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Information synergy: adding unambiguous quality information rescues social information use in ants

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Abstract

Animals have access to many alternative information sources when making decisions, such as private information (e.g. memory) and social information. Social insects make extensive use of social information. However, when intentional social information (e.g. pheromone trails in ants) conflicts with private information (e.g. route memories), insects often follow their private information. Why is this? We propose that it is an asymmetry in information content between these two information sources that drives the neglect of social information. In ants, workers with certain information about the quality of a food source (memory) ignore valuable social information (pheromone trails) because the pheromone trails encode only a very ambiguous measure of food quality. This leads to a testable hypothesis; the addition of unambiguous quality information should rescue social information following. To test this, we trained ants to a poor quality (0.25M) food source, and then provided an alternative path along with either 1) no information, 2) a pheromone trail, 3) a 0.2µl droplet of 1.5M sugar solution, providing unambiguous quality information, or 4) both a trail and a droplet. When either no or only one information source was provided (1-3), most ants (60-75%) continued following their own memory. However, the addition of unambiguous quality information to a trail (4) rescued trail following: when both a pheromone trail and a sugar droplet were provided, 75% of ants followed the trail. We propose that information content – what type of information a source can convey, and what is its ambiguity, is a strong driver of which type of information is attended to.

Key words:

Information conflict; information use strategies; recruitment; social information; information asymmetry; Certainty Effect; ambiguity avoidance

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Introduction

Animals have access to many types of information. These can be broadly separated into private information, which is available only to the individual animal, and public information, which is available to other animals as well [1]. Private information includes genetic information and non-genetic information such as internal states and, importantly, memories. Public information includes all observable cues, such as the colour of a flower. An important subset of public information is social information, which is information related in some way to other animals. These may be incidental cues, such as the presence of conspecifics at a resource, or intentionally produced signals, such as the waggle-dance of a honey bee.

Multiple information sources may provide information about the same thing. For example, both the colour and the odour of a flower patch, and whether other bees are dancing for that patch, might inform a bee about whether and where food is available in the environment [2,3]. These multiple information sources may interact in a variety of ways. Information may be used hierarchically, with one being used whenever it is available, and if it is not the next on the list is used [4]. When information sources agree, they may act additively or synergistically to improve behaviour. For example, ants which have private information about a food source (memory) which agrees with social information (a pheromone trail leading in the same direction) walk 25% faster than ants with either only one or none of these information sources [5]. These information sources also act additively by causing more ants to follow a pheromone trail [6]. Bumblebees which have experienced a novel flower odour in the nest (public information) are more likely to exploit the novel flowers, but only once they have tasted a flower scented with this novel odour (private information) [7].

A particularly interesting situation is when information sources conflict. One option in such situations is to weight information from different sources and produce and an intermediate value [6,8,9]. An alternative is to rely on one type of information and ignore the others. In some situations, such as choosing a path at a trail bifurcation, an intermediate option is not available. Different strategies might be undertaken due to different ecological conditions or the state of individual animals, and understanding what strategies animals use to decide which information to follow is a very active field of research [10–14]. Information use strategies can be broadly divided in to *when* strategies (when to use which information type) and *who* strategies (whose information to use) [15].

Evidence supporting various information use strategies has been described in wide array of taxa, including insects, fish, lizards, rats, and humans [16–19]. Information use strategies have been especially well researched in social insects such as ants and bees, as in these groups social

[1] Our definition of private information deviates somewhat from that of Danchin et al. [1], who consider public information more-or-less synonymous with social information. We consider social information a subset of public information.

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information has the potential to play a very large role [see 11,20 and references therein]. Social insects also represent a special case, since there are not usually expected to be any conflicts of interest in many situations requiring communication, such as foraging and nest-site selection. This should, at face value, strengthen the role of explicit social signals such as pheromone trails or waggle-dances. However, somewhat surprisingly, in most cases in which such intentionally produced social information is conflicted with private information, the ants and bees predominantly follow their own memories [21–29]. This was found not to be the case in only a few instances [23,30]. This preference could have strong implications for colony level behaviour, preventing colonies from optimally exploiting their environment.

Why do ants and bees so often underweight or ignore the directional information provided by their sisters? Explanations of information use strategies have been made in terms of the reliability of an information source – how often using one type of information is associated with a positive outcome, or how outdated the information is (e.g. [14,31]), or the cost of acquiring new information [32–34]. However, what has not been considered is the *information content* of different types of information.

Economists, and later behavioural ecologists, distinguish between two types of situations with an unknown outcome: risk and ambiguity (or uncertainty) [35–37]. The term 'risk' refers to a situation where the mean result or probabilities of a situation are known, but the precise value at any one time is not. A gamble on a six-sided die is thus a risky proposition: the average score is 3, the probability of any one side is 1/6, but the precise value on each roll is unknown. By contrast, 'ambiguity' or 'uncertainty' refers to a situation where neither the mean nor the variation is known; a gamble on a die with an unknown number of sides is thus gambling under ambiguity.

When faced with ambiguity, humans have been found to behave in a manner inconsistent with the predictions of expected utility theory, the standard economic theory of human behaviour. Specifically, humans are found to display *ambiguity aversion.* Given a choice between a risky and an ambiguous proposition, humans overwhelmingly prefer the risky proposition, although there is no *a priori* rational reason for them to do so [38,39], (but see [37] for a Baysian perspective). This was famously described by the Ellsberg paradox [38]. He gives the example of a single choice, in which you are offered to pull one ball out of one of two urns. One urn contains an equal mix of red and black balls, the other contains an unknown ratio of red to black balls. Pulling out a red ball is rewarded with $100, but the black ball is unrewarded. The urns are thus a risky and an ambiguous proposition, respectively. Most people choose the urn with the known distribution. Related to this, Kahneman and Tversky, in their famous Prospect Theory paper [40], describe *the Certainty Effect*. Here, subjects overweight certainty, and are willing to pay a premium to move from a risky to a

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certain situation. For example, people usually prefer $3000 with certainty to an 80% chance of $4000, although the expected payoff of the gamble is $3200. Effectively, subjects are willing to pay $200 for certainty. Ambiguity aversion has also been documented in non-human primates [41,42].

A similar situation may be happening in social insects experiencing an information conflict. Imagine an ant which has found a poor quality food source. It is shuttling back and forth to this food source, and knows the quality of this resource with certainty. It then encounters a pheromone trail leading in a different direction. This pheromone trail was deposited by another ant, which had discovered a good food source. It would be in both of the ants' interests for the ant exploiting the poor food to follow the pheromone trail. However, this often does not happen, even if the recruitment to the alternative direction is very strong [21–29]. Why is this? We propose this is due the (lack of) information content of the social communication signal. The pheromone trail provides only very noisy, imprecise, and ambiguous information about the quality of a food source. Pheromone trail strength varies with resource quality, time since discovery, recruitment rates, and the individual pheromone depositions behaviour of ants: A strong trail may lead to a good food source exploited by a few ants, or to a poor one exploited by many ants; a weak trail may lead to a poor food source, or to a good one which has been unproductive for a while, or to a newly discovered food source. Importantly, there is a very large variation in the amount of pheromone deposited by individual ants to food sources of the same quality [43]. With no strong evidence that the new food source is better, the forager avoids paying the costs of attempting to find an advertised food source [32,44,45], and falls back on exploiting the food source she knows about.

This hypothesis leads to a testable prediction: If a worker foraging on a poor food source can be given unambiguous information about the quality of a better food source a pheromone trail advertises, she should follow the trail pheromone. Here, we set out to test this prediction.

Materials and methods

Study species and maintenance

We used 8 queenless colony fragments of the black garden ant, *Lasius niger* (Linnaeus), collected from eight different colonies on the University of Regensburg campus. Colonies were housed in a plastic box (40×30×20cm) with a layer of plaster on the bottom. Each box contained a circular plaster nest (14cm diameter, 2cm high). Colonies contained c. 1000 workers and small amounts of brood. The ants were fed *ad libitum* on 1M sucrose solution supplemented with *Drosophila melanogaster* fruit flies. Colonies were deprived of food for four days prior to each trial to

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give high and consistent motivation for foraging and pheromone deposition. Water was provided *ad libitum*.

Experimental procedure

10 different experimental treatments were carried out in total, coded A-J. An overview of the different treatments is provided in table S4 in the supplement. All treatments were variations on a central design. The aim of the experiments was to test whether ants with a well-established memory of finding food on one arm of a Y maze can be induced to search a newly-presented alternate arm by the provision of various information sources. The information sources provided could be a pheromone trail, a small droplet of sucrose (simulating trophallaxis), a novel scent in either the droplet or on the newly presented path or both, or a combination of these. The scent treatments were added to test whether similar droplet and pathway odours cause a further increase in trail follow, as there could thus be an associative link between the quality of the droplet and the odour of the new runway. However, as there was no effect of the various odour treatments (see supplement S1 for details) we pooled our data into treatments groups for the final analysis, depending on the types of information presented to the ants, and the quality of the original feeder to which it was trained. This resulted in 5 treatment groups: i) no information (treatments A and B), ii) only a droplet of 1.5M sucrose just before the bifurcation (treatments C-E), iii) only a pheromone trail on the new path (treatment F), vi) both a pheromone trail and a droplet (treatments G-I), and finally v) a pheromone and a droplet for ants trained to 1.5M sucrose (treatment J).

A trial began by allowing an ant onto the apparatus via a drawbridge. The drawbridge led to a Y maze with one arm drawn out just out of reach of the ants, to form an L maze (Figure 1). The arm that was out of reach (left or right) was systematically varied. The arms of the maze were 10cm long and 1cm wide, narrowing to 2mm wide at the junction. The arms of the maze were covered with paper overlays. The overlay on the stem of the maze was unscented, while the overlay on the arm of the maze was scented with either rosemary or lemon essential oil – the odour used was systematically varied between trials. Odour impregnation was achieved by storing the paper overlays in a sealed plastic container containing one 0.1ml drop of essential oil on a glass petri dish for at least 24 hours. An acetate sheet affixed to the end of the L maze arm acted as a feeder. A large drop of 0.25M sucrose solution (1.5M in treatment J), flavoured similarly to the L maze arm leading to it, was placed onto the feeder. Sucrose solutions were flavoured by adding 10µl essential oil per 100ml sucrose solution, following Czaczkes *et al.* [46]. Once the ant found the feeder it was marked with a dot of acrylic paint on the abdomen, and allowed to return to the nest. While the ant was in the nest,

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unloading her sucrose load, the paper overlays on the stem and arm were replaced by fresh overlays, to remove any trail pheromone the ant might have laid. The ant was then allowed to make 3 further return visits to the same feeder, resulting in 4 visits to the original feeder in total. This is sufficient to ensure that, even given the relatively low quality of food, most ants will return to this arm of the maze given a choice (Oberhauser, Koch and Czaczkes, submitted, see also data below).

While the ant was in the nest prior to its fifth return to the feeder, the feeder from the original arm of the Y maze was removed, and access to the second arm was given. The new arm was either marked with a pheromone trail (treatments F - J) or not (treatments A-E). This pheromone trail was produced by immersing 8 worker hindgut glands in 2ml of dichloromethane (DCM), following von Thienen *et al*. [47]. 5.6µl of this mixture was applied in an even line along the paper overlay covering the arm, using a capillary tube (Servoprax GmbH, Germany). This amount was calculated to produce a pheromone trail of a realistic strength [47], and in control trials elicited a trail following accuracy of 82% (594 / 715), which is indistinguishable from those recorded from naïve ants following a reasonably strong naturally-deposited trails as reported by Czaczkes et al. [48] (82-83% accuracy). See supplement S1 for detailed methods and results regarding the artificial pheromone trail.

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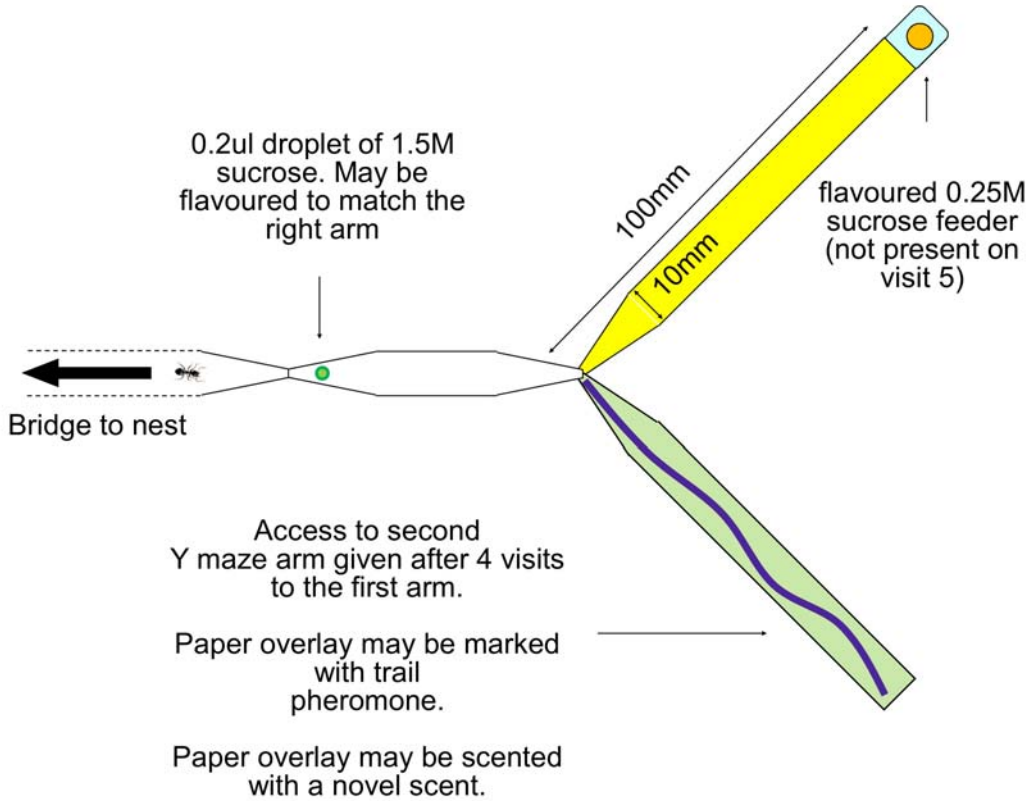

Figure 1 – experimental setup. Ants are first trained for 4 visits on a Y maze with access to only one arm (here the top arm, in yellow in the figure but not coloured in the experiment), leading to a 0.25M sucrose feeder flavoured with lemon or rosemary (1.5M in treatment J). On the 5th outward journey the second arm of the Y maze (here bottom, green) is added, and the feeder removed. The new arm may be marked with a pheromone trail and/or scented with a novel scent (lemon or rosemary). Additionally, a small (0.2µl) droplet of 1.5M sucrose may be placed after a narrowing of the stem before the bifurcation, which the ant can drink but will not become satiated from. The droplet may be flavoured to match the new Y maze arm scent or may be unflavoured.

The new arm was also either scented (treatments B, D, E, H, I, J) with a different scent to that of the original arm, or was not (treatments A, C, F, G). Lastly, a small (c. 0.2µl) droplet of sucrose either was (treatments C, D, E, G, H, I, J) or was not (treatments A, B, F) placed on the stem of the Y maze, before the bifurcation but just after a narrowing of the stem. This ensured that the ant contacted the droplet as it walked towards the bifurcation. This droplet was either flavoured similarly to the scent on the newly presented runway (treatments E, I, J) or was unscented (treatments C, D,

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G, H). The droplet was large enough for the ant to detect and drink, but not enough to satiate the ant [49], which proceeded onwards after drinking the droplet. This droplet was designed to simulate trophallaxis. Trophallaxis is used in the nest to unload food, and also provides ants with information about the food available in the environment [50–53]. This information is attended to very strongly [51,54]. *L. niger* ants can often be observed performing trophallaxis away from the nest, and recipients of these trophallactic interactions usually continue on their outwards journey afterwards (TJC, personal observation). Unfortunately, we could not reliably achieve such on-trail trophallaxis with the trained ant under controlled experimental conditions.

We then noted which arm of the Y maze the ant chose. We took two choice measurements: the initial decision, as defined by the ant crossing a line 2cm from the bifurcation, and the final decision, as defined by the antennae of the ant reaching the end of the Y maze arm. As the ant reached the end of the Y maze, it was allowed to walk onto a piece of paper and replaced on the path leading to the Y maze, before the location of the sugar droplet. This allowed us to make 10 repeated measures of each ant. After 10 such measurements the ant was permanently removed from the colony. The number of ants tested in each treatment is given in table S7 in the supplement.

Statistical analysis

Since the initial decision (crossing a line 2cm from the bifurcation) and the final decision (reaching the end of the arm) rarely differed (<5% of cases), we analysed only the final decision. While we collected 10 data points per ant to increase the potential power of our experiments, we finally decided to perform a conservative analysis by only considering the first decision made by the ants. This avoids the possibility of ants becoming frustrated in later trials. Initial data exploration revealed a leftward side bias, which is not uncommon in the behaviour of ants or other animals [55], and so training side was also added to the model. Finally, colony identity was added as a random effect. This resulted in the following model:

$$\text{Decision} \sim \text{treatment.group} + \text{training.side}$$
$$+ \text{(colony as a random effect)}$$

As the data is binomial we used a binomial error structure. Data were analysed in R v.3.4.1 [56] using generalised linear mixed models from the LME4 package [57]. Model fit was checked using the DHARMa package [58].

We also tested whether the decisions of each group differed significantly from random using two tailed exact binomial tests.

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Following Benjamin et al. [59] we set significance level for hypothesis testing at p = 0.005, terming p-values greater than that but smaller than 0.05 'suggestive'. However, due to the limitations of using p-values alone, we provide estimates and confidence intervals for all effects.

Results

The type of information available to a forager strongly influenced her decision of whether or not to follow her memory. For ants trained to 0.25M sucrose, given just an unmarked novel path on the Y maze, most ants (75%) choose to follow their own memory (figure 2), significantly more than chance (two tailed binomial exact test, 46/61 followed their memory, mean = 0.75, 95% C.I. range = 0.63 – 0.86, $p < 0.0001$). The addition of a small 1.5M sucrose droplet does not significantly change the choices made by the ants, who still preferentially follow their memory (binomial test, 60/87, mean = 0.69, 95% C.I. = 0.58 – 0.78, P = 0.0005). The addition of a pheromone trail on the novel arm still resulted in most ants (60%) following their memory, but this result was not different from random choice (binomial test, 18/30, mean = 0.6, 95% C.I. = 0.41 – 0.77, p = 0.36). These three groups do not differ significantly from each other (GLMM, $z \leq 1.90$, $p \geq 0.057$, for details of all pairwise comparisons, including estimates for each comparison, see table S1 in supplement S1).

However, a striking synergistic effect of presenting a pheromone trail and a sucrose droplet was found. If both were presented, only 25% of ants chose to follow their memory, with 75% choosing to follow the novel path. This is significantly fewer than chance (binomial test, 23/92, mean = 0.25, 95% C.I. = 0.17 – 0.35, $p < 0.0001$) and differs significantly from all other groups provided with less information (GLMM, $Z \geq 2.97$, $P \leq 0.0029$).

The effect of presenting both information sources depends on the relative quality of the droplet presented and the food quality the ant was trained on. If ants were trained on 1.5M sucrose, 53% of ants chose to follow their memory, which does not differ from random choice (binomial test, 16/30, mean = 0.53, 95% C.I. = 0.34-0.72, p = 0.86). This is a non-significantly, but suggestively, greater than for the ants receiving the same information, but trained on poorer food (GLMM, z = 0.23, p = 0.020), and also suggestively less than the ants receiving no information (GLMM, z = -2.56, p = 0.011). It is not significantly different from the ants receiving either one information source (GLMM vs only droplet, z = 1.95, p = 0.051, vs only pheromone z = 0.60, p = 0.55).

The entire dataset on which these results are based in provided in online supplement S2.

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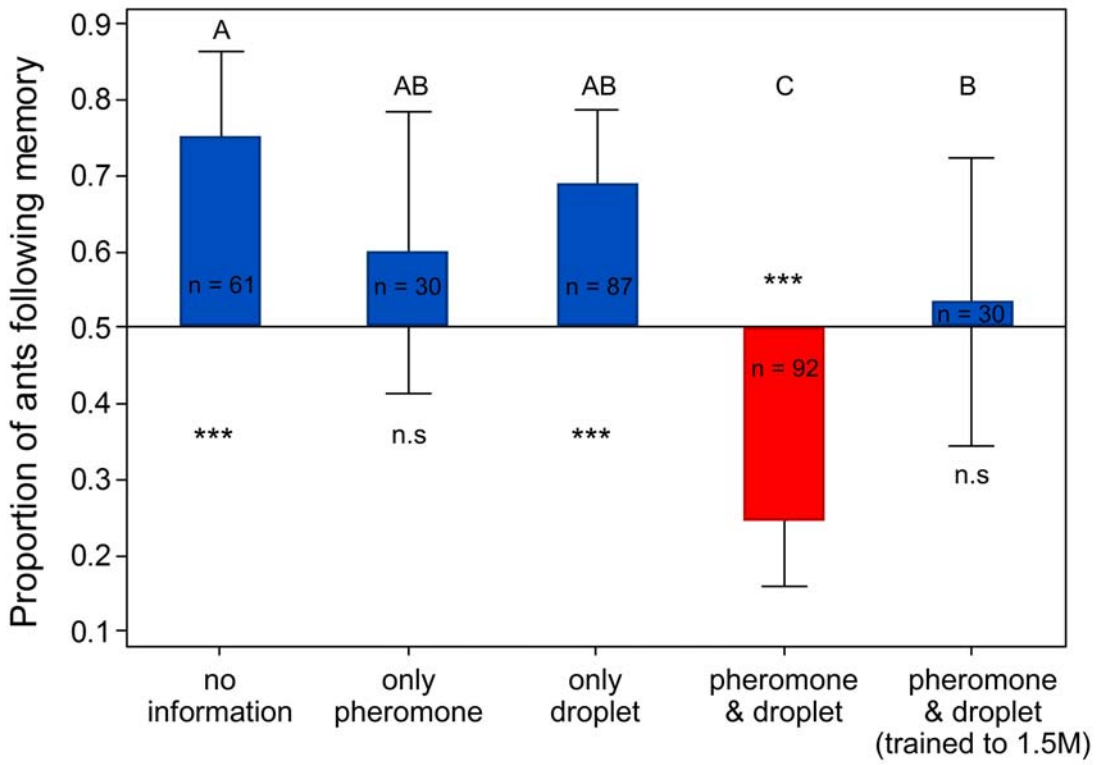

Figure 2 – proportion of ants following their memory down the original Y-maze arm as a function of what other information was available to them. Ants may have had either no information about the new Y-maze arm, a pheromone trail on the new arm, a small 1.5M sucrose droplet before the bifurcation, or a pheromone trail and a droplet. In most groups ants were trained to 0.25M sucrose, but in one group they were trained to 1.5M sucrose. Whiskers are 95% C.I. for the mean. Letters indicate groups that are significantly ($P < 0.005$) different from each other. "***" and "n.s." signify groups that are either significantly different from 0.5 (exact binomial test, $P < 0.0001$), or not different from 0.5 ($P > 0.05$), respectively. Sample sizes per group are show in the bars. Detailed statistical analysis results are presented in tables S1 and S2 in online supplement S1.

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Discussion

By providing unambiguous information about the quality of other resources in the environment the information asymmetry in a communication system was rebalanced. This rescued pheromone following behaviour in our experiment. When ants had no information about alternative food sources in the environment, they predominantly (75%) chose to continue exploiting their private information, returning to the sure but poor quality (0.25M) feeder. When ants were provided with the information that better food exists in the environment (a small 1.5M sucrose droplet), they nonetheless predominantly (69%) returned to the poor quality feeder they knew about. Even when a strong pheromone trail led in the opposite direction, 60% of the ants continued to exploit the known, poor quality feeder. However, when social information (a pheromone trail) and unambiguous quality information (the sugar droplet) was provided, the behaviour of the ants completely reversed, with 75% of choices made for the unknown, but advertised, route.

Information use strategies have been divided into '*when*' and '*who*' strategies – when should information be used, and who should one listen to [15]. Here, we propose considering information use in terms of a '*what*' strategy – what is the information content of an information type, and what is its' level of ambiguity? Social information sources such as pheromone trails and honey bee waggle-dances do not provide unambiguous quality information, while private sensory information does. While pheromone trails and waggle-dances do encode some information about food quality, this information is extremely imprecise and noisy, both due to individual variation in responses to fixed food quality [43,60] and due to the effect of time and foraging patterns on these information sources (see introduction for details). We propose that is it this ambiguity in social information, or the certainty of the private information, which causes otherwise valuable social information to be neglected. Our data supports this claim.

Understanding information use strategies in terms of information asymmetry can explain previously puzzling findings. Leadbeater and Florent [7] unexpectedly found that bumblebees do not rate social information above personal experience, even when their personal experience becomes outdated. Bumblebees which had experienced a novel odour in the nest (social information) were just as unlikely to sample novel flowers scented with this odour as bees which did not experience the novel odour in the nest. Both groups continued choosing known-odour flowers, even when those flowers became unproductive. However, once the bees with the social information did, eventually, sample the novel flowers, they were much more likely to switch to the novel flowers than the group without social information. This is directly analogous to the situation we report: neither private sensory information providing reliable quality information (sampling the novel flowers), nor social information (smelling the novel odour in the nest) is sufficient to make bees change their choices.

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However, when both are provided together (here, after the first sampling of the novel flower), bees are willing to switch.

Similarly, understanding information use in terms of information quality can explain situations in which social information does override personal information. This is because in such cases, the social information is actually based on personal, sensory information, which provides unambiguous quality information. For example, Dunlap et al. [14] and Smolla et al. [61] find that social information alone can drive decision making during flower choice in bumblebees, and that social information even outweighs private information when the two compete [14]. This result could be understood through the psychological concept of blocking [20]. However, differences in information content between the two information sources can also explain these results: in these studies the social information is actually private information, based on making associations between a social cue (the presence of a conspecific) and the direct personal experience of the forager with the flower [20]. There is thus no quality ambiguity. Indeed, if ambiguity exists, it is lower in the social information: the forager not only has her own experience of finding the flower acceptable, but also the presence of a conspecific suggests that the conspecific also finds the flower acceptable, resulting in more weight of information about quality for the socially advertised flower. Likewise, Josens et al. [54] describe how trophallactic interactions with a forager providing scented, untainted food can cause foragers to accept similarly scented food tainted with poison, which they would otherwise avoid. Here again, the social information component is based in direct sensory experience of the food (trophallaxis), and the reason the ants overweigh this information over their own later sensory information are similar to those described for the bumblebee examples above.

Also supportive of the information content hypothesis is the response of ants whose receive unambiguous information that alternative food qualities are *not* better – the ants trained to a high quality 1.5M feeder in our experiment. Both paths (apparently) led to equally good food sources, so there was no particular reason to prefer either, and indeed ants chose both feeders equally often.

Finding drops of liquid honeydew lying around on a trail is not a common situation in nature. However, we argue that our results are analogous to an ant receiving a trophallactic interaction, either on the trail or in the nest. Returning ants often perform trophallaxis with multiple partners on returning to the nest, and these partners are then themselves likely to go out to forage. Similarly, dancing honeybees often engage in trophallaxis with followers. Ants receiving trophallaxis may even respond as if they have themselves successfully foraged, depositing trail pheromone when otherwise only successful ants do so [62]. Ants can also occasionally be seen to perform trophallactic interactions on the trail, with receivers continuing on their outwards journey afterwards (TC, pers. obs.). Information gained during trophallactic interactions seems to be particularly well attended to –

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even more so than information gained while foraging [51,54]. This information, gained in the nest or on the trail, can then drive information use. Indeed, provision of unambiguous quality information, may well be a major role of most trophallactic interactions, especially those occurring on a trail. Provision of information about food associated cues such, as the odour of the shared food [50,54], is also no doubt important, although we could not find any role for food odour in the current experiment (see supplement S1).

Trophallactic networks within a nest are complex [63]. Social insect colonies contain a high proportion of apparently taskless individuals ([64] and references therein), which can be divided into inactives and interactives [65]. Interactives have a more central place in interaction networks within the colony [64,65]. If they also receive trophallactic interactions from many foragers and food receivers, they may act to homogenise the various food qualities being returned to the nest, providing a reading of the average food being brought into the colony. Foragers interacting with these ants may then compare this reading to their current exploited food source. If they find their own food source to be worse, they may begin to follow social information. It has already been shown that ants which receive high quality food via trophallaxis are less willing to accept medium quality food, and vice versa for ants receiving poor quality food [Wendt & Czaczkes, in prep]. It is also known that ants which have experienced higher quality food source avoid exploiting poorer but otherwise acceptable food source discovered en-route [66]. Using newly developed imaging technologies allows the flow of food via trophallaxis in a colony to be tracked and quantified [67], opening the possibility to empirically test these suggestions. Such an information use pattern would correspond to the strategy “copy if better”, a strategy normally ignored, as direct quality comparison is not usually considered possible.

Finally, we note that while our results are consistent with ambiguity aversion or the Certainty Effect playing a role in insect behaviour, they do not constitute a direct test of either of these related, but distinct, effects. The memory of the ants can be considered certain, while the pheromone trails ambiguous. Thus, the ants may be following their memory due to its certainty, or avoiding the pheromone trail due to its ambiguity. Moreover, our different treatments likely affected the subjective probabilities of receiving a particular reward each ant assigned to each path. Only by repeatedly testing the same ant in both a risky and an ambiguous situation could one demonstrate that the behaviour of the ants truly deviates from standard economic behaviour, as described by expected utility theory. It is intriguing that the results of this study are in line with the ‘Certainty Effect’ from Prospect theory, while ants also perceive value relative to a reference point – another key aspect of Prospect theory [Wendt & Czaczkes, in prep].

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Here, we explored how three different information sources, one private and two public, interacted. In doing so, we found evidence that the information content of an information source is a key driver in whether it will be heeded or not. Uncertainty avoidance or the Certainty Effect [38,40] could be the driver behind the repeated findings that social insects often preferentially follow their own memory over the communications of their nestmates. We propose that as well as considering 'when' and 'who' strategies for information use, 'what' is an important question to ask: what type of information can be provided. Social insects, and animals in general, demonstrably use complex mechanisms to decide which information to attend to, and integrate information from a wide variety of sources in order to do so.

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