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Myrmica rubra Ants Are More Communicative When Young: Do They Need Experience?

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The role of experience in the development of communication in animals is a matter of special interest to many ethologists and psychologists. Ants are known to possess sophisticated and flexible communication systems based mainly on their antennal movements (Reznikova & Ryabko, 2011). However, it is still enigmatic whether young ants need stimulation performances by adults to develop their communication capacities. Experiments with pairwise interactions of *Myrmica rubra* ants revealed significant differences in individual behavior and the mode of communication in callow (newly emerged) and adult workers. Adult ants are much more mobile than callow ones, and they switch their behavior depending on what partner they interact with, whereas callows behave independently. Adults communicate with callows and queens much longer than with other adults. Both callows and queens seem to be rather attractive to adults, although in different ways. Adults pay close attention to callow ants and initiate prolonged antennal contacts with them, touching their bodies and not leaving them alone. Young (callow) ants appear to be more communicative than adults, and they are equally ready to communicate with each other and with adults. Antennal movements are slow and clumsy in young ants, and they often switch from communication to other activities. It is likely that patterns of antennal movements in callows change gradually. Peculiarities of the mode of communication enable us to speculate that young ants need prolonged contacts with adult nestmates to gain the experience of communication. Some parallels with the development of communication skills in vertebrate species are considered.

Keywords: ants, antennal contacts, communication, experience, ontogenetic development, behavior

Supplemental materials: <http://dx.doi.org/10.1037/com0000067.supp>

The role of experience in the development of communication in animals is a matter of special interest to many ethologists and psychologists. Animal studies have been mainly concentrated on vocal communications. Thorpe (1958) reared chaffinches *Fringilla coelebs* in isolation and determined which aspects of their songs are innate and which have to be learned from adults. This study has been greatly expanded upon by Marler (1997) and many other researchers (for reviews, see Jarvis, 2006;

Slater, 2003). Gottlieb (1965, 1997/2014) demonstrated that in ducklings imprinting on the maternal vocalization rests on hearing their own contact vocalizations before they hatch, and thus normal species-typical responses to communication signals rely critically on experience in this species. We know now that some birds (Jarvis, 2006) and a few mammalian species, from whales (for a review, see Filatova et al., 2015), dolphins (Favaro et al., 2016), and elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005) to mice (Arriaga, Zhou, & Jarvis, 2012) can modify their vocalizations in response to auditory experience. However, the relations between learned and non-learned mechanisms of signal production and receiver decoding remain unknown in most of the studied species.

The mode of life of social insects is wholly based on communication that includes different sensory modalities, such as acoustic, tactile, visual, and odor signals (Hölldobler & Wilson, 1990; Tautz, 2008). There is evidence, though scarce, of learning aspects of communication in bees and ants. The “dance language” of honeybees is known as one of the most sophisticated animal communication systems (Seeley, 1995; Tautz, 2008; Von Frisch, 1967). Experiments with mixed colonies of two species of honeybee indicated that Asiatic honeybees can decode the dances of European honeybees, and this suggests the possibility of social learning between the two honeybee species, which would be based on interspecies communication (Su et al., 2008).

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In ants, social learning between a pair of species was experimentally demonstrated by means of field experiments in which *Formica pratensis* learned from *F. cunicularia* how to get food from a maze (Reznikova, 1982, 2007a). This does not mean that ants can decode specific signals: they may rather rely on characteristic movements and trajectories of members of the scouting species in the maze. However, this means that they can learn by observation from another species. Long-term laboratory experiments revealed a symbolic communication system in highly social ant species, which is possibly even more complex than that of honeybees (Reznikova & Ryabko, 1994, 2011). This communication system can be classified as “language behavior.” Language behavior, a term much more inclusive than “language,” is defined as a communication system that includes referential signals and means for transferring information about remote events (Reznikova, 2007b, 2017). Language behavior has been demonstrated in several highly social species, including not only ants but also some primates and the honey bee (for a detailed review, see Reznikova, 2007a). The cognitive flexibility of ants’ communications (Reznikova, 2007b, 2008) enables us to hypothesize the existence of a learning component in their language behavior (see Reznikova, 2017). However, it is not known yet whether young ants need lessons from adults to develop their communicative capacities.

Antennal mode of communication is a good candidate for studying the role of social experience in the development of communication in ants. Measuring exactly the duration of antennal contacts between scouting ants and their followers, Reznikova and Ryabko (1994, 2011) revealed the existence of a complex symbolic language behavior in red wood ants; that is, their ability to transfer information about coordinates and numbers of objects and flexibly optimize their messages. Using the same experimental “binary tree” paradigm, Frasnelli, Iakovlev, and Reznikova (2012) discovered lateralization in antennal contacts during trophallaxis (liquid food transfers from mouth to mouth) in red wood ants, which is closely connected with their social interactions and communication.

Ontogenetic development of antennal communication in ants had been studied in *Camponotus vagus*. Filming of pairwise interaction among callow workers and older ones during trophallaxis revealed that units of antennal movements become more complex and coordinated in maturing ants (Bonavita-Cougourdan & Morel, 1984; Morel, 1986). However, these investigations were limited to trophallaxis and did not consider ants’ communication in a context of other vital situations such as brood caring, recruiting nestmates to new food sources, alerting them to danger, and so forth. To our knowledge, after these studies there were no attempts to study the role of social experience in ontogenetic development of antennal communication in ants.

Here, as a first step, we investigate differences in the mode of behavior and communication during pairwise interactions among callow (young) workers, older workers, and queens in *Myrmica rubra*. The species chosen is a favorite one in recent behavioral ant studies because of its highly structured colonies, placid temperament, learning abilities, and distinctive and relatively slow movements (Chapman, Thain, Coughlin, & Hughes, 2011; Pamminger, Foitzik, Kaufmann, Schützler, & Menzel, 2014).

Method

Ant Housing

We collected a polygynous colony of *Myrmica rubra* (about 1,000 workers with about 30 queens and much brood) from a mixed pine-birch forest near Novosibirsk and placed it into two artificial plaster nests. The nests were covered with a glass pane and a removable cardboard cover to maintain darkness. The nests were placed on the plastic arena (80 × 60 cm), which was subjected to daily variations of the natural light cycle. The food (sugar syrup and small meal warm larvae) was renewed on the arena every day. Light callow workers less than 7 days old were chosen for experiments. Adult workers of unknown age were taken from the arena where they actively moved. The nests were kept in the laboratory for 5 days before the testing began, and the subsequent experimental work lasted 10 days.

Experimental Observations

For experimental observations, the ant was placed into each of two Petri dishes connected by a short tunnel. During the first 2 min a partition blocked the tunnel; then it was removed, and ants could move freely between the dishes. From that moment video records were taken on, which lasted from 15 to 80 min. Ants were tested in pairs (dyads): Callow–Adult (CA), 5 dyads; Adult–Adult (AA), 7 dyads; Callow–Callow (CC), 5 dyads; Queen–Adult (QA), 7 dyads. Each dyad was tested once. Video records were made by a digital video camera recorder DCR-SX44 (Sony).

After the session, both ants were labeled to avoid using the same individuals twice, and returned to the basic laboratory colony.

Video Analysis

Video records (8 hrs in total) were analyzed with the use of The Observer 10 XT (Noldus Information Technology) and VLC media player, reducing the playback speed when necessary to 1/8.

Two types of data were analyzed: behaviors and contacts. In the first case, a 10-min segment from each session was extracted. To do this, we removed the initial 1-min interval, and then considered the 10-min segment which started from the first “long” (not less than 3 s) contact between ants. In the second case, all fragments of videos containing interactions between ants were extracted from each session.

The following behavioral elements were recorded:

d = moving straight;

r = circular movement along the walls of a Petri dish;

w = vertical movement on the walls of a Petri dish;

s = staying motionless;

t = exploratory touching of a substrate (the bottom and the walls of Petri dish) by antennae;

g = self-grooming;

i = antennal interaction with a partner (antennae-to-antennae);

f = touching the partner’s body with antennae;

p = passages from one dish to the other.

Total duration (in seconds) of each of the behavioral elements per 10 min was measured, with an exception of “p,” which was measured as the number of events.

When exploring ants' contacts, we singled out those fragments of the video recordings that contained ants' interactions. The following types of contacts were distinguished:

“antennal” = contacts started from the “antennae-to-antennae” interaction (they lasted from seconds to tens of seconds);

“touch” = contacts started from touching a partner's body with antennae (also lasted from seconds to tens of seconds);

“transient” = contacts lasted less than a second; in these cases an ant seemed not to distinguish between partner's body and details of its environment.

The number and the duration of contacts were registered. For “touch” and “antennal,” the initiator was registered, that is, the ant that touched a partner with its antenna first.

Results

Ants' Behavior in Different Dyads

In total, 24 ten-min sessions with 24 dyads were analyzed. The results expressed as medians are considered.

When comparing behaviors of two adult ants placed together (AA dyads) with those of adult ants in the company of callow ants (CA dyads; Figure 1A), one can see that in the first situation ants spent significantly more time on straight (d: $U = 13, p \leq .05$) and circular movements (r: $U = 13, p \leq .05$), and less time touching a partner (f: $U = 7, p \leq .01$).

When comparing behaviors of adult ants in AA dyads with behaviors of adult ants in the company of queens (QA dyads; Figure 1A), one can see that in the first situation ants spent significantly more time moving straight (d: $U = 10, p \leq .01$) and in circles (r: $U = 3, p \leq .01$), moving vertically on the wall (w: $U = 0, p \leq .01$), exploratory touching the substrate (t: $U = 9, p \leq .01$), and contacting the partner with antennae (i: $U = 20, p \leq .05$); they spent significantly less time staying motionless (s: $U = 2, p \leq .01$) and performing self-grooming (g: $U = 15, p \leq .05$).

It is worth noting that adult ants and queens in the company of each other (QA; Figure 2D) displayed quite a similar behavior, which looked almost synchronized.

In sum, the presence of either a callow ant (in CA dyads) or a queen (in QA dyads) influenced the behavior of an adult worker in much the same way; namely, the adults became less mobile and preferred to stay near the partner.

When comparing behaviors of two callow ants placed together (CC dyads) with those of callow ants in the company of adult ones (CA dyads; Figure 1B), one can see no reliable differences.

When adult workers were placed into the set-up together with callow ones (CA dyads; Figure 2A), callows displayed much less mobility than adults: they spent significantly less time moving straight (d: $U = 4, p \leq .05$) and vertically on the wall (w: $U = 2, p \leq .05$), and more time staying motionless (s: $U = 3, p \leq .05$). In the company of each other (CC dyads), callow workers also displayed less agility in comparison with pairs of adult ants (AA dyads; Figure 2B): they spent less time moving straight (d: $U = 23, p \leq .01$) and in circles (r: $U = 14, p \leq .01$). Independent of whether they were partnered with another callow ant, or with an adult ant, callows behaved similarly, being just less mobile than adults. Our observations showed that whereas behavioral elements were clearly defined and separated from each other in adults, in callows such behavioral elements as exploratory touching the

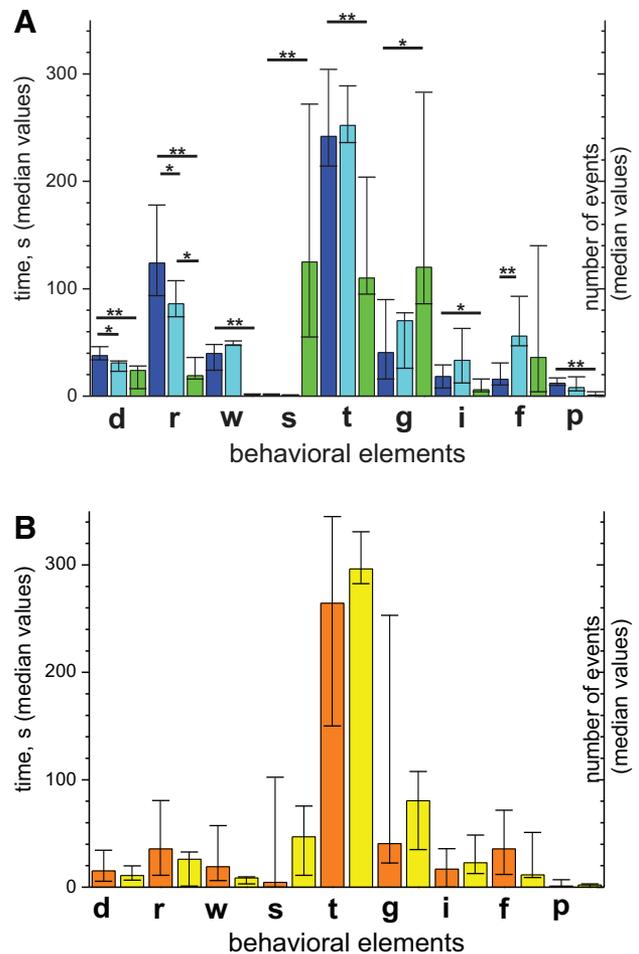


Figure 1. (A) Behavior of an adult ant as a partner in AA (adult–adult), dark gray (blue); CA (callow–adult), gray (cyan); and QA (queen–adult), white (green) dyads. Observation time is 10 min. The sample size was 12 for the adults, 5 for the callows, and 7 for the queens. Behavioral elements observed are as follows: d = moving straight; r = circular movement; w = vertical movement; s = staying motionless; t = touching of a substrate; g = self-grooming; i = antennal interaction with a partner; f = touching the partner's body; p = passages between the dishes (see Method section). For all behavioral elements except “p,” the total length of the episodes is shown (see left ordinate), whereas “p” is expressed as number of the episodes (see right ordinate). The lower and the upper error bars correspond to the 25% quartile and 75% quartile values, respectively. Mann–Whitney U test: ** ($p \leq .01$) and * ($p \leq .05$). (B) Behavior of a callow ant as a partner in CC (callow–callow), dark gray (orange) and CA (callow–adult), white (yellow) dyads. Observation time is 10 min. The sample size was 10 for the callows in homogenic dyads and 5 for the callows in heterogenic dyads. Designations of behavioral elements on the x -axis are the same as in Panel A. For all behavioral elements except “p,” total length of the episodes is shown (see left ordinate), whereas “p” is expressed as the number of the episodes (see right ordinate). The lower and the upper error bars correspond to the 25% quartile and 75% quartile values, respectively. Mann–Whitney U test: $p > .05$. See the online article for the color version of this figure.

substrate, self-grooming, and contacts with the partner were somehow blurred, and different elements could blend: sometimes a callow worker touched the partner with one antenna and explored the substrate with the other one (Figure 3A), or cleaned the other

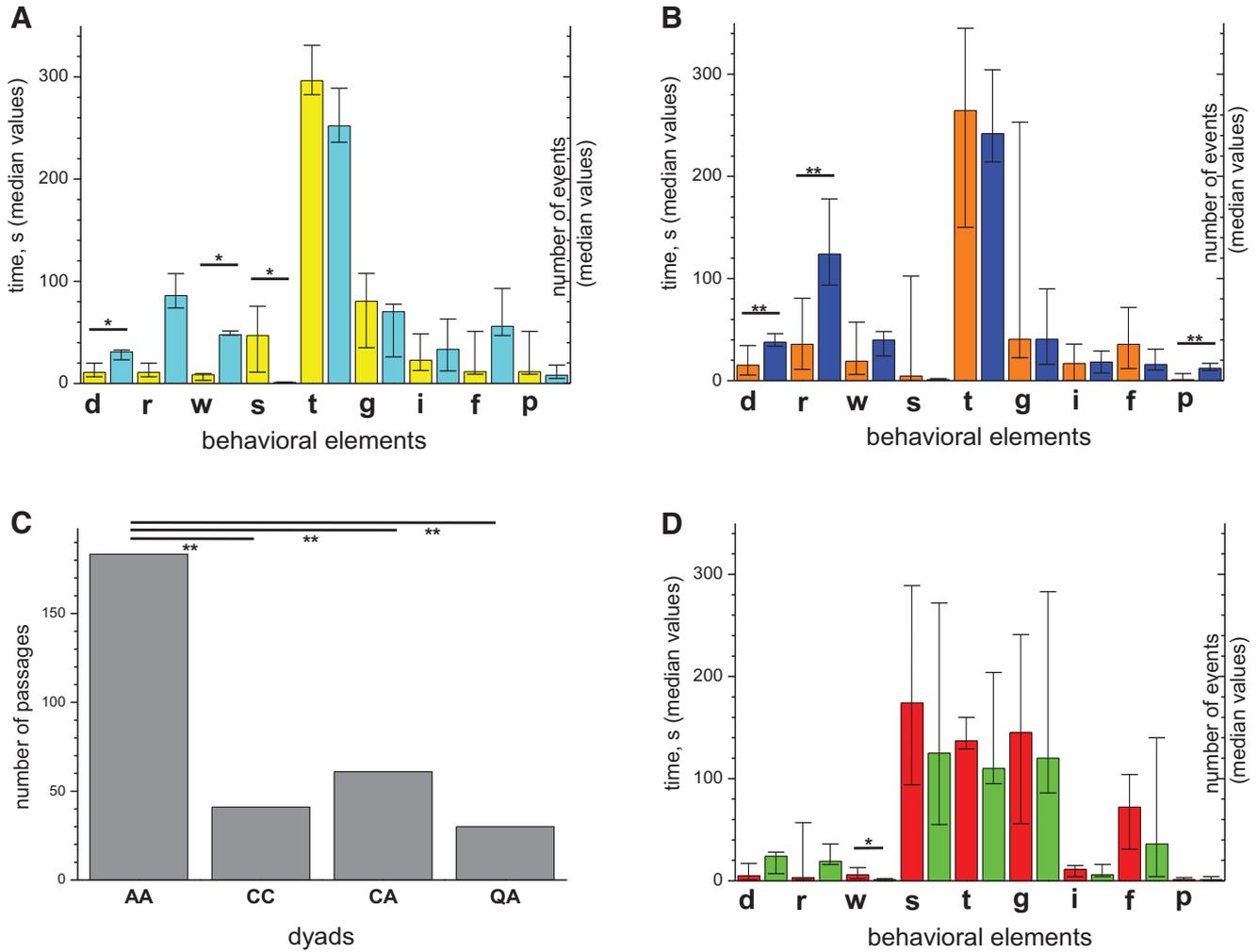


Figure 2. A. Behaviors of a callow ant—white (yellow) versus an adult ant—dark gray (cyan) during pairwise interaction. Observation time is 10 min. The sample size was 5 both for the adults and for the callows. Designations of behavioral elements on the x -axis are the same as in Figure 1. For all behavioral elements except “p,” total length of the episodes is shown (see left ordinate), whereas “p” is expressed as number of the episodes (see right ordinate). The lower and the upper error bars correspond to the 25% quartile and 75% quartile values, respectively. Mann–Whitney U test: * ($p \leq .05$). (B) Behaviors of a callow ant in CC (callow–callow) dyad—white (orange) versus an adult ant in AA (adult–adult) dyad—dark gray (blue). Observation time is 10 min. The sample size was 12 for the adults and 10 for the callows. Designations of behavioral elements on the x -axis are the same as in Figure 1. For all behavioral elements except “p,” total length of the episodes is shown (see left ordinate), whereas “p” is expressed as number of the episodes (see right ordinate). The lower and the upper error bars correspond to the 25% quartile and 75% quartile values, respectively. Mann–Whitney U test: ** ($p \leq .01$). (C) Number of passages in different dyads (AA—adult–adult; CC—callow–callow; CA—callow–adult; QA—queen–adult). The sample size was 12 for the ants in AA dyads, 10 for the ants in CC dyads, 10 for the ants in CA dyads, and 14 for the ants in QA dyads. Observation time is 10 min. Total numbers of passages between the dishes made by the both partners are shown. The data obtained in all dyads of each type are summarized. Mann–Whitney U test: *** ($p \leq .01$). (D) Behaviors of a queen—white (red) versus an adult ant—dark gray (green) during pairwise interaction. Observation time is 10 min. The sample size was 7 both for the adults and for the queens. Designations of behavioral elements on the x -axis are the same as in Figure 1. For all behavioral elements except “p,” total length of the episodes is shown (see left ordinate), whereas “p” is expressed as number of the episodes (see right ordinate). The lower and the upper error bars correspond to 25% quartile and 75% quartile values, respectively. Mann–Whitney U test: * ($p \leq .05$). See the online article for the color version of this figure.



Figure 3. (A) A callow ant (right) is touching the partner with one antenna, and exploring the substrate with the other one. (B) A callow ant (right) is touching the partner with one antenna, whereas cleaning the other antenna. See the online article for the color version of this figure.

antenna (Figure 3B). The video fragments illustrated typical CC and CA contacts are available online as supplemental materials.

We compared the number of passages from one dish to another made by members of different dyads during 10 min sessions. This parameter reflects the general mobility of ants. From Figure 1A one can see that in AA dyads an adult ant made more passages than in AQ dyads ($p: U = 3, p \leq .01$). From Figure 2B one can see that callow ants in CC dyads made less passages compared with adult ants in AA dyads ($p: U = 8, p \leq .01$). We also compared the total number of passages made by both members of the dyads (Figure 2C). This parameter is significantly higher in AA dyads, in comparison with CC ($U = 8, p \leq .01$), CA ($U = 18.5, p \leq .01$) and QA ones ($U = 6, p \leq .01$).

The Mode of Communication Among Ants in Different Dyads

We compared the number and the duration of contacts in ants being placed into the set-up with different partners. Number of

contacts (Figure 4A) was much higher in AA dyads in comparison with CC ($U = 5, p \leq .05$), CA ($U = 1, p \leq .01$), and QA ones ($U = 3, p \leq .01$). There were no differences in the number of contacts among CC, CA, and QA.

The average duration of contacts (Figure 4B) in AA dyads was much smaller than in CC (Student's test: $t = 2.7, p \leq .05$), CA (Student's test: $t = 2.4, p \leq .05$), and QA (Student's test: $t = 4.7, p \leq .01$). As a result, a part of the contacts in the total time budget in AA dyads was the smallest (Figure 4C): mean values differed significantly between AA and CC ($U = 6, p \leq .05$), as well as between AA and QA ($U = 3, p \leq .01$).

Three types of contacts were compared in different dyads. One can see from Figure 5C that in AA dyads "transient" contacts constitute a half of the total number of all interactions, whereas numbers of "antennal" and "touch" contacts were almost equal. In CC dyads, the three types of interaction constitute almost equal parts (Figure 5D). In CA and QA dyads (Figures 5A and 5B, respectively), "transient" contacts constitute about 20%. The part of "antennal" contacts was the largest in CA dyads; that is, more than a half, and the part of "touch" contacts was the largest in QA dyads (also about a half).

In CA and QA dyads, we registered which member initiated a contact, that is, touched the partner first. There was a significant difference in one situation only (Figure 5A): being placed into the setup with a callow worker (CA), an adult one initiated both "antennal" and "touch" contacts (Fisher's exact test for "antennal": $\Phi_{emp.}^* = 1.979, p \leq .05$; for "touch": $\Phi_{emp.}^* = 1.934, p \leq .05$). Behavioral observations showed that while adult ants mutually touch each other (in AA dyads), being paired with a callow worker an adult worker actively touches the partner's body and antennae, whereas a callow ant stands still.

Discussion

Adult Workers Switch Their Behavior in the Presence of Queens and Callow Workers

Our study reveals significant differences in the behavior of adult and callow *Myrmica* ants. Adult ants are much more mobile than young ones, and they spend more time on different forms of active behavior. The most characteristic difference between adult and callow workers is that adults switch their behaviors depending on what partner they interact with, whereas callows behave independently of the partner.

When finding itself sharing the setup with a queen or with a callow worker, an adult worker significantly decreases its own exploratory activity and mobility and switches to the interaction with the partner. One can suggest that both queens and callows are somehow attractive to adult ants, although in different ways.

When meeting with a queen, an adult worker contacts it, which usually starts with mutual touching, and then remains near the queen, giving her long contacts and performing self-grooming. It is worth noting that the total duration of adults' self-grooming episodes significantly increases in the presence of a queen. Insect grooming movements have been classified as "nibbling," where cleaning is performed by the insect's mouthparts, "rubbing," where the appendage sweeps back and forth in continuous contact over another body part, and "scraping" which consists of unidi-

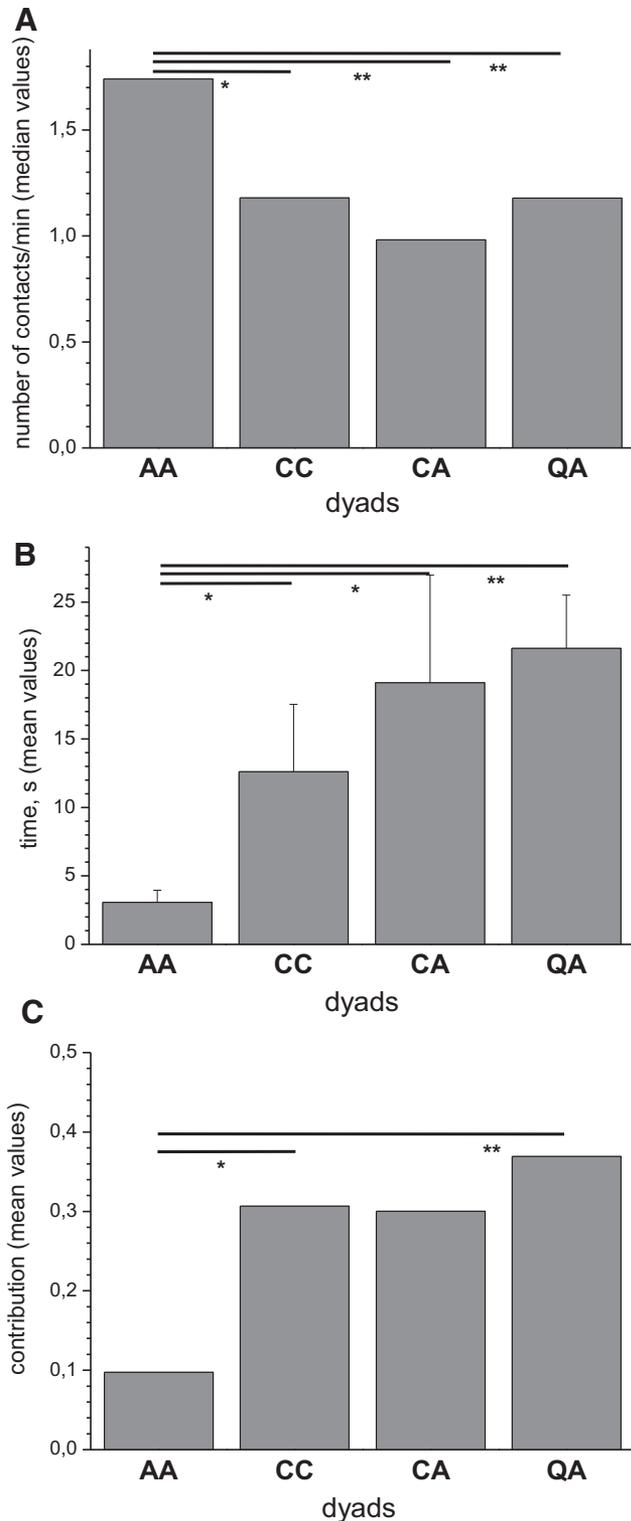


Figure 4 (opposite)

rectional movements performed by the cleaning structure (Hackmann, Delacave, Robinson, Labonte, & Federle, 2015). All these elements were observed in *Myrmica* ants. It is likely that, staying near a queen, a worker reapplies hydrocarbons, which are responsible for nestmate recognition, on its cuticle through self-grooming, similar to the behavioral pattern described in several ant species (see Detrain, Deneubourg, & Pasteels, 1999).

It is well known that in ant societies the queen controls workers' fertility by pheromones (Hölldobler, Wilson, 1990) and hydrocarbon labels (Endler et al., 2004) and serves as a key factor in the maintenance of both behavioral characteristics of the workers and the organization of the colony (Brian & Hibble, 1963; Vienne, Errard, & Lenoir, 1998). Even parts of a queen's corpse attract workers (Brian, 1973). Workers usually do not lay eggs in the presence of a fertile queen, but in many species they do so when the queen is removed. This effect has been explained by manipulative, that is, dishonest, queen control or honest fertility signaling (Heinze & d'Etorre, 2009). There are different hypotheses about how the queen prevents workers from breeding (for the reviews see: Endler et al., 2004; Heinze, 2004; Heinze & d'Etorre, 2009); in any case, the queen somehow governs workers' behavior by attractiveness, and not by aggression. To our knowledge, our study provides the first, though preliminary, observations on how adult ants change their behavior in the presence of a queen.

In the presence of a callow worker, an adult one also decreases its mobility and prefers to stay near the callow one, frequently giving it long antennal contacts. That an adult worker prefers to stay near a callow one and contacts it as it would a queen, although in a somewhat different manner, suggests that callows are attractive to adults. One can propose some behavioral (and rather anthropomorphic) hypotheses like "babyness," "loneliness," and so on in the "artificial world," which callow ants encounter outside a nest being placed into the experimental apparatus.

As far as "babyness" is concerned, callow ants are known to possess some character distinctive features, strongly associated with age, which possibly attract adults the same way as infantile features in many vertebrate species do (Lorenz, 1943). Callow workers seem to be characterized by a "cuticular chemical insignificance" followed by a "chemical integration" period when they

Figure 4 (opposite). (A) Frequency of contacts in the different dyads (designations of dyads on the *x*-axis are the same as in Figure 2C). Ordinate values are obtained from the total number of contacts within a dyad normalized to the total time of the experiment. The sample size was 7 (adult–adult—AA dyads), 5 (callow–callow—CC dyads), 5 (callow–adult—CA dyads) and 7 (queen–adult—QA dyads). Mann–Whitney *U* test: ** ($p \leq .01$) and * ($p \leq .05$). (B) Duration of contacts in the different dyads (designations of dyads on the *x*-axis are the same as in Figure 2C). The average time of interaction between the partners is shown together with the SEs. The sample size was 7 (AA dyads), 5 (CC dyads), 5 (CA dyads), and 7 (QA dyads). Student's test: ** ($p \leq .01$) and * ($p \leq .05$). (C) Time contribution of contacts in the different dyads (designations of dyads on the *x*-axis are the same as in Figure 2C). Ordinate values are obtained from the total length of contacts within a dyad normalized to the total time of the experiment. A part of contacts in the total time budget is expressed as a fraction of unity. The sample size was 7 (AA dyads), 5 (CC dyads), 5 (CA dyads), and 7 (QA dyads). Mann–Whitney *U* test: ** ($p \leq .01$) and * ($p \leq .05$).

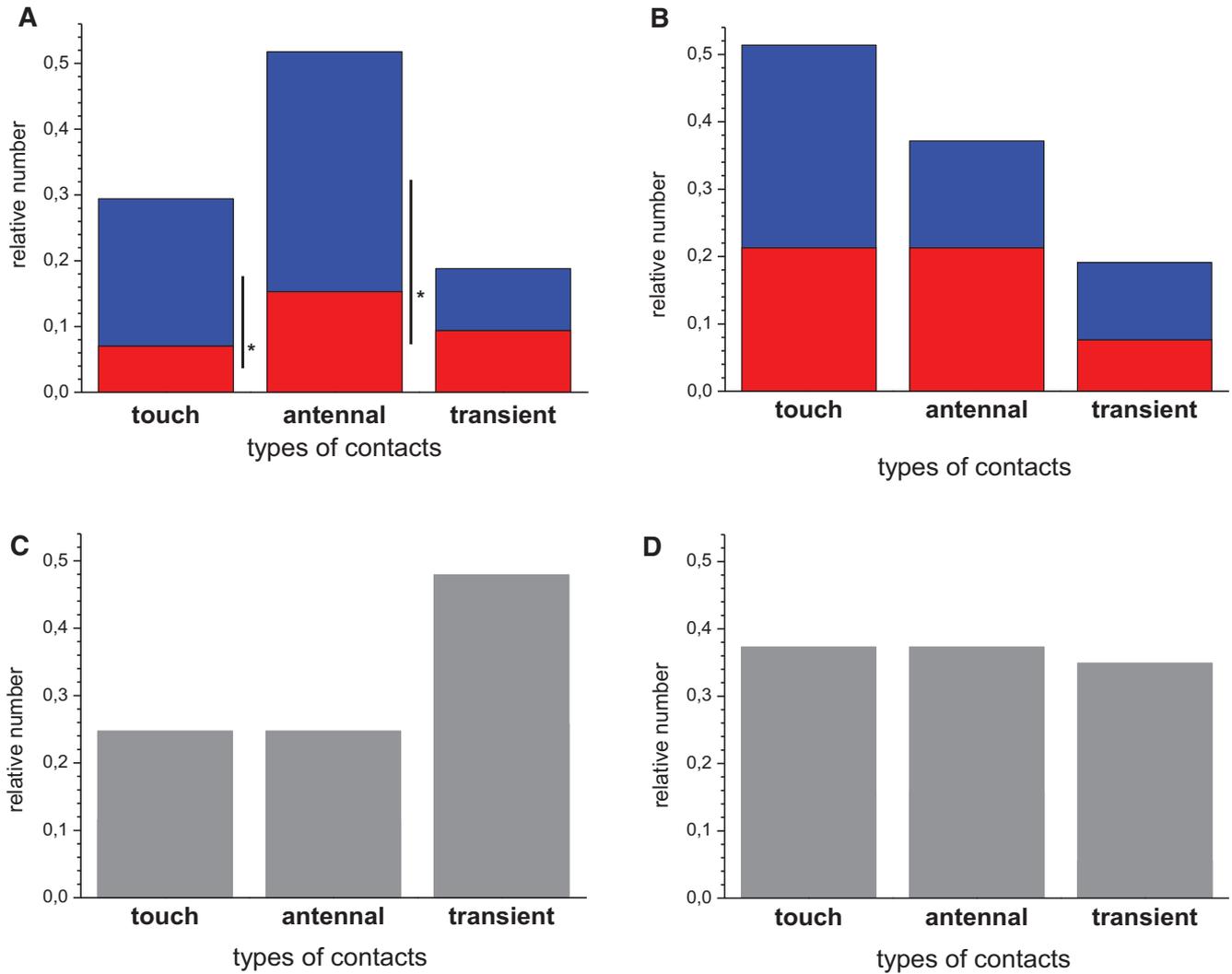


Figure 5. A. Distribution of contacts among the types (“antennal”—started from the “antennae-to-antennae” interaction; “touch”—started from touching a partner’s body; “transient”—the contacts shorter than 1 s; see Method) and initiators of contacts in CA (callow–adult) dyads (the sample size was 5). Total time of observation is 90.63 min; total number of contacts is 85. Parts of the contacts of given types are expressed as fractions of unity. The contacts initiated by an adult ant are shown in black (blue); the contacts initiated by a callow ant are shown in gray (red). Exact Fisher’s test: * ($p \leq .05$). (B) Distribution of contacts among the types (the designations on the x-axis are the same as in Panel A) and initiators of contacts in QA (queen–adult) dyads (the sample size was 7). Total time of observation is 174.07 min, total number of contacts is 183. Parts of the contacts of given types are expressed as fractions of unity. The contacts initiated by an adult ant are shown in black (blue), the contacts initiated by a queen are shown in gray (red). (C) Distribution of contacts among the types (the designations on the x-axis are the same as in Panel A) in AA (adult–adult) dyads (the sample size was 7). Total time of observation is 95.53 min; total number of contacts is 190. Parts of the contacts of given types are expressed as fractions of unity. (D) Distribution of contacts among the types (the designations on the x-axis are the same as in Panel A) in CC (callow–callow) dyads (the sample size was 5). Total time of observation is 132.62 min; total number of contacts is 126. Parts of the contacts of given types are expressed as fractions of unity. See the online article for the color version of this figure.

acquire the “gestalt” of the colony and learn the associated template (Lenoir, Fresneau, Errard, & Hefetz, 1999). Cuticular hydrocarbons are initially stored in the postpharyngeal gland (PPG) and shared among individuals (Ichinose & Lenoir, 2009). Callows have underdeveloped PPG and ovaries (Ichinose & Lenoir, 2009).

It was observed in *Cataglyphis iberica* that workers’ chemical profiles vary with their age group and gradually converge from a “callow profile” with specific hydrocarbons to a profile characteristic of mature workers (Dahbi et al., 1999). Early analysis of cuticular lipids of *Myrmica incompleta* revealed 19 hydrocarbons

(Howard et al., 1990), whereas further analyses resulted in the identification of 111 substances (Lenoir et al., 1999). It has been demonstrated in several species of ant that callow workers are more likely to be accepted into alien colonies than 1-week-older workers, which may be linked to weak aggressive behavior, but also to the weak signal they possess on their cuticle (for a review see: Lenoir et al., 1999). Ichinose and Lenoir (2009) studied the ontogeny of the hydrocarbon profile in *Aphaenogaster senilis*. In this species, the total quantities of both cuticular and PPG hydrocarbons increased with age from 0 to 20 days after emergence and then stabilized. Under individual social isolation, cuticular hydrocarbons increased as normal, but the total quantity of hydrocarbons never increased from the initial low level. This effect of social isolation on the hydrocarbon level, together with the correlation between the development of PPG and ovary, support our hypothesis that callows attract adults by some features of specific “ant-babyness.”

Ants Are More Communicative When Young

When comparing the total number of contacts, we found that they were much higher in adult ants encountering each other, and there were no differences in the number of contacts in other dyads (CC, CA, and QA). However, the average duration of contacts between two adult ants is much smaller than in all other dyads. “Transient” contacts constitute a half of the encounters among adult workers. On the contrary, when encountering with a callow ant, or with a queen, an adult one gives both of them long contacts. In these cases 80% of all contacts are composed of “long” ones. Unlike contacts with a queen, which usually start from touching a partner’s body, contacts among an adult worker and a callow one more often start from antennal contiguity. Adult workers initiate both antennae-antennae and antennae-body contacts with young ants in most of the cases. An adult worker actively touches the callow worker’s body whereas a callow ant stands still keeping its antennae motionless. On the contrary, during encounters among two callow ants there are no differences between the relative numbers of contacts starting from antennal and body touching, nor of “transient” ones.

In general, young ants appeared to be more communicative than adult ones. They display longer duration of contacts, and contacts constitute the larger part of the total time budget in callows than in adults. It is worth noting that the average duration of contacts between two callow workers is the same as between callow and adult ones. This means that young workers are equally ready to communicate both with each other and with adult ones.

Do Young Ants Need Experience to Develop Communication?

We revealed some trends in the modes of communications and individual interactions in callow *M. rubra* ants. Let us consider the main peculiarities of this early postimaginal period in ants.

Ants are known to begin learning some signals and even communicating long before eclosion. Cross-fostering experiments, in which larvae were introduced in an alien adoptive colony, where they developed until the pupal stage and then

transferred back to their original colony, revealed preimaginal olfactory learning in formicine ants (Carlin & Schwartz, 1989; Isingrini, Lenoir, & Jaisson, 1985) and in *Aphaenogaster senilis* (Signorotti, Jaisson, & d’Ettorre, 2013). In *M. scabrinodis*, sclerotized pupae generate sounds by a stridulatory organ and thus attract attention of workers (Casacci et al., 2013). Thus, newly hatched ants are equipped with some skills of olfactory and acoustic communication, and they are ready to gain further experience in different forms of communication including “antennal code.”

The early postimaginal period has been described in some ant studies as a sensitive period for a variety of behavioral patterns and tasks such as cocoon recognition (Jaisson, 1972; Le Moli & Mori, 1982), recognition of nestmates (Pfenning, Gamboa, Reeve, Shellman-Reeve, & Ferguson, 1983; Le Moli & Mori, 1984), aggression (Errard, 1984; Reznikova & Iakovlev, 2008), and brood care (Champalbert & Lachaud, 1990). Early social experience has a strong effect on the development of trophallaxis in *Camponotus vagus* because callow workers deprived of relations with mature workers from before hatching showed a slower behavioral ontogenesis than workers that hatched within their colony (Morel, 1986).

It is worth noting that relations between “innateness” and experience in ants appear to be closer to those in vertebrate species than we thought before. In particular, it has been demonstrated in some vertebrate species that the ability to recognize vitally important objects is often based on specific key stimuli that “trigger” the corresponding responses. For example, experiments demonstrated that tammar wallabies perceive predators as a natural category (Griffin, Evans, & Blumstein, 2001). Experiments with human infants showed that schematic drawings of spiders (presumably objects of “inborn fear”) attracted the attention of five month olds more than schemes chaotically composed of the same elements (body, head, extremities). Yet children who had seen realistic pictures of spiders paid greater attention to “incorrect” images. Thus, the actualization of the innate pattern resulted in singling out its characteristic features which began to be recognized and compared with the template (Rakison & Derringer, 2008). Our experiments first revealed similar regularities in *Formica* ants: they have innate templates for recognizing some vitally important objects, need some triggers to start particular behavioral patterns, and some experience to develop these behaviors. For example, *Formica* s. str. have an innate template for recognizing enemies such as carabid beetles (Reznikova & Dorosheva, 2004, 2013), and ladybird imagines (Novgorodova, 2015). Deprivation experiments with red wood ants (Reznikova & Novgorodova, 1998; Reznikova, 2007a) showed that to develop such a sophisticated behavioral stereotype as aphid tending, ants needed trigger stimuli from their symbionts. However, when the mode of interaction with aphids had been completed, naive ants still needed much more social experience with older workers to develop optimal division of labor within groups of aphid tenders.

Why speculate about the role of experience in the development of communication in ants? Although we know that ants can exchange messages by means of antennal movements (see Reznikova, 2017), almost nothing is known about the ontogenetic development of their antennal communication. The ob-

served differences in the manner of antennal contacts between young and adult *Myrmica* ants enable us to suggest that patterns of antennal movement in callows change gradually. We speculate that young ants might need the “training” stage to develop the informative antennal communication. From our preliminary observations in the presented study, we suggest that callow ants need awkward bouts of slow antennal movements which somehow resemble the babbling vocal bouts produced by human infants and by neonates in some vertebrate species (e.g., Bolhuis, Okanoya, & Scharff, 2010; Elowson, Snowdon, & Lazaro-Perea, 1998; Goldstein, King, & West, 2003; Knörnschild, Behr, & von Helversen, 2006; Snowdon & Elowson, 2001; Wilbrecht & Nottebohm, 2003). One could argue that pupae stridulation in *Myrmica* ants could be considered a form of acoustic “babbling” (Casacci et al., 2013): the sounds generated by worker pupae were similar to those of workers but were emitted as single pulses rather than in long sequences characteristic of adults. All of these examples concern vocal practice rather than gestural communication. It would be interesting to compare ants’ early antennal movements with first awkward communication gestures in chimpanzees (Hobaiter & Byrne, 2014) and elephants (Poole & Granli, 2011). Moreover, further experiments are needed to establish whether ants require teaching from adults to develop their antennal communication and whether they can transfer information about a target by their clumsy and slow antennal movements.

Conclusion

Although ants are known to possess sophisticated and flexible communication system, it is still enigmatic whether young ants need experience to develop their language behavior (see in: Reznikova, 2017). Experiments with pairwise interactions of *Myrmica rubra* ants revealed significant differences in individual behavior and the mode of communication in callow workers and adult ones. Adult ants are much more mobile than callow ones, and they switch their behavior depending on what partner they interact with, whereas callows behave independently. Adults communicate with callows and queens much longer than with other adults. Both callows and queens seem to be rather attractive to adults, although in different ways. Adults pay close attention to callow ants, initiate prolonged antennal contacts with them touching their bodies and not leaving them alone. Young (callow) ants appear to be more communicative than adults, and they are equally ready to communicate with each other and with adults. Antennal movements are slow and clumsy in young ants, and they often switch from communication to other activities. It is likely that patterns of antennal movements in callows change gradually. These peculiarities of the mode of communication enable us to suggest that young ants need prolonged “training” contacts with adult ants to gain the experience of communication.

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