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Ants adjust their pheromone deposition to a changing environment and their probability of making errors

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Animals must contend with an ever-changing environment. Social animals, especially eusocial insects such as ants and bees, rely heavily on communication for their success. However, in a changing environment, communicated information can become rapidly outdated. This is a particular problem for pheromone trail using ants, as once deposited pheromones cannot be removed. Here, we study the response of ant foragers to an environmental change. Ants were trained to one feeder location, and the feeder was then moved to a different location. We found that ants responded to an environmental change by strongly upregulating pheromone deposition immediately after experiencing the change. This may help maintain the colony's foraging flexibility, and allow multiple food locations to be exploited simultaneously. Our treatment also caused uncertainty in the foragers, by making their memories less reliable. Ants which had made an error but eventually found the food source upregulated pheromone deposition when returning to the nest. Intriguingly, ants on their way towards the food source downregulated pheromone deposition if they were going to make an error. This may suggest that individual ants can measure the reliability of their own memories and respond appropriately.

1. Introduction

Uncertainty poses a significant problem for animals, especially when facing a changing environment. To overcome uncertainty, animals must continually gather information about their surroundings [1]. Central place foragers often have a well-developed memory [2–4]. In addition, social animals can share valuable information, such as patch productivity, safety and quality [5–7]. In many social insects, such as honeybees and ants, information transfer has become key to their ecological success. Many ants deposit pheromone trails from a food source to their nest, thereby recruiting other foragers and increasing food intake [8]. Because the chance of an ant to follow a specific pheromone trail at a bifurcation is proportional to the relative amount of pheromone on either side of the bifurcation [9,10], modulation of pheromone deposition strongly influences collective decision-making, and thus colony success [7]. Pheromone deposition is therefore modulated according to factors which impact on foraging success, such as resource quality, colony need and perceived path use [7,11,12]. However, reliance solely on trail pheromones may be risky, as accidentally depositing pheromone inappropriately could result in an erroneous information cascade [13,14], and indeed, behavioural rules are in place to avoid such events [15]. On complex paths, memorizing a route becomes more difficult, resulting in poorer-quality information and an increase in navigational errors [16].

Similarly, in a changing environment, social information can become rapidly outdated. This brings particular difficulties to ants, as pheromone trails cannot be quickly removed. Honeybees can prevent nest-mates from recruiting to a dangerous food source, when too much nectar is being retrieved, or to competing nest sites during nest-relocation, by using a stereotyped 'stop' signals [5,17,18]. Pharaoh's ants, *Monomorium pharaonis*, are reported to deposit a 'no entry' pheromone marker on the trail that does not lead to a food source, preventing other foragers from taking the wrong route, and it is conceivable that such a 'no entry'
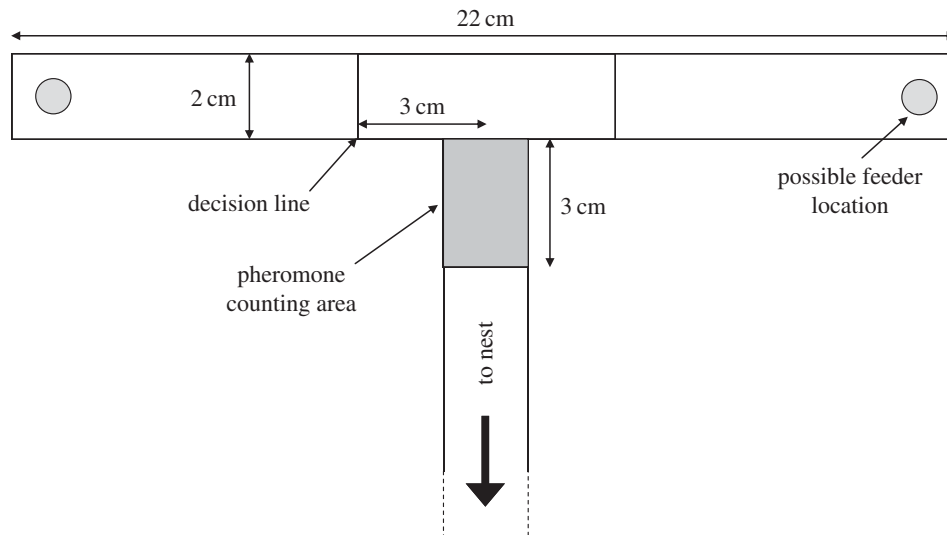
Figure 1. Experimental T-maze. Pheromone depositions were counted in the grey rectangular area. Ants were considered to have chosen one arm of the T-maze when their antennae had crossed a decision line. In every experiment, the feeder was first placed at the end of one arm of the T-maze, and after a set number of visits by the ants moved to the other arm.

pheromone could be deployed on outdated routes [19]. However, apart from the one example in Pharaoh's ants, no other stop signals have been reported in ant organization.

An alternative method by which ant colonies could prevent redundant information from being harmful would be to upregulate the production of new information. In concrete terms, this would entail upregulating pheromone deposition in response to an environmental change.

To test this, we trained ants to a feeder location, and then changed the environment by changing the feeder location. We hypothesized that ants would respond to this change by upregulating pheromone deposition.

2. Material and methods

(a) Housing and maintenance of the ants

Colonies of the black garden ant, *Lasius niger*, were collected on the campus of the Ludwig-Maximilian University in Munich, and housed in plastic foraging boxes (40 × 30 × 20 cm) with a layer of plaster of Paris on the bottom. Each box contained a circular plaster nest (14 cm diameter, 2 cm high). Colonies were queenless with 1000–2000 workers and small amounts of brood. Colonies were fed three times per week with Bhatkar diet, a mixture of egg, agar, honey and vitamins [20]. While being from a queenless colony may slightly affect the behaviour of ants, this is unlikely to affect the result of this experiment, as small amounts of brood were present in the nests [21,22]. Colonies were deprived of food for 4 days prior to each trial to give high and consistent motivation for foraging and recruitment. Water was provided ad libitum.

(b) Experimental procedure

A colony was given access to a plastic T-maze (stem 15 cm long, head 22 cm, width 2 cm) via a drawbridge (figure 1). The T-maze and drawbridge were covered in printer paper overlays. Lines on the T-maze head 3 cm from the centre of the stem acted as 'decision lines', with ants whose antenna crossed the line being scored as having taken that direction. A bright light was placed to the right of the T-maze to act as an obvious landmark, and the experiment was carried out in a room containing many other landmarks the ants could use to form a route memory. A drop of 1 molar sucrose (Merck KGaA, Darmstadt, Germany) solution was placed on a small plastic platform at the end of one arm of the T-maze and acted as a feeder.

The first five ants to reach the feeder were individually marked on the abdomen with a dot of acrylic paint, and all other ants were removed and replaced in the foraging box. This prevented unmarked ants from visiting the feeder, depositing pheromone or otherwise interfering with the experiment. Unmarked ants were then prevented from entering the T-maze using the drawbridge. The marked ants were allowed to perform either 1, 3, 5, 10 or 15 visits to the feeder (training phase). The location of the feeder was then switched to the other arm of the T-maze. The variation in the number of training visits was implemented in order to characterize the foraging persistence of the ants, results of which are presented elsewhere [23]. Trained ants began by searching the old feeder location, but eventually discovered the new feeder location, and then were allowed to make further return trips to the feeder (testing phase). During both the outwards (towards the feeder) and return (towards the nest) journey, the number of pheromone depositions performed by each ant was counted on the 3 cm section of the T-maze stem nearest to the T-maze head (figure 1). Pheromone deposition in *L. niger* is a highly stereotyped behaviour, and easily quantified by eye [7]. The arm chosen by each ant at each visit was also noted. As the presence of trail pheromone itself reduces pheromone deposition [16], the paper overlay covering the T-maze head was either removed whenever an ant walked over it (pheromone-removed treatment) or was left in place throughout the experiment (pheromone-allowed treatment). Once all the marked ants had made a correct decision (as defined by the decision lines) on at least three consecutive visits to the new feeder location, the ants were removed from the colony, and the experiment ended. Each colony was tested twice at each level of training visits, once with pheromone being removed and once with pheromone remaining in place. In half of the experiments the training visits were to the right, and on the other half to the left. This was randomly assigned. A total of 413 ants from eight colonies were tested.

(c) Statistical analysis

Statistical analyses were carried out in R v. 3.1.0 [24] using generalized linear-mixed models [25]. Following Forstmeier & Schielzeth [26], we included in the tested models only factors and interactions for which we had a priori reasons for including.

As the pheromone deposition behaviour of ants heading towards the food source (outgoing) and ants returning to the nest is known to be very different [15,16,27], we analysed the behaviour of outgoing and returning ants separately. As multiple data points were collected from each individual
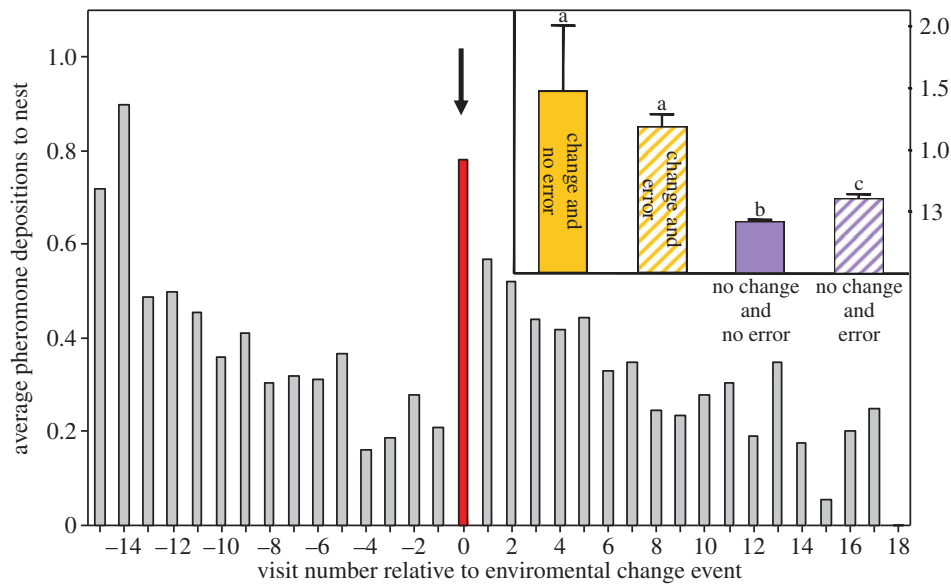
Figure 2. Main figure: mean pheromone depositions of ants returning from the food source to the nest, by the visit number relative to the food source location change. Note that pheromone deposition is upregulated immediately after experiencing the change event. For clarity, this figure shows data only from experiments in which ants made 15 training visits to the original feeder location before the food source location was changed. See the electronic supplementary material figure S1 for similar figures from all change treatments. Inset: mean pheromone depositions of returning ants by whether or not they had experienced an environmental change event, and whether or not they had made a branch choice error before finally locating the food. This figure shows data from both ants which did and did not deposit pheromone. See the electronic supplementary material, S1 for two similar figures (figures S2 and S3) for deposition probability of ants and deposition intensity of depositing ants. Electronic supplementary material, S1 also contains all statistical results for the *post hoc* pairwise analyses. (Online version in colour.)

and multiple ants were tested per colony, ant and colony identity were added as random effects, with ant identity nested inside colony identity. Binomial data (pheromone deposited or not) were modelled using a binomial distribution and logit link function. Count data (number of pheromone depositions for ants, which deposited pheromone at least once) were modelled using a Poisson distribution using a log link function.

The following model formulae were used, and each model was run twice; once for outgoing and once for returning ants.

To test whether an environmental change elicits a change in pheromone deposition:

pheromone deposited or not OR number of pheromone

depositions = pheromone.removed? + visit

+ directly.after.switch

+ (random effects: ant nested within colony)

With 'pheromone.removed?', 'visit' and 'directly.after.switch' as fixed effects.

As Czaczkes *et al.* [16] found that ants which had made an error while outgoing deposited more pheromone when returning, we also tested for this effect. Furthermore, in an initial survey of the data, it seemed that ants *which were about to make an error* decreased their pheromone deposition. We also tested explicitly for this effect. The model formulae used were as follows:

(for returning ants)

pheromone deposited or not OR number of pheromone

depositions = just.made.an.error? + directly.after.switch

+ (random effects: ant nested within colony)

(for outgoing ants)

pheromone deposited or not OR number of pheromone

depositions = will.make.an.error.this.visit?

+ directly.after.switch + (random effects: ant nested

within colony)

With 'just.made.an.error?', 'will.make.an.error.this.visit?' and 'directly.after.switch' as fixed effects.

Finally, to explicitly disentangle the effects of making an error and of experiencing an environmental change, we performed *post hoc* pairwise comparisons between the four possible combinations of error/no error and change/no change. Likewise, to explicitly disentangle the effort of making an error and travel direction, we performed *post hoc* pairwise comparisons between the four possible combinations of error/no error and travelling outwards/returning to nest.

3. Results

(a) Response of ant to an environmental change

Immediately following a change in feeder locations, trained ants that had found a changed feeder position dramatically increased the number of pheromone depositions on their way back to the colony. The proportion ($Z = 7.61$, $p < 0.001$) and the number ($Z = 5.53$, $p < 0.001$) of depositions increased (main figure in figure 2). This was true of both ants which had correctly followed their memory to the old (now empty) feeder location, and those ants which had mistakenly taken the wrong path to the new (now rewarding) feeder location (figure 2 inset).

Conversely, outgoing ants, which had just experienced an environmental change on their previous visit, were less likely to deposit pheromone ($Z = -2.71$, $p = 0.0067$) even though they all did eventually relocate the feeder during the previous visit. However, of the ants that did choose to deposit pheromone, the number of pheromone depositions performed did not change ($Z = 0.81$, $p = 0.42$). Surprisingly, whether or not pheromone was removed from the stem of the maze had no effect on either deposition probability (outgoing $Z = 1.43$, $p = 0.15$, returning $Z = 1.45$, $p = 0.15$) or intensity (outgoing

$Z = 0.99$, $p = 0.32$, returning $Z = 0.93$, $p = 0.35$). As reported previously [16,27], in later visits, ants were less likely to deposit pheromone (outgoing $Z = -8.51$, $p < 0.001$, returning $Z = -8.02$, $p < 0.001$), and when they did, they did so less intensely (outgoing $Z = -6.49$, $p < 0.001$, returning $Z = -5.85$, $p < 0.001$) in later visits.

(b) Response of ant to making an error

When returning to the nest after eventually finding the feeder, ants which had just made an error increased both the probability ($Z = 6.40$, $p < 0.001$) and intensity ($Z = 2.03$, $p = 0.043$) of pheromone deposition, even after any effect of environmental change had been taken into account (figure 2 inset and figure 3). *Post hoc* analysis revealed that the upregulation of pheromone deposition in response to an environmental change and in response to making an error are separate phenomena (see figure 2 inset and electronic supplementary material, S1 for statistical test results).

Most surprisingly, outgoing ants *which were about to make an error* were significantly less likely to choose to deposit pheromone ($Z = -6.19$, $p < 0.001$, see figure 3 and electronic supplementary material, S1 and figure S4). However, of the ants that chose to deposit pheromone, the intensity of pheromone deposition was unchanged (see the electronic supplementary material, S1 and figure S5).

4. Discussion

We found that ants strongly upregulate pheromone deposition in response to an environmental change. This might also be seen as ants upregulating pheromone deposition on finding a new, unexpected, food source. Decision-making systems based on positive feedback loops, such as the ants' pheromone-based recruitment, are very adept at reaching collective decisions, but are susceptible to becoming trapped in initial decisions [28–30]. This is because pheromone trails leading to initially chosen options become so strong as to out-compete any incipient trails to new options. Even if a better resource is found, the strong recruitment of a few ants cannot produce a trail strong enough to compete with the established trail. Likewise, algorithms based on positive feedback and ant colony optimization (ACO) can also suffer from early convergence and becoming trapped in local optima [31], as early paths strongly constrain future exploration of the available options by the algorithm. By implementing a rule upregulating pheromone deposition after an environmental change, colonies and ACO algorithms may be able to respond more rapidly to environmental changes, by facilitating the breaking out from previous decisions.

However, this response is seemingly only open to systems composed of agents with a memory. Only by comparing the previous situation to the current one can an environmental change be noted. However, an alternative behaviour, which does not require a memory, would be for ants to upregulate pheromone when returning on an unmarked path, and in fact, pheromone deposition of returning ants is higher on unmarked paths [7,15,32]. Decision-making in biological systems is characterized by multiple redundant or complementary mechanisms, and it is thus perhaps not surprising to find two separate mechanisms, which seem to fulfil the same role. A further alternative to upregulating recruitment in the face of environmental change would be
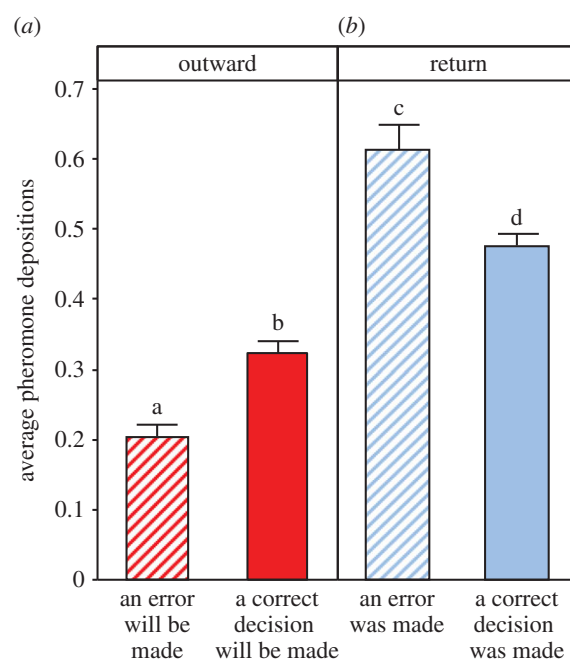

Figure 3. When travelling outwards towards a food source, ants deposited less pheromone if they were going to make an error at an upcoming bifurcation. When returning to the nest, ants which had made an error deposited more pheromone than ants which had made a correct decision. Different letters denote statistically significant values. These patterns are mainly driven by the proportion of ants choosing to deposit pheromone, and not by the modulation of the number of pheromone depositions by depositing ants. See the electronic supplementary material, S1 for similar figures (figures S5 and S6) in which pheromone laying probability and intensity are separated and for statistical details. Data from all visits and all treatments are pooled for clarity in this figure. (Online version in colour.)

to downregulate recruitment to the old food location. Indeed, honeybees can employ a piping signal to stop recruitment to dangerous food sources, and to prevent decision-making deadlocks [5,17,18]. We might expect honeybees, which have an excellent memory, to also show an upregulation in recruitment when faced with an environmental change. Likewise, it may be fruitful to search for a downregulation signal in ant recruitment systems. In honeybees, downregulation might be more straightforward, as individual dancing bees may be targeted. As ants deposit a pheromone trail and then leave, other mechanisms, such as perhaps a 'no entry' signal [19], might need to be employed.

Another potential benefit of responding to a changing environment by upregulating pheromone deposition would be in maintaining the pheromone trail as an 'external memory' [8]. Positive-feedback-based systems tend to converge on a single decision—a process termed 'symmetry breaking' [30,33]. By upregulating recruitment to new or underused resources such convergence may be avoided. Computer scientists tellingly have implemented rules strengthening underused parts of a network, specifically to prevent early convergence [34]. Other mechanisms for coping with environmental change include reducing the intensity of recruitment, or using more linear positive feedback mechanisms, such as individual recruitment [29,35–37].

The apparent response of ants to making an error by upregulating pheromone deposition on the return journey has been described previously [16]. Intriguingly, we also found that outgoing ants which went on to make an error deposited less pheromone. This seems to imply that the ants can judge the

quality of their own memories, and respond accordingly: if the ant does not trust its own memory, it deposits less pheromone. The ability to assess the quality of a memory (known as meta-memory judgement, which is an aspect of metacognition) is a highly advanced cognitive ability, which has previously only be demonstrated in mammals and some birds [38–41]. Social insects, such as ants and honeybees, are often found to have impressive cognitive abilities, such as making generalizations (e.g. something being similar or different to something) and learning abstract relationships between stimuli [42–45]. Nonetheless, it is hard to believe that such tiny-brained animals are capable of such an advanced cognitive feat. However, a recent study showed that honeybees are capable of selectively 'opting out' of difficult choices [46], although the authors stopped short of definitively claiming that metacognition was being used. Their study could not disentangle metacognition from simple association of the more difficult stimulus with the 'opt-out' decision. While our study avoids this particular pitfall and other problems which plague demonstrations of metacognition [47–49] (see the electronic supplementary material, S1), it was not designed specifically to address this question. Thus, one could conceive of several alternative explanations for our findings, which do not invoke metacognition. For example, it is possible that a third factor which we did not control, e.g. age, may predict both pheromone deposition and learning accuracy (although the opposite pattern found for returning ants speaks against this example). Individual variation between ants may also have caused the correlation we report. We therefore do not claim a definitive demonstration of metacognition in ants. Nonetheless, our findings, alongside similar results from honeybees [46], are suggestive of metacognitive abilities in social insects. As Smith [40,47], one of the founders of the field of metacognition, warns: we must also be careful that over-stringent demands for demonstrations of cognitive abilities do not cause us to 'throw the baby out with the bathwater'.

Ants and social insects, in general, have a wide variety of elegant behavioural rules, which allow them to reach adaptive collective decisions in an ever-changing environment. The combination of individual cognitive abilities, such as a memory, alongside the ability to communicate information, allows for added complexity [8,23]. Whether or not they also possess metacognitive abilities, social insects demonstrate an impressive array of behavioural adaptations. While we have learned a great deal about social insect organization, and applied some of what we have learned, there are clearly many more aspects left to apply, and much more to learn about how social insects make decisions.

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