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Food information acquired socially overrides individual food assessment in ants

Roxana Josens[1] · Analia Mattiacci[1] · Jimena Lois-Milevicich[1] · Alina Giacometti[1]

Abstract

Social insects rely on sophisticated communication channels and on individual decision making to achieve efficient foraging behavior. Through social interactions, individuals can acquire information inadvertently provided by a nestmate such as in trophallaxis. During this mouth-to-mouth food exchange, food receivers can perceive the odor of the food delivered by the donor and thus associate this odor with a food reward. Through individual experience, workers are able to perceive characteristic information of the food they have found and to evaluate food quality. Here, we determined which information, social or individual, is prioritized by the carpenter ants *Camponotus mus* in a foraging context. We exposed receiver ants to a deterrent and harmful food with the same odor they had previously learned in the social context of trophallaxis. We determined on which information individual ants based their decision to forage, whether on their individual evaluation of food quality or on the previously acquired social information. We show that the odor experienced in a trophallactic contact overrides individual food assessment to the extent that ants collect the deterrent food when the odor coincided with that experienced in a social context. If ants were exposed individually during a similar time to a food

with the odor and afterwards, they were confronted with the same odor paired with the deterrent substance, and they rejected the deterrent food, contrary to what occurred when the odor was experienced in a social context. These results show that olfactory appetitive experiences in the social context play a fundamental role for subsequent individual foraging decisions. Individuals can acquire information by interacting directly with the environment or through social interactions with other individuals. Individual and social information may induce informational conflicts so that it is crucial to determine when it is worth ignoring one sort of information in favor of the other. Social insects are useful models to address this question: individuals evaluate and learn about their environment and rely on sophisticated communication systems. Here, we show that carpenter ants receiving social instructions, leading them to forage on a toxic food, overcome their natural rejection of this food, despite its noxious effects. Social instructions are, therefore, powerful enough to induce the consumption of food that would be otherwise rejected on the basis of the ants' individual evaluation. Thus, although eusociality seems to favor sacrificing individual assessments in favor of social information, the resulting 'social obedience' may not always be adaptive.

Roxana Josens and Analia Mattiacci contributed equally to this work.

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✉ Roxana Josens
  roxy@bg.fcen.uba.ar

[1] Laboratorio de Insectos Sociales, Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, IFIBYNE, CONICET, Ciudad Universitaria Pab. II. (C1428 EHA), Buenos Aires, Argentina

Significance Statement

Individuals can acquire information by interacting directly with the environment, or through social interactions with other individuals. Individual and social information may induce informational conflicts so that it is crucial to determine when it is worth ignoring one sort of information in favor of the other. Social insects are useful models to address this question: individuals evaluate and learn about their environment and rely on sophisticated communication systems. Here we show that carpenter ants receiving social instructions leading them to forage on a toxic food, overcome their natural rejection of this

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food, despite its noxious effects. Social instructions are, therefore, powerful enough to induce the consumption of food that would be otherwise rejected on the basis of the ants' individual evaluation. Thus, although eusociality seems to favor sacrificing individual assessments in favor of social information, the resulting 'social obedience' may not always be adaptive.

Keywords Social information · Individual information · Ants · Olfaction · Foraging · Recruitment

Introduction

Individuals can acquire information by interacting directly with the physical environment (*personal information*) or, in a social context, through interactions with other individuals or their products (*social information*) (Danchin et al. 2004). Social information can be transferred through signals—stimuli specifically designed by natural selection to convey information—or through cues—stimuli provided inadvertently by individuals and not designed explicitly for communication purposes (inadvertent social information (ISI); Danchin et al. 2004). In the latter case, individuals inadvertently leave cues that can be used as publicly available information by other individuals (Danchin et al. 2004).

Social insects are useful models to understand the interplay between socially and individually acquired information (Leadbeater and Chittka 2007; Grüter et al. 2010; Grüter and Leadbeater 2014). They possess sophisticated communication systems including ritualized behaviors and a broad spectrum of chemicals mediating several behavioral functions. Social insects also use cues in an adaptive way in a variety of contexts. For instance, during recruitment, honey bees exchange scented food via mouth-to-mouth contacts (trophallaxis) so that receivers can acquire olfactory information about the food source visited by the donor (ISI) (Farina et al. 2005, 2007; Arenas et al. 2007; Balbuena et al. 2012). Odor cues acquired in this context later drive the foraging choices of receivers (Farina et al. 2005; Balbuena et al. 2012). A similar scenario can be found in the carpenter ant *Camponotus mus*: during trophallaxis, receiver ants perceive the odor of the nectar offered by a donor and use this information afterwards to localize the nectar source (Provecho and Josens 2009).

Besides acquiring inadvertent information in a social context, social insects are well known for their capacity to perceive and use cues to master their environment efficiently, be it in a foraging and/or in a navigation context, i.e., in situations where an ant or a bee depends to a large extent on its individual performance. In the last decades, bees and ants have emerged as model organisms for understanding associative learning and cognition (Dupuy et al. 2006; Josens et al.

2009; Giurfa 2007, 2013; Guerrieri and d'Ettorre 2010) precisely because they have the ability to use a variety of sensory cues as predictors of positive or negative outcomes (food, nest, punishment, etc.).

The picture emerging from these two scenarios is one in which social insects benefit from social and/or personal information so that both can potentially drive their decision-making process. However, multiple information sources can be sometimes conflicting. It was suggested that individuals should rely on social learning rather than individual learning whenever they can, because the use of social information is generally considered to be highly beneficial (Rendell et al. 2010), particularly in social species.

Several studies have addressed the potential conflicts between social and personal information. In the case of social insects, these studies take place in the context of appetitive search, where insects are forced to make a decision when a memory acquired in an individual context is conflicting with a memory acquired in a social context (bees, Biesmeijer and Seeley 2005; Grüter et al. 2008; Grüter and Farina 2009; Grüter and Ratnieks 2011; bumblebees, Leadbeater and Florent 2014). In other cases, a memory acquired in an individual context is in conflict with a communication signal (as a pheromone trail for ants) (Rosengren and Fortelius 1986; Harrison et al. 1989; Traniello 1989; Quinet and Pasteels 1996; Grüter et al. 2011). Most studies have showed that personal information overrides social information, in particular when the food source of the personal information is still profitable. Such conflicts take place before reaching the food, which commonly implies choosing the way towards the source. In this study, we tackled the question of what may occur if the conflict is about the quality of the food the recruited forager found; i.e., the conflict takes place after reaching and tasting the food. What may occur if the food encountered is different from that to which the ant was recruited for: does she prioritize her individual assessment of food quality at the expense of the previously acquired social information? To answer this question, we determined if a harmful substance known to be a strong deterrent for carpenter ants (Fernández 2001; Sola et al. 2013) becomes, nevertheless, acceptable if associated with an odorant present in the food exchanged via trophallaxis.

Materials and methods

Animals

For all experiments, we used seven queenright colonies of *C. mus* from the province of Santiago del Estero (Argentina), reared in the laboratory during more than a year at approximately constant temperature (25 ± 2 °C) with natural light-dark cycles. Colonies varied from 400 to 3000

workers approximately. Artificial nests were built with plastic containers with a base (30 × 35 cm) coated with plaster and walls (23 cm height) painted with Fluon to prevent ants from escaping. Animals were able to move freely within the nest and had access to fresh water. Between experiments, ants were fed with canned meat, tuna and dead insects (cockroaches and bees) as a source of protein and diluted honey solution as a source of carbohydrates. During the experiments, nests were subjected to a diet with a slight decrease of carbohydrates in order to maintain constant the motivation for feeding during the data collection period.

Solutions

A basal solution of sucrose 20 % (w/w) was offered and combined with linalool (5.55 μl/l) as the olfactory cue (O) and/or boric acid 5 % (w/v) as the deterrent toxic compound (D). Boric acid usually acts as a feeding deterrent to *C. mus* when contacted with mouthparts, but not as a deterrent odor. Its presence in the sucrose solutions generates reduced acceptance, less volume ingested and feeding time, and lower intake rates when the colony has low requirements of carbohydrates; i.e., foragers have low motivation for foraging nectar (Sola et al. 2013).

Depending on the experiment, the solution offered could have the olfactory cue or not: O+ or O−, respectively, and the deterrent compound or not: D+ or D−, respectively. Thus, by combining these elements, we could obtain four sucrose solutions: (1) basal solution (O− D−), (2) odor solution (O+ D−), (3) deterrent solution (O− D+), and (4) deterrent odor solution (O+ D+).

A boric acid concentration of 5 % (w/v) was chosen because it generates high deterrence response in *C. mus* when feeding motivation is low (Fernández 2001; Sola et al. 2013). For the odor concentration, preliminary tests were made, comparing the acceptance of a control solution without odor versus solutions with decreasing concentrations of linalool. The 5.55 μl/l concentration was the first at which equal acceptance of both solutions offered occurred.

Working solutions were separated into aliquots, placed in Eppendorf tubes, isolated in airtight bags (one per type of solution), and frozen, in order to avoid contamination with fungi or other odors. Every week, solutions were replaced by new ones. Prior to each data recording day, the sugar concentration of the thawed aliquot was verified with a refractometer (A. Kruss model HR18-HR92). Only those solutions which kept the initial concentration of 20 % (w/w) sucrose were used in the experiments.

Experimental conditions

We attempted to control the experience of the experimental individual while recreating the natural context in which an ant evokes a previous socially acquired olfactory memory for foraging decisions. We recorded data on days without rain, as we had observed that such external climatic condition may affect some aspects of foraging behavior in the laboratory (RJ, pers. obs.). Every day, we evaluated all the treatments and the treatment order was varied at random throughout the experiment.

The foragers chosen for the experiments were similar in size among treatments. Once data collection was completed, the experimental animals were frozen to avoid pseudoreplication and odor or deterrent compound from entering the nest.

Experiments

1. Control: effect of the compounds on feeding

We aimed at testing whether there was an effect of odor (O) and/or deterrent compound (D) on feeding behavior. For this purpose, individual feeding responses were quantified for the four solutions mentioned above (n = 33 for each solution).

Each trial began by placing an individual ant on a wooden bridge that led to a feeding arena, which was separated from the bridge at the time the ant entered. In the arena, the ant found a drop of one of the solutions which represented an ad libitum source. To prevent cross-contamination between solutions, each drop was placed on an acrylic base (0.5 × 0.5 cm) that was removed and replaced with a new one for each recording. All tests were conducted under an air extractor placed vertically 25 cm above the solution.

Each ant was weighed before (initial weight = ant weight; in mg) and after (final weight = ant weight plus load weight; in mg) ingestion on a digital balance (Mettler Toledo AG285; resolution = 0.01 mg). Thereafter, we calculated the amount of solution ingested (mg) as the difference between the final and initial weights.

2. Response to scented and unscented deterrent solutions after trophallaxis

For this experiment, five different nests were used. This assay was conducted during summer and early fall, because at this time of the year, the foraging activity for this species increases under natural conditions (Falibene and Josens 2014).

The aim of this experiment was to compare the feeding behavior on a deterrent solution under two treatments: ants that had experienced an odor during trophallaxis (odor group) versus ants that had not experienced that odor during trophallaxis (non-odor group). The underlying hypothesis necessarily requires that the deterrent compound acts as such by generating a decrease in the feeding response, so that we are able to evaluate if the presence of the odor experienced previously in the social context overrides the deterrent effect of the solution found. If this is the case, the odor group should display a

higher feeding response than the non-odor group. As previously mentioned, this compound only produces deterrence when the colony has low motivation, but not when the colony is highly starved (Sola et al. 2013); as in the latter case, both solutions—with and without the deterrent compound—are equally ingested. It was therefore imperative to validate the presence of a deterrent effect in the experimental colonies. To confirm this, at the beginning of each recording day, we evaluated the motivational status of an experimental colony by means of a simple test. Each day before recordings, two ten individual groups were offered a sucrose solution: one a basal solution (O− D−) and the other a deterrent solution (O− D+). We recorded the acceptance of each solution. The conditions needed to perform the subsequent experiment were that the basal solution was accepted by at least 80 % of individuals and the deterrent solution only by 60 % or less. If basal solution (O− D−) was highly rejected, we concluded that the motivation was too low; in such a case, donor ants tend either to reject the solution offered initially or not to perform trophallaxis (McCabe et al. 2006).

During the first phase of the experiment, couples of ants of similar weight were selected and placed in small flasks, one couple per flask (radius of 2 cm and height of 3 cm with background of plaster and walls painted with Fluon), and kept there for a 90-min acclimatization period.

In the second phase of the experiment, one ant was removed from the flask and gently placed on a wooden bridge that led to a foraging arena (2 × 3 cm), where a sucrose solution was offered (0.5 µl) without the deterrent compound (D−); for a half of the ants, this solution was scented (O+), and for the other half, unscented (O−). The ant was marked with chalk dust on her gaster while drinking. Once the intake was finished, the ant (the donor) was removed from the foraging arena and gently put back with her partner (the receiver). We observed if they performed trophallaxis; otherwise, after 10 min, the couple was discarded. In case they performed trophallaxis, we recorded the time until it started (*trophallaxis delay* (s)) and how long it lasted (*trophallaxis duration* (s)).

We compared the feeding behavior on the deterrent solution in the two groups of receivers: (1) *odor group*, in which the donor ant fed on an odor solution (O+ D−) and then the receiver ant found an odor deterrent solution (O+ D+), and (2) *non-odor group*, a group that has no olfactory cue added; i.e., the donor ant fed on a (non-odor) solution (O− D−) and then the receiver ant found a (non-odor) deterrent solution (O− D+).

Once the first trophallaxis event was finished, the receiver ant was weighed again (initial weight; mg) and put in the foraging arena, in which a drop of a deterrent solution (D+) was offered, in a volume that represented an ad libitum source. If the receiver ant did not contact the drop before 4.5 min, it was discarded and not considered for any analysis.

We measured the following variables on the receiver ant: *feeding time*, *initial* and *final weights*, and *amount of solution ingested* (mg). Feeding time was defined as the time (s) during which the ant mandibles were in contact with the solution. Ants were weighed before and after feeding to obtain the initial and final weights. Solution ingested was calculated as explained for the control.

3. Response to scented and unscented deterrent solutions after an individual odor experience

Trophallaxis duration can vary from a second to more than 2 min (Provecho and Josens 2009). We wondered whether one personal experience of similar duration with the odor sucrose solution (O+ D−) could affect the decision making when later the ant found a deterrent solution with the same odor previously experienced (O+ D+). In other words, our aim was to verify if—in experiment 2—the effect on the odor-deterrent-solution feeding was induced by the experience of odor with sucrose *within the social context provided by the trophallaxis*, rather than on simple previous exposure to the odor and the sucrose.

For this experiment, two different nests were used. In this assay, each experimental ant visited the foraging arena twice. In a first visit, we offered a drop of a sucrose solution with or without the odor added (O+ or O−, respectively). The ant was weighed before and after feeding, so we obtained the mass of solution ingested in the first visit. Then, she was placed with a group of five nestmates, so that she could unload her crop. Afterwards, the ant was weighed again and gently placed in the foraging arena for a second visit. Only ants that had unloaded at least 90 % of the ingested weight at the first visit were used for the second visit. We compared three groups of ants. One group received sucrose solution (without odor or deterrent added) in the first and second visits (O− D−/O− D−), another group received sucrose solution in the first visit and deterrent solution in the second (O− D−/O− D+), and the last group received odor solution in the first visit and deterrent solution with the same odor in the second (O+ D−/O+ D+).

4. Field assay

We considered that the data obtained in the laboratory experiment might have an application in urban ant control. Sugary toxic baits are commonly used for controlling most of the urban ant species. Such commercial baits are used in *one single step*. Even though they are effective when feeding motivation is high, sometimes—when feeding motivation is low—they are not accepted. We wondered whether our result was likely to be used in the latter situation in order to manipulate decision making in a natural colony in an urban setting. We worked in Hurlingham (province of Buenos Aires, Argentina; 34° 35′ 15″ S–58° 38′ 26″ W) in an area where *C. mus* was extremely abundant. In fact, this species caused considerable damage in structures (building materials, wood,

insulation of roofs, etc.) and electrical apparatus in that entire neighborhood (AM and RJ, pers. obs.). In this area, we worked within a property of about 16 m front by 60 m deep, which contained various one-floor constructions in a large garden with scattered trees and flowerbeds with plants. Assays were conducted during March and April 2013 in days in which we found intermediate motivation conditions, i.e., when basal solution was accepted and deterrent solution was partially rejected, and not in other scenarios.

Our aim was to replicate the situation of the odor group in the laboratory experiment. For each of these assays, we first searched for two sites exhibiting the same ant activity on the trails. One observer located at each site on the trail counted the number of ants crossing a line in one direction during 1 min, five times at intervals of 1 min. The mean of these counts had to be the same or very similar for the two sites to be chosen. In those sites (henceforth, *stations*), we then offered a certain volume of sucrose solution (20 % *w/w*) simultaneously on a rectangular plastic plate (4 × 2.5 cm). Depending on the assay, these solutions could be with odor or not (O+ or O−, respectively; linalool 5.55 μl/l) and with the deterrent substance or not (D+ or D−, respectively; boric acid 4 % *w/v*).

Each assay started by offering a drop of 0.5 ml of a given solution in each of the two stations, and the activity of ants around the drop was quantified for 30 min. The count at both stations was conducted simultaneously by two people trained and using the same criteria of quantification. We counted in situ how many ants touched the drop and how many of them stayed feeding for at least 5 s. Thus, acceptance (%) was calculated by dividing the number of ants that had ingested for at least 5 s out of the total number of ants that had contacted the drop.

Experimental series

Control: This assay allowed verifying that when the deterrent solution acted as such, the presence of our odor did not promote per se an increment in the acceptance of the deterrent solution. We offered odor deterrent solution (O+ D+) at one station and odor solution (O+ D−) at the other station. We conducted this assay twice in two different places with different nest separated ca. 15m one from each other: replicas a and b, respectively.

Experiment: Our aim was to compare the current protocol for ant controlling by commercial baits, in which the toxic bait—possibly deterrent—is applied in a *unique step with no odor added*, with an alternative protocol in *two steps with odor*. For that, we offered in one station the opportunity to experience as a *first phase* the solution with the odor without deterrent, so that ants were able to recruit and establish trophallaxes in a similar situation to that in the laboratory experiment, i.e., receiving this olfactory cue as social information.

Then, in a *second phase*, we offered in the same station the deterrent solution with the same odor.

In this experiment, two different stations were located on a long trail. In one of these stations, we first delivered sucrose solution with odor; then, in the second phase, we offered the solution with odor and the deterrent compound. In the other station, we first offered sucrose solution with the deterrent compound, and then in the second phase, we repeated this treatment. Thus, one difference between the two stations is that in one, there was odor in both phases (station O) while, in the other, there was non-odor in both phases (station NO). The stations were separated by approximately 7 m.

Thus, on the first day of recording (first phase), we offered, at station O, odor solution (O+ D−) and, simultaneously at station NO, a drop of non-odor deterrent solution (O− D+). Once the recording was finished, we left 5 ml of the corresponding solution at each station. Both solutions were housed in four Eppendorf tubes with a small cotton plug at the tip to avoid dripping but allowing ants to ingest through it.

The next morning (ca. 15 h later), as the solution in station O was totally ingested and the trail continued having a high activity, we passed onto the second phase. We offered a deterrent solution in both stations: in station NO, non-odor deterrent solution (O− D+), which was the same solution offered the previous day as it can be done with commercial baits, and in station O, odor deterrent solution (O+ D+). In station O, ants had the opportunity to associate the odor with a sugar solution and, on the following day, they found a deterrent solution with the same odor previously learned (as it was designed in the laboratory experiment).

Statistical analysis

In experiments 1 and 2, the same five different nests were used, while in experiment 3, two different nests were used. Based on preliminary studies and previous experiences, we knew that the factor nest (as a random factor) does not explain much of the variability of the data, in particular when compared with the motivational state of foragers. To confirm this, we analyzed three different GLMM models for each experimental variable. We used a log transformation for some variables that were asymmetrical. The most basic and simplest model had only one factor, treatment (fixed effect); the next model had two factors, treatment and nest (random effect); and finally, the more complex model had three factors, treatment, nest, and the interaction (also a random effect). We performed a comparison between the three-factor and the two-factor models using a likelihood ratio test, and we found no differences between them ($P > 0.05$) for all variables. Afterwards, we compared the two-factor and the one-factor models and again we found no significant differences between them ($P > 0.05$) for all variables. Given that all models were equal, nest as a factor does not explain a significant part of

data variation. This result confirms, therefore, our original assumption on the lack of relevance of between-nest variability. Therefore, the nests used in each experiment were pooled for data analysis.

The mass ingested of the four solutions offered in experiment 1 was compared by a two-way Kruskal-Wallis test (Sokal and Rohlf 2000, p. 446). For experiment 2, all behavioral variables were analyzed by a Mann-Whitney U test. The general significance level used was 5 % in all experiments. In experiment 3, differences among treatments were evaluated by means of a Kruskal-Wallis test for each of both visits, and when significant, multiple comparisons of mean ranks for all groups were made afterwards. The general significance level used was 1 %.

For each field assay, we conducted a chi-square test of homogeneity to compare both stations.

Results

1. Control: effect of the compounds on feeding

Ants involved in the treatments of this experiment had the same initial weight (Kruskal-Wallis test: $H_3 = 0.61$, $P = 0.89$, $N = 132$).

Ants ingested significantly less food when the solution contained the deterrent compound (O+ D+ and O− D+; two-factor Kruskal-Wallis test: factor D; $H_1 = 10.2$; $P < 0.05$). No significant decrease of ingestion was detected when the solution contained the odorant (O+ D− and O+ D+; two-factor Kruskal-Wallis test: factor O; $H_1 = 0.25$; $P > 0.05$, not significant (NS)), and no significant interaction between both factors was found (two-factor Kruskal-Wallis test: interaction O × D, $H_{OD} = 3.11$; $P > 0.05$, NS).

2. Response to scented and unscented deterrent solutions after trophallaxis

The odor in the solution ingested by the donor modified neither the trophallaxis delay nor trophallaxis duration [Mann-Whitney test: $U_{(42)} = 220.5$, $P = 0.61$, NS (Fig. 1(a)), and $U_{(42)} = 199$, $P = 0.32$, NS (Fig. 1(b)), respectively].

Next, we measured the feeding behavior of receivers which had experienced or not the odorant via trophallactic exchange. The receivers of both groups (odor and non-odor) used in this analysis had the same initial weight (Mann-Whitney test: $U_{(42)} = 232.5$, $P = 0.83$). The feeding time varied significantly between treatments (odor vs. non-odor: Mann-Whitney test: $U_{(39)} = 110.5$, $P = 0.0098$; Fig. 2, inset). Ants that had experienced a non-odor solution during trophallaxis spent a reduced period of time contacting the odorless deterrent solution at the food source (O− D+), usually no more than 10 s. On the contrary, ants that had experienced an odor solution during
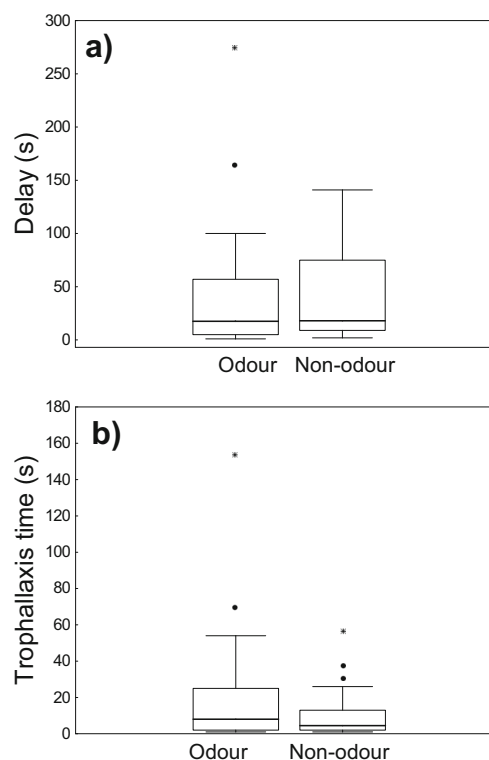

Fig. 1 *a* Delay (s) until trophallaxis and *b* duration (s) of the first trophallactic contact between two groups of ants: in one group, the donor fed on an odorless sucrose solution (non-odor group; $N = 22$) and the other on an odor one (odor group; $N = 22$). *Thick horizontal lines* represent the medians, *boxes* show the 25th and 75th percentiles, and *whiskers* show non-outlier range. *Dots* and *asterisks* indicate outliers. There were no significant differences between groups for both variables (Mann-Whitney test)

trophallaxis spent more time ingesting the deterrent solution with the known odor (O+ D+), in an average of 41 s.

The frequency distribution of feeding times (Fig. 2) showed important differences between both experimental groups: in the non-odor group, 52 % of the ants had contacts with the solution of ca. 1 s, while in the odor group, only 15 %. Conversely, in the odor group, 50 % of the ants had feeding times longer than 30 s, while in the non-odor group, only 10 %. Therefore, the odorant experienced during trophallaxis induced longer feeding times of the deterrent solution.

The feeding time alone does not provide a complete account of the decision-making process of receiver ants. A fundamental variable to consider is the quantity of deterrent solution ingested by the receiver ant. For the odor group, the mass of solution ingested was significantly higher than that of the non-odor group [odor group: 1.3 ± 0.3 mg (mean ± SE); non-odor group: 0.3 ± 0.1 mg (mean ± SE); Mann-Whitney test: $U_{(42)} = 98$, $P = 0.0008$; Fig. 3]. In the frequency distribution of ingested food mass, 77 % of the ants of the non-odor group had null loads or loads that were below 5 % of their own weight, while in the odor group, these categories dropped to
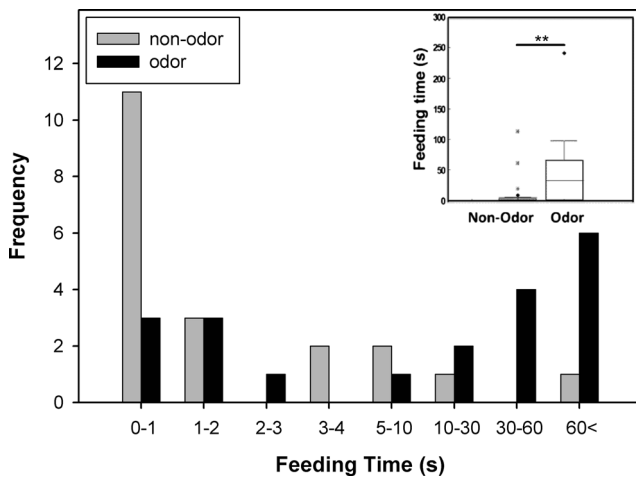
Fig. 2 Frequency distribution of the times of ingestion on a sucrose solution added with a deterrent compound. For one group, the deterrent solution was added with an odor (O+ D+). These ants have previously received by trophallaxis a sucrose solution with the same odor (odor group: *black bars*). For the other group, no odor was added in the solution received by trophallaxis (O− D−) nor in the deterrent solution (O− D+) found in the foraging arena (non-odor group: *gray bars*). *Inset* feeding time (s) on a deterrent solution for the two mentioned groups of ants ($N_{non-odor} = 21$ and $N_{odor} = 20$). *Thick horizontal lines* represent the medians, *boxes* show the 25th and 75th percentiles, and whiskers show non-outlier range. *Dots* and *asterisks* indicate outliers. **$P < 0.01$, Mann-Whitney test

32 %, consistently with higher ingestion of the deterrent solution. Therefore, a pre-exposure to the contingency sugar-odor experienced in the social context of trophallaxis induced a longer feeding time and more mass ingested of a deterrent solution.

Short (≤5 s) and long (>5 s) trophallaxes led to the same result: a similar percentage of receivers drinking the scented deterrent solution for more than 5 s (64 and 67 %, respectively). Therefore, it seems that the duration of trophallaxis did not play a determinant role for the receiver's acceptance or rejection of the scented deterrent solution at the food source.

3. Response to scented and unscented deterrent solutions after an individual odor experience

In this experiment, we studied whether a similar result could be obtained in a second visit if the contingency sugar-odor was experienced *individually* in a first visit to the source. All ants used in this experiment were of similar size (ANOVA: $F_{2,41} = 0.73$, $P = 0.49$).

As shown in Fig. 4, the mass ingested in the first visit was similar for all three groups as in all cases the food did not contain the deterrent substance (Kruskal-Wallis first visit: $H_2 = 4.70$, $P = 0.095$, $N = 44$). On the contrary, the mass ingested in the second visit varied between treatments as the presence of the deterrent substance in two cases (2 and 3; see above) decreased ingestion regardless of the presence of the odorant (Kruskal-Wallis second visit: $H_2 = 28.23$, $P < 0.0001$,
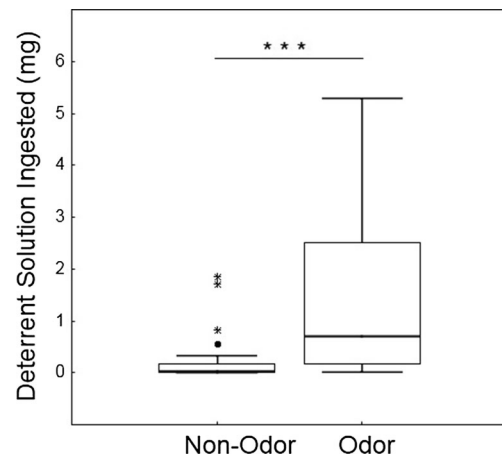

Fig. 3 Deterrent solution ingested (mg) by ants that previously received sucrose solution by trophallaxis. Two groups are compared: odor group, in which ants found the deterrent solution with the same odor (O+ D+) and had previously received during trophallaxis (O+ D−; $N = 22$), and non-odor group, in which no odor was added in any of the two instances (O− D− in trophallaxis and O− D+ at the source; $N = 22$). *Thick horizontal lines* represent the median, *boxes* show the 25th and 75th percentiles, and *whiskers* show non-outlier range. *Dots* and *asterisks* indicate outliers. ***$P < 0.001$, Mann-Whitney test

$N = 44$). Only the control group which experienced the same sucrose solution during two consecutive visits ingested the same mass of solution. Therefore, a simple pre-exposure to the contingency sugar-odor per se does not promote more acceptance of the deterrent solution.
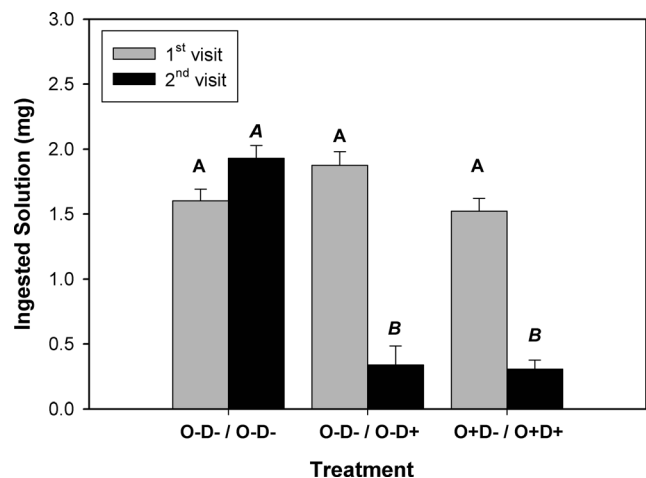

Fig. 4 Solution ingested (mg) with or without odor added (O+ or O−, respectively) and with or without a deterrent compound added (D+ or D−, respectively). A solution was offered to each ant in two consecutive visits to a foraging arena (visit 1/visit 2). Three treatments were compared: O− D−/O− D− ($N = 15$), O− D−/O− D+ ($N = 15$), and O+ D−/O+ D+ ($N = 14$). At visit 1, the ingested mass did not differ among treatments (*uppercase letters in common* means no differences; Kruskal-Wallis test). At visit 2, the ingested mass decreased with the presence of the deterrent compound regardless the presence of odor (*uppercase italic letters in common* means no differences; Kruskal-Wallis test). Differences at $P < 0.01$

4. Field assay

Control

Both replications (a and b) yielded the same result: the deterrent solution was less accepted than the solution with no deterrent compound (homogeneity test: $P < 0.001$; Fig. 5). In agreement with the results obtained in the laboratory (see Exp. 1), field ants, with an odor experience that was unknown to us, also rejected the deterrent compound irrespective of the odor presence in the food.

Experiment

We compared two protocols for toxic bait acceptance: one was the current protocol used for commercial baits in one step (the same bait offered in the first and second phases), and the other considered two different phases. In the first phase, both stations showed a similar activity in the first 10 min (from the placement of the drop until the 10th minute), while in station NO, four ants touched the drop, five ants did the same in station O, and all the ants rejected the drops in both stations. In the second 10 min (from 10 to 20), differences between stations became observable: in both stations, seven ants touched the drop, but while all ants rejected the deterrent solution (station NO), four ants drank more than 5 s on the odor solution (station O). In general, for the time recorded and as expected, the deterrent solution (O− D+), present in station NO, was rejected by the ants (Fig. 6(a)); most of the ants that touched the drop available in station NO rapidly went away without feeding. On the contrary, the scented solution available in station O (O+ D−) was highly accepted as it had no deterrent substance. In this case, more than half of the ants that touched the drop fed on it for more than 5 s. Therefore, food acceptance was significantly different between both stations in the first phase (homogeneity test: $P < 0.001$; Fig. 6(a)).

In the second phase, both solutions had the deterrent compound. However, they were not equally rejected (homogeneity test: $P < 0.001$; Fig. 6(b)). At station NO, the odorless deterrent solution still presented a low acceptance that was similar to that of the first phase. On the contrary, at station O, the deterrent solution which presented the same odorant that was previously experienced with pure sucrose solution was highly accepted.

We highlight that *C. mus* ants foraging on station O during the second day (i.e., when the deterrent and harmful substance was then available on it) defended fiercely this resource against other ant species which tried to get close to the station. This was never observed at station NO; on the contrary, recruitment was almost inexistent in this station and ants bypassed this source by changing the direction of their trail (i.e., generating a semicircle of about 30 ± 10 cm away from station NO). Although ant activity (i.e., the number of ants
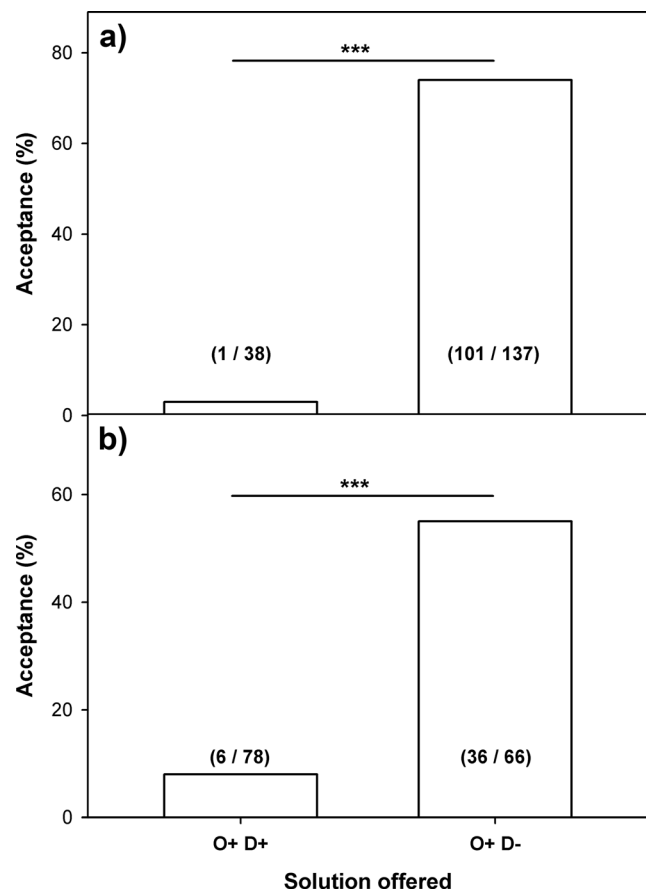

Fig. 5 Field study. Two stations were evaluated simultaneously for the acceptance of a given sucrose solution: in one station, odor deterrent solution (O+ D+) was offered, while in the other, odor solution (O+D−). *Acceptance (%)* is the percentage of ants that drank for at least 5 s out of the number of ants that touched the drop offered. *a, b* Two repetitions of the same assay were performed. In both repetitions, the result was the same; the presence of the odor does not compensate the deterrent effect. *Numbers in parentheses* is the number of ants that drunk over 5 s out of the number of ants that touched the drop. ***$P < 0.001$, homogeneity test

walking on the trail) was similar in both trails, very few ants touched the food drop available in station NO during the second experimental phase due to the bypassing arc of their trajectory.

Discussion

This is the first study that has tackled a conflict between social and individual information in which a social instruction contradicts the perception of a toxic compound being experienced while the decision whether feeding or not is being made. In both experiments, in controlled laboratory conditions as well as in the field, ants perceived the deterrent compound in the solution and behaved consequently by rejecting this harmful
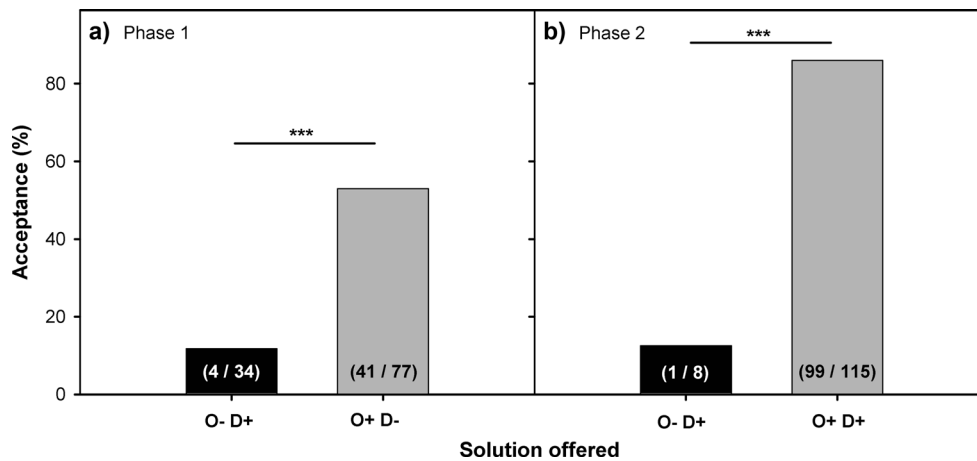
Fig. 6 Field study. *Acceptance (%)* is the percentage of ants that drank for at least 5 s out of the number of ants that touched the drop offered in two stations. The two stations were located in a trail of ants (station NO in *black* and station O in *gray*) and evaluated simultaneously for the acceptance of a sucrose solution in two phases. *a* In the first phase, in station NO, a non-odor deterrent solution (O− D+) was offered, while in station O, odor solution (O+ D−). *b* In the second phase, the next day, the solution was the same for station NO (*black bar*; O− D+), but in station O, a deterrent solution with the same odor as on the previous day was offered (*gray bar*; O+ D+). *Numbers in parentheses* is the number of ants that drunk over 5 s out of the number of ants that touched the drop. ***P < 0.001, homogeneity test

food. However, when the deterrent solution was presented with the odor that matched with the odor ants had experienced in a social context of trophallaxis, they accepted the deterrent solution regardless of its deterrent quality. Animals instructed to forage and confronted with a toxic compound overcame their aversion and fed on it, a behavior that non-instructed animals did not exhibit. Thus, contrary to prior studies, in our work, the individual information accessible to foragers was not a memory acquired in a previous foraging bout but their individual sensing of toxic food. Here, the individual expectation generated by social information overrides the individual assessment of food toxicity. Moreover, memories are known to be labile, they might be vulnerable to disruption and extinction, and associations might be replaced or reversed (Komischke et al. 2002; Devaud et al. 2007; Eisenhardt 2014; Müssig et al. 2010). Besides, existent personal information can become outdated (Grüter et al. 2008). All these arguments do not apply for our study, as the information of the harmful food is gained at the moment, the ant should make a decision. In most studies about social and individual information conflicts, workers must decide between available options in an appetitive search regarding *where* to forage, to nest, etc. (Aron et al. 1993; Rosengren and Fortelius 1986; Harrison et al. 1989; Grüter et al. 2008, 2011; Stroeymeyt et al. 2011; Leadbeater and Florent 2014), whereas for our study, the decision is *whether* to forage or not on toxic food. Thus, our results show how the assessment of a harmful compound is overridden by social information.

When an ant is recruited to a non-familiar source of nectar, she interacts with the recruiter ant and, usually, trophallactic contacts are established between them. Trophallaxis allows the receiver to acquire chemical information about the source,

particularly olfactory cues (before contacting the solution) and gustatory cues, e.g., the composition of the nectar (when contacting the solution). As there is no other information available about the food source, these keys become the most relevant in this context, and only a brief contact is enough to establish an olfactory memory (Provecho and Josens 2009) as seen in bees (Farina et al. 2005, 2007). Probably in this situation, not only is associative learning involved but also attention processes towards these particular cues as information providers. This memory is used for short-distance nectar localization once the ant reaches the source, and enables her to move towards the source of the smell (Provecho and Josens 2009). Then, when the receiver ant finds and contacts the nectar with her mouthparts, she can detect the physicochemical properties thereof. In the case of the deterrent solution, it was clear that its presence can be perceived by the ants causing deterrence. This was observed in the control experiment of laboratory and the field assays, and the results are consistent with previous works with the same ant species (Fernández 2001; Sola et al. 2013). An assessment of the deterrent solution without the previous social experience would make the solution reprehensible. However, the recruited ant prioritized social information on the assessment made by her partner over the information gathered by herself. Consequently, she acted accordingly and behaved as if she had found the sucrose solution to which she was recruited.

A similar situation was explored by Roces (1990), when he studied odor use during recruitment in leaf-cutting ants. There, a scout foraged on a scented valuable resource, odor impregnated flakes. Then, other nestmates were recruited, finding at the foraging site filter paper disks some with the same scent and some with a different scent. These recruited ants used the

learned cue as a decision criterion during food collection. However, in this study, there was no specified data about the context in which the odor information was gathered: it cannot be discarded that recruited ants may have come in contact with the scented flake that the scout may have dropped. This case might be considered as an individual contact with the food, rather than a socially mediated signal. Moreover, there was no quantification or control of the cumulative experience with the odor for each individual ant. Furthermore, ants may gain experience with odor-impregnated disks carried by a returning worker on the trail (Howard et al. 1996). On the other hand, filter paper is not a toxic resource and perhaps also serves as a substrate for the fungus garden, in sharp contrast with our boric acid bait. This compound is toxic for ants in general (Klotz et al. 1997) and also for *C. mus* in particular, generating a lethal effect when ingested by workers (Sola et al. 2013). In another study by Roces (1993), recruitment information provided by the scout affected the velocities towards the source and back to the nest of recruited leaf-cutting ants *Acromyrmex lundi*. Contrary to our study, there is indeed an individual assessment of the resource quality in this leaf-cutting ant, which is modulated by the information received during recruitment. This individual assessment of food quality was evinced as no ant showed trail laying while returning to the nest having found a poor quality of resource regardless of the food found first by the scout. On the contrary, if they found a better resource, there was a higher percentage of trail layers. This suggests that, in leaf-cutting ants, even when the information received by the scout is relevant and modulates the motivation of recruiters, there is an individual assessment at the moment the recruited ant finds the resource (Roces 1993).

The central point here is to understand in which situations the social information is preferred over the individual information. Since the colony in eusocial insects acts as a reproductive unit, it is not expected that there is manipulation or deception tactics by any forager of the colony, i.e., giving false information in order to get an individual benefit. Dismissing the possibility of manipulation, the information provided by the recruiter ant should always lead to greater efficiency in terms of group gathering and, therefore, precedence of this social information would be favored by natural selection. This makes sense if we assume that the evaluation or the assessment of resource quality demands time and/or attention certainly longer than the immediate acceptance of the same resource by the single *matching* with the olfactory memory established. It is often assumed that individual learning is more costly than social learning to make decisions (but see Seeley 1983), because of the risk of making errors, costs that will result at least in a waste of time (Laland 2004). Hence, if only scouts evaluated the resource but not recruited ants (which just find and transport it to the nest), it would result in a very useful tactic to quickly forage and dominate or even monopolize a resource in the frame of a strategy of cooperative foraging. This might be particularly important in competitive environments with food sources that present great concurrence with other ant species.

Using social information per se does not warrant success, because environments change and individuals thus expose themselves to different environmental conditions. Therefore, the shorter the time involved in receiving and reacting to social information, the more reliable this information is. In nature, in such a short time frame, most situations probably present consistent individual and social information about the quality of a given source, and therefore, individuals might be able to use social information blindly to act as a colony more efficiently. The question that still remains is, if the personal assessment, once the ant has already found the nectar, really involves any additional cost or time.

This simple rule of thumb to make decisions can also cause colonies to become trapped in suboptimal foraging situations: some ants and bees show a reduced ability to switch to better food sources after foraging at a food source of low quality that is already being exploited (Detrain and Deneubourg 2008; Schmidt et al. 2006; in *C. mus*: RJ, pers. obs.). Furthermore, as our field assay showed, ants became trapped and defended a harmful food source.

Theoretical studies in this field pointed out that the level of energy reserves might be a particularly important state variable that can affect the use of social information (Barta and Giraldeau 2000) in the context of group foraging. We restricted the conditions under which we evaluated our hypothesis both in the laboratory and field assays. That means that our results may not necessarily apply to other scenarios, for example, under heavy starvation conditions.

It is evident that not all the individuals respond equally; a scout seems to evaluate the source quality and reject a deterrent solution regardless of the odor presence. The recruited ants that experienced the odor in the context of trophallaxis were more willing to accept and defend this harmful resource.

There are many examples of vertebrate species capable of learning what to eat from conspecifics such as rats which present *socially-induced* preferences. A simultaneous exposure to a given food odor together with another rat results in an enhanced preference for this food, while an exposure to an odorant food alone (without the social context) does not (Galef 1989, 2012). In a similar way, in our study, ants exposed to food with a given odor in a non-social context did not accept the deterrent solution with this odor in the following visit to the source. On the contrary, the ants that experienced the odor solution in a social context (experiments 2 and 3) accepted the deterrent solution.

In carpenter ants, trophallaxes, even for a few seconds, affect both the odor choice in a Y-maze (Provecho and Josens 2009) and the decision making once contacting a food with the odor (the present study). It was suggested that this social context of recruitment increases arousal so it might

facilitate the probability to establish these olfactory memories (Menzel and Müller 1996; rev. Farina et al. 2012). In a similar way, just a few minutes of interaction between rats is enough to affect diet preferences (Galef 2003). Rats do not require a direct contact between observer and demonstrator, but the presence of food odor and a volatile compound emanated from the breath of a peer (Galef and Wigmore 1983). On the other hand, when a couple of ants in a flask did not perform trophallaxis, the potential receiver had no contact with the sugar solution; then, while in the Y-maze, instead of choosing the arm with the pre-exposed odor, she chose the arm with a novel odor (Provecho and Josens 2009).

Only when rats are exposed to live demonstrators—even when they were anesthetized—the subsequent preference for the food is generated (Galef and Stein 1985; Galef et al. 1985; Galef and Kennett 1987). Preference enhancement depended on exposure to a diet within a context provided either by demonstrator's breath or by carbon disulfide (CS_2) present therein (Galef et al. 1988). If ants use other stimuli (such as pheromones, cuticular hydrocarbons, tactile stimulation, etc.) that might improve the learning of the food scent during trophallaxis is a question that remains to be studied, as well as if the social information involved leads to robust, long-term olfactory memories.

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