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Research article

Label familiarity and discriminatory ability of ants reared in mixed groups

C. Errard[1, 2, *] and A. Hefetz[1, 3]

[1] *Laboratoire d'Ethologie Expérimentale et Comparée, Université Paris Nord, CNRS 2214, F-93420 Villetaneuse, France*
[2] *Present address: Laboratoire d'Ethologie et Pharmacologie du Comportement, Faculté des Sciences et Techniques, Parc de Grandmont, F-37200 Tours, France, e-mail: errard@balzac.univ-tours.fr*
[3] *Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv 69978, Israel, e-mail: hefetz@ccsg.tau.ac.il*

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Summary

The discriminatory ability of the ant *Manica rubida* was tested using mixed species groups composed of *M. rubida* and *Formica selysi*. We recorded the response of *M. rubida* reared in homospecific or heterospecific groups towards postpharyngeal glandular secretions (applied on a nestmate) of *F. selysi* that originated from various homo- or heterospecific groups. The reaction of the ants depended largely on the source of the scent applied, and tends to suggest a hierarchical system for deciphering the odour. The ants exhibited a diminishing degree of aggression that corresponded to an increase in the degree of odour familiarity. The most aggressive encounters were manifested when *M. rubida* ants from homospecific colonies were exposed to the glandular secretions of *F. selysi* ants from homospecific colonies. A lesser degree of reaction was noted when *M. rubida* from mixed species were tested with similar alien secretions. At the other extreme, heterospecific *M. rubida* ants exposed to a completely familiar signal (that of *F. selysi* nestmates) did not elicit any overt aggression. Intermediate reactions occurred when the secretion was only partially familiar. The introduction of completely alien elements e.g., the occurrence of alkenes and alkadienes characteristic to *F. selysi* but barely present in *M. rubida* from homospecific colonies, appeared to elicite the highest aggression. On the other hand, in *M. rubida* from heterospecific groups, all the signal elements were familiar but the overall composition deviated from the aquired template. We hypothesize that the deciphering of the odour may be hierarchical and that the template to which the odour is compared is acquired. Moreover, since the odour is dynamic, template plasticity must follow. Acquisition of the template is not a permanent event, but has to be reinforced via constant perception of nestmates' odours.

Introduction

Nestmate discrimination is nearly ubiquitous in the social insects. Exclusion of unrelated individuals prevents robbery, predation and parasitism, enables mono-

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[*] Author for correspondence.

polization of resources in defended territories, and helps in eliminating neighboring competitors (Wilson, 1971). It has been further demonstrated that nestmate recognition is attributed to olfactory non-volatile substances borne on each individual's cuticle, that are shared by all nestmates and vary between nests (Howse, 1975; Bradshaw and Howse, 1984; Blum, 1987; Howard, 1993). Indirect evidence such as the species as well as colony specificity that is as predicted for recognition signals, suggests that among the cuticular lipids, hydrocarbons are responsible for the discriminatory activity (Bonavita-Cougourdan et al., 1987; Morel et al., 1988; Henderson et al., 1990; Nowbahari et al., 1990). Each colony member possesses its own cues, that are correlated with the genotype, and is influenced by the social and physical environment (Gamboa et al., 1991). In parallel, each individual should possess a sensory template encoding the labels likely to characterize nestmates. A "decision rule" concerning the magnitude of discordance between the template and the encountered individual is used to determine appropriate subsequent behaviour (Breed and Bennett, 1987). For example, an individual whose labels match another individual's template is accepted as a colony member, whereas an individual whose labels deviate from the template may be attacked, as a function of the degree of tolerance which determines the decision rule (Holmes and Sherman, 1983).

Although each member of the colony may possess an individual odour composition, in large colonies discrimination between a nestmate and an alien conspecific can be possible through the formation of a colony odour common to all its members (Crozier and Dix, 1979). It was recently shown that in *Cataglyphis niger* (André, 1881) this "Gestalt odour" is achieved by an exchange of hydrocarbons between nestmates (Soroker et al., 1994). The same results were observed in artificial mixed groups of *Formica selysi* (Bondroit, 1918) and *Manica rubida* (Latreille, 1902) workers, in which the ants acquire some of the components characteristic of their allo-specific-nestmates, thus achieving a unifying hydrocarbon profile (mixture of the odours of the two species) in the cuticle (Bagnères et al., 1991; Errard, 1994a). The two species cohabited without aggression, presumably because workers of both species shared the same mixed species odour.

In two different species, *Cataglyphis niger* (Soroker et al., 1994) and *M. rubida* (Hefetz et al., 1996), it was demonstrated that the postpharyngeal gland plays a role in nestmate recognition. Application of an alien postpharyngeal gland secretion on the cuticular surface of ants elicited a similar aggression by nestmates as that manifested towards alien ants. Conversely, application of nestmates' postpharyngeal gland secretion on alien ants reduced the aggression towards them and made them more acceptable within the environment of the nest.

The link between cuticular lipids and postpharyngeal gland secretions was demonstrated by indirect and direct means. There is a chemical congruency between the content of the postpharyngeal gland and the cuticule composition (Bagnères and Morgan, 1991). Moreover, by using radiolabelled tracers it was shown that there is an exchange of hydrocarbons between the postpharyngeal gland and the epicuticle of the individual ants as well as between nestmates via trophallaxis and grooming (Soroker et al., 1994; Soroker et al., 1995). More relevant to the present work, the same phenomena are observed in mixed species groups of *F. selysi* and *M. rubida*. The occurrence of the respective heterospecific components in the epicuticle of members of such groups (Bagnères et al., 1991), reflects the mixture that is already present in the postpharyngeal gland (Hefetz et al., 1992). These group specific blends are obtained and maintained by continuous mutual exchanges between the members of the group through trophallaxis and allogrooming (Vienne et al., 1995).

Much of the work on between-colony discrimination has focused on the source and nature of colony-specific labels and on the origin of templates. However, the mechanisms for such discrimination are less well known. The use of mixed species group provides a good system to address such questions. The specific use of groups composed of *M. rubida* and *F. selysi* has an additional advantage, since the putative recognition cues differ considerably between the genera. *F. selysi* secretion is composed of at least 50% alkenes and alkadienes that are almost completely absent in *M. rubida* (Bagnères et al., 1991; Hefetz et al., 1992). In terms of the label, we artificially obtained a mixture of specific composition in one group (the mixed species group), while retaining the pure specific composition in the homospecific mother colonies, reared under different social condition.

In the present paper, we tested the response of *M. rubida* workers reared under different social condition (e.g., homo- or heterospecific groups) towards postpharyngeal glands exudates of *F. selysi* reared under various social conditions (odours with different degrees of familiarity). We also addressed the question of whether ants reared in a mixed species group recognize only their nestmates' odours (group or colony odour) or the corresponding allospecific odours in general (genus or species odour).

Materials and methods

Ants, preparation of mixed species groups

The species studied, *Manica rubida* (Myrmicinae, oligogynous species) and *Formica selysi* (Formicinae, monogynous species), were collected from the same biotope (French Alps: altitude, 800 m) in June 1994. These colonies (four colonies of each), constituting the "mother colonies" containing queens, brood and workers, were reared in the laboratory in Paris in nest-tubes (180 × 17 mm) fitted at one end with a water container and covered with black cardboard. Each nest was placed in a plastic box (280 × 275 × 85 mm) that served as a foraging arena. The colonies were reared at 20 ± 3 °C under natural photoperiod, and were regularly fed with honey/apple mixture and mealworms *ad libitum*.

For the formation of the mixed colonies, ants that were less than five hours post-emergence were removed from their respective natal nests and combined into a queenless single mixed species group (25 mixed groups including 10–15 workers of each species). The ants were kept as a mixed species group for at least 2 months before they were taken for testing or for dissection of the postpharyngeal gland.

Observations: aggression tests

The bioassay was comprised of encounters between six *M. rubida* nestmates, taken either from a homospecific (mother colony) or a heterospecific colony (mixed

Table 1. Summary of the experimental groups depicting the social structure of the group from which the test *Manica rubida* were taken, and the origin of the postpharyngeal gland exudate that was applied to the tested ant

Abbreviation	Origin of the *M. rubida* ants	Source of the postpharyngeal gland
MHm (FHm)	Homospecific nests: MHm	*F. selysi* from a homospecific colony (FHm)
MHt (FHm-d)	Heterospecific nests: MHt	*F. selysi* from an alien homospecific colony (FHm-d)
MHt (FHm-p)	Heterospecific nests: MHt	*F. selysi* from the parent homospecific colony (FHm-p)
MHt (FHt-d)	Heterospecific nests: MHt	*F. selysi* from a different mixed species group (FHt-d)
MHt (FHt-s)	Heterospecific nests: MHt	*F. selysi* from the same mixed species group (FHt-s)

species group). One of these nestmates was marked with a color dot on the abdomen and served as the test ant. Table 1 lists the origin of the test ants and the source of the postpharyngeal gland secretions used in the encounters. In all the encounters, the behaviour of the ants towards the marked ant was recorded. Each test comprised two consecutive encounters (2–3 minutes between the first and second encounter). In the first (control) encounter the marked ant was untreated, whereas in the second (test) encounter it was treated with a postpharyngeal gland secretion from various sources. The control is to verify that the color dot we mark the ant with is not affecting the behavior of the other ants (visual cues) and also to set a base line behavior before each test to reduce individual variability in the different tests. For the application of postpharyngeal gland exudates, ants were dissected in water under stereomicroscope and their gland was removed and placed on the tip of an entomological pin. This was immediately applied to the test ant by crushing it on the thorax and smearing the secretion as evenly as possible over the entire body of the ant. A single gland was used for each test.

Encounters were conducted for 3 minutes in a Petri dish (90 mm diameter). Before each encounter, the marked ant was allowed to acclimate by isolating it in a glass tube for one minute in the Petri dish. Each encounter began by removing the glass tube and recording the reaction of the ants towards the marked nestmate according to the following index of aggression: 0 = inspection and antennal contact, 1 = threat as indicated by mandibular opening, 2 = biting, 3 = curling the abdomen in stinging attempts.

The frequencies and duration of each behavioural component were registered using a micro-computer (Psion® event recorder, Aware, Paris, France) and the overall aggression exhibited in each encounter was calculated as follows:

$$\frac{\sum_{i=1}^{n} AI_i \cdot t_i}{T}$$

where AI_i and t_i are the aggression index and duration of each act respectively, and T is the total interaction time defined as the sum of times in which the ants were in physical contact.

Statistical tests (ANOVAS) revealed that the control encounters in the different experiments were not significantly different (Fisher PLSD $p > 0.1$). Therefore, for comparison between treatments, each control encounter was subtracted from the respective test encounter, and this new variable served for comparison among the various treatments using ANOVA. Since antennal inspection manifests a behaviour related to recognition it could be used, independently, as a criterion for recognition of the treated ant. The duration of the antennal contacts (seconds) within a manipulation, i.e., control vs test, were compared using a Non Parametric Paired Sign test. The statistical program used for all statistic is "Statview for Macintosh".

All the behavioral test were unidirectional because the response of *F. selysi* is almost always avoidance and escape and it is difficult to quantitate.

Results

In all the control encounters (i.e., the first encounter of each test) the *M. rubida* workers did not react aggressively towards nestmates. Each time two ants met, whether this involved the marked ant and a nestmate or encounters between any of the other nestmates, they antennated each other briefly and then continued walking. The behaviour of the ants was different when the introduced (marked) ant was treated with a postpharyngeal gland secretion. As soon as the treated ant was encountered by one of its nestmates it was antennated extensively (mean antennation time per contact per test was 1.89 ± 1.63 s for the control encounters and 4.41 ± 5.98 s for the test encounter $p < 0.001$; Non Parametric Paired Sign test). Following physical contact between the ants further reaction took place; its character depended on the nature of the glandular deposit (Fig. 1).

Ants that originated from a homospecific *M. rubida* colony were apparently more sensitive to the scent of the postpharyngeal gland secretion of *F. selysi*, since they reacted significantly more aggressively towards their treated nestmate than did *M. rubida* reared in mixed species group. The best indication of this phenomenon can be seen in the comparison between experiments MHm (FHm) and MHt (FHm-d) (cf. Table 1). In both experiments the tested ants encountered a postpharyngeal gland secretion dissected from ants that belonged to a homospecific *F. selysi* colony that was unfamiliar. In the case of the homospecific *M. rubida*, the ants were presumably never exposed to a secretion of *F. selysi*. When workers of *M. rubida* from a mixed species group were used, the postpharyngeal gland was taken from a homospecific *F. selysi* colony that was different from the parent colony from which the specific mixed species group was formed (FHm-d). This comparison clearly demonstrated higher aggression of the homospecific ants towards the treated nestmate (1.06 ± 0.77 for MHm (FHm) vs. 0.50 ± 0.56 for MHt (FHm-d). Fisher's PLSD, $p = 0.0007$).

As depicted in Figure 1, among the experiments involving *M. rubida* from mixed species groups the application of postpharyngeal gland of a *F. selysi* from the same mixed species group was the least effective. In fact, in this experiment, in contrast to all other experiments performed, the test encounter was not significantly different from the control encounter ($p = 0.15$ paired *t*-test), and the behaviour of the

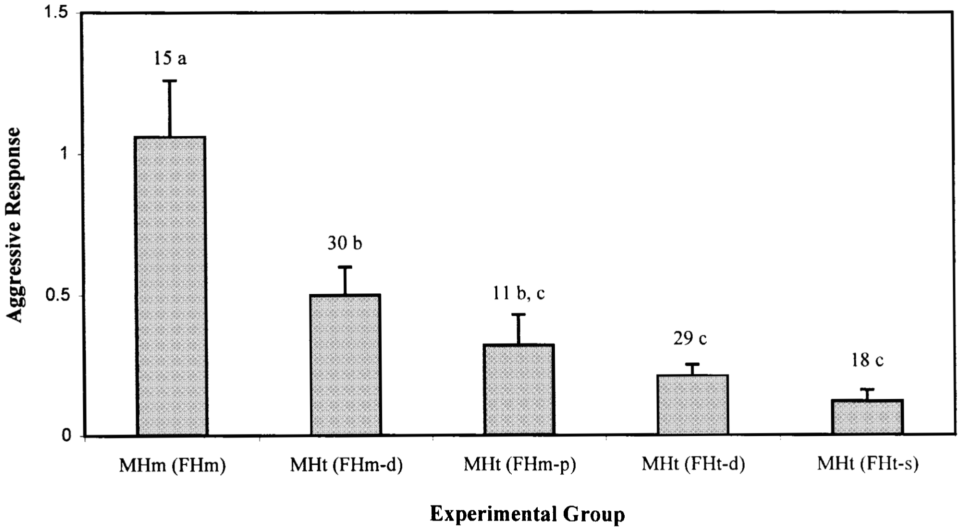

Figure 1. Aggression (expressed as treatment – control) of *Manica rubida* towards nestmates that were treated with postpharyngeal gland exudates from *Formica selysi* from various sources. Different letters represent the groups which differed significantly (ANOVA)

ants towards their introduced, treated, nestmate was that of passivity as in the control encounter. Comparison between the experiments using *M. rubida* from mixed species groups further revealed a gradual decrease in the aggressive response depending on the nature of the glandular secretions. The most effective was the postpharyngeal gland secretion of *F. selysi* workers that were taken from a homospecific colony that was different from the parent colony of the *F. selysi* members of the mixed species group. It was significantly more effective at eliciting aggression than secretions taken from *F. selysi* belonging to a mixed group, irrespective of whether it was from the same group (MHt (FHm-d) vs MHt (FHt-s) 0.5 ± 0.5 vs 0.12 ± 0.15, $p = 0.006$) or from a different mixed species group (MHt (FHm-d) vs MHt (FHt-d)(0.5 ± 0.5 vs 0.21 ± 0.23, $p = 0.017$). An intermediate response was obtained when the secretion extracted from *F. selysi* individuals from the homospecific parent colony was tested. The reaction of the *M. rubida* workers towards a nestmate applied with the latter secretion was milder when compared to application of a secretion of ants from a different homospecific colony, but this difference was not statistically significant. On the other hand, aggression was higher than in the cases when a secretion of ants from a mixed species group was used (irrespective of the type of mixed species group), but again this difference was not statistically different. It should be noted that the reaction towards an ant applied with a postpharyngeal gland secretion of ants from a different mixed species group was stronger than that towards ants applied with postpharyngeal gland secretion from the same mixed species group, although this difference was not statistically significant.

Inspection times (seconds) of the marked ants were always higher after the ants were treated with the glandular secretion (Table 2). A look at the mean differences

Table 2. Average inspection time (second) per contact spent by *Manica rubida* workers antennating their nestmate. Values in the column "T-C" are expressed as mean differences between the test experiment (the marked ants was treated with postpharyngeal gland secretion from various sources) and its corresponding control (marked ant left untreated) encounters. Statistical differences were determined by paired *t* tests

Experiment	n	Test Mean ± SE	Control Mean ± SE	T-C Mean ± SE	P
MHm (FHm)	15	4.33 ± 2.93	2.64 ± 2.57	1.69 ± 2.96	0.04
MHt (FHm-d)	30	4.37 ± 9.52	1.93 ± 0.97	2.43 ± 9.39	0.17
MHt (FHm-p)	11	5.98 ± 6.07	1.40 ± 0.48	4.58 ± 5.72	0.02
MHt (FHt-d)	29	4.83 ± 3.69	2.05 ± 2.16	2.79 ± 3.60	<0.001
MHt (FHt-s)	18	2.94 ± 2.25	1.24 ± 0.32	1.69 ± 2.12	<0.001

between the test encounters and the corresponding control encounter reveals a short inspection time per contact in two cases. When the secretion was unfamiliar (e.g., MHm (FHm) overt aggression ensued, following a short inspection. Short inspection per contact was also characteristic of the encounter in which a familiar odour was used (e.g., MHt (FHt-s), but this time the ants continued to move about without any noticeable change in behaviour. The longer inspection time per contact characterized the encounters when the secretion was seemingly familiar enough not to provoke overt aggression, but different enough to elicit longer inspection at each contact. In these three cases (MHt (FHm-d); MHt (FHm-p); MHt (FHt-d), we again observed a gradual response depending on the nature of the glandular secretion. Noteworthy is the result of a comparison between the aggressive response and inspection time between the tests in which either a nestmate's postpharyngeal secretion or a secretion from an alien mixed species group was used. There were no significant differences in aggression in these two cases, yet when the less familiar secretion was used, inspection time was roughly doubled at each contact. In a similar fashion, when we compared the two secretions that originated from the alien and parent homospecific colonies, the inspection time at each contact with ants smeared with postpharyngeal gland secretion from alien colonies was lower than that observed when the secretion came from ants that were reared in the parent homospecific colony.

Discussion

The results of this study corroborate the role of the postpharyngeal gland in nestmate recognition. As in earlier studies (Soroker et al., 1994; Hefetz et al., 1996), it was shown that ants that are applied with an alien odour are discriminated against and aggressed by their nestmates. However, the use of mixed species groups showed that the reaction of the ants depended largely on the source of the odour signal applied, and tend to suggest a hierarchical system for deciphering the signal. There was a diminishing degree of aggression exhibited by the ants that corresponded to an increase in the degree of odour familiarity. The most pronounced effect was when *M. rubida* from homospecific colonies were utilized and glandular secretion from a homospecific *F. selysi* was tested. This reaction, towards an unfamiliar signal, was similar in its magnitude to the reaction of homospecific *M. rubida* towards a nestmate that was treated with postpharyngeal gland secretion of an alien *M. rubida* (Hefetz et al., 1996). At the other extreme, heterospecific *M. rubida* ants exposed to a completely familiar signal (secretion extracted from *F. selysi* reared in the same mixed species group) did not demonstrate overt aggression towards the treated nestmate. Intermediate reactions were present when the secretion was only partially familiar, when *M. rubida* from mixed species group were tested with alien or parent homospecific *F. selysi* secretions, or with a *F. selysi* postpharyngeal gland secretion from another mixed species group.

These results suggest that there are different levels of recognition that may operate hierarchically. The stronger response of the homospecific ants towards *F. selysi* secretion give an insight into the possible hierarchical process of discrimination. Ants from an *M. rubida* homospecific colony were presumably never exposed to the alkenes and alkadienes that characterizes the secretion of *F. selysi*. Because the alien secretion applied on the test ant entirely masks the ant's own odour (Hefetz et al., 1996), the exposure of a completely alien element on the epicuticle of a nestmate elicited an immediate and full aggressive response. On the other hand, for *M. rubida* reared in mixed species group, alkenes and alkadienes constitute a natural part of the secretion. This familiarity may explain the reduced reaction of these ants, although we can not exclude the possibility that ants reared in mixed species groups are inherently less aggressive than their conspecifics reared in homospecific groups. Experiments using mixed species that are composed of additional species may resolve this question.

The differences observed in inspection times seem to support the above hypothesis. When the secretion is completely alien, or utterly familiar, recognition is swift and the appropriate reaction ensues immediately. However, when the signal is composed of both familiar and alien elements, more attention is paid by the ants, presumably in order to decipher the signal properly. We hypothesize that identifying the major components of the secretion constitutes the first discriminatory step, followed by a more acute discrimination based on the minor component present in the secretion.

The fact that in artificially mixed species group, the heterospecific members are recognized as nestmates and are integrated as a homogenous group, implies that the template they utilize is acquired through learning. Nestmates of both species acquire exogenous (allospecific) odour cues, exhibiting phenotypes that an individual's genome cannot specify in advance; so the chemical characteristics of the allospecific surrounding individuals must be acquired through experience (Errard, 1994b). Carlin and Hölldobler (1983) have reported similar results obtained in interspecific mixed colonies of carpenter ants (*Camponotus* sp.). They have shown that the principal mechanism of nestmate recognition appear to be odour labels that originate from the queen and are distributed among, and learned by, all adult members of the colony.

Given that the acceptance or rejection of an individual depends on the degree to which the label and template of the two partners overlap, we may suppose that within a natural colony, in which the individuals will recognize only their nestmates, there is inherited co-variation in template and label or that individuals learn to recognize their nestmates soon after metamorphosis. In fact, there are several types of template formation that explain how social insects might integrate different cues to discriminate nestmates from non-nestmates (Breed and Bennett, 1987). Crozier and Dix (1979) have developed two models to explain colony recognition. Under the "Individualistic" model, each individual keeps its own odour. Workers of one colony are hostile as long as there is no genotypic identity. This model can only apply in small colonies. Otherwise, the "Gestalt" model postulates that chemical cues are transferred among workers, resulting in a mixture of odours that is unique to the colony. In this last case, each recognition cue (gestalt odour) might be learned by nestmates, forming a gestalt template or a mean template, and an individual might tolerate a certain level of derivation from the gestalts. The results obtained with the artificial mixed groups fit the "Gestalt" model in which recognition takes place by memorisation through familiarisation with nestmates during a sensitive period.

As the odour characteristics may be continuously variable (as cues are constantly exchanged between nestmates and refreshed at the individual level) (Breed and Bennett (1987), consequently the template has to be reinforced via constant perception of nestmates' odours. In fact, the template would not appear to be fixed with time, but to be dynamic and continuously subjected to signal exchange among the colony members and vary as a function of the colony's composition through learning. The parallelism between the mechanisms involved in the formation of the label in mixed species groups and normal homospecific colonies, enables us to conclude that the phenomena pertaining to the nature of the template in mixed species group may be also relevant in natural colonies.

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