

Density of Antennal Sensilla Influences Efficacy of Communication in a Social Insect

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Submitted February 18, 2013; Accepted June 19, 2013; Electronically published October 9, 2013

Dryad data: <http://dx.doi.org/10.5061/dryad.7c9q7>.

ABSTRACT: Effective communication requires reliable signals and competent receptors. Theoretical and empirical accounts of animal signaling focus overwhelmingly on the capacity of the signaler to convey the message. Nevertheless, the intended receiver's ability to detect a signal depends on the condition of its receptor organs, as documented for humans. The impact of receptor organ condition on signal reception and its consequences for functional behavior are poorly understood. Social insects use antennae to detect chemical odors that distinguish between nestmates and enemies, reacting aggressively to the latter. We investigated the impact of antennal condition, determined by the density of sensilla, on the behavior of the weaver ant *Oecophylla smaragdina*. Worker aggression depended upon the condition of their antennae: workers with fewer sensilla on their antennae reacted less aggressively to nonnestmate enemies. These novel data highlight the largely unappreciated significance of receptor organ condition for animal communication and may have implications for coevolutionary processes in animal communication.

Keywords: signal receiver, nestmate recognition, chemical communication, antennae, *Oecophylla smaragdina*, signal detection error.

Introduction

It is widely understood that effective communication requires a combination of reliable signals and sensitive receptors, allowing the receiver to detect the signal precisely and thus behave accordingly. At the organismic level, the field has been largely dominated by an interest in the degree to which signals provide accurate or honest information about the signaler (Kotiaho 2001; Maynard Smith and Harper 2003; Searcy and Nowicki 2005; Johansson and Jones 2007; Botero et al. 2010; Számadó 2011; Stevens and Ruxton 2012). While there have been some investigations into how receiver strategies might act as a selection pressure on signals (Johnstone 1994; Hailman 2008; Broom and Ruxton 2011), the impact of the condition of

the receptor organs on the capacity of the receiver to detect and/or interpret the signal has rarely, if ever, been investigated in species other than humans (Roth et al. 2004; Bovo et al. 2011), and much of this interest is at the genetic and neurobiological level (e.g., Frasnelli et al. 2011).

The receptor component of visual and auditory sensory systems deteriorates with age in humans and other vertebrates, although the relative importance of senescence, environmental damage, or both remains unclear (Roth et al. 2004; Limburg and Keunen 2009; Bovo et al. 2011). Less is known about the effect of these long-term processes on olfactory sensory systems, despite their crucial role in foraging and mating success, social interactions, and avoidance of enemies, all of which depend upon the accurate detection of chemical signals and cues (Wyatt 2003). The antennae of insects are essential for acquiring chemical information, yet they are also subject to substantial wear and tear (Seabrook et al. 1979). While neurophysiological studies of insects reveal variation in response to chemical signals with age (Seabrook et al. 1979; Blaney et al. 1986; Vetter and Visscher 1997), this typically reflects the very early days of adult life. Whether the condition of the receptor organ affects the individual's ability to detect a signal and respond appropriately is apparently unknown.

The profoundly cooperative behavior of social insects relies on a combination of chemical and tactile signals, typically detected through the antennae. In particular, social insects rely on chemical signals to distinguish between colony mates and other enemies, thereby ensuring the integrity of the colony and preventing nonnestmates from exploiting colony resources (Crozier and Pamilio 1996; d'Ettorre and Lenoir 2010; van Wilgenburg et al. 2011; Sturgis and Gordon 2012; van Wilgenburg and Elgar 2013). The chemical signals involved in colony mate recognition are nonvolatile cuticular hydrocarbons, comprising a mixture of alkanes, alkenes, and methyl-branched alkanes (van Wilgenburg et al. 2011). An individual worker discerns the identity of another individual by sweeping

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and/or brushing her antennae against the cuticle of her counterpart, thereby obtaining information about the profile and typically responding aggressively if it is not a nestmate (d’Ettorre and Lenoir 2010; van Wilgenburg et al. 2011; see also Brandstaetter et al. 2008).

It is widely recognized that there is both inter- and intraspecific variation in the nature of the response of ants to nonnestmate conspecifics, but the source of this variation has not been widely examined (Sturgis and Gordon 2012). The primary focus is how ecological and social factors might modify workers’ response to nonnestmates, including seasonal changes (Mabelis 1979; Ichinose 1991; Katzerke et al. 2006), territoriality (Whitehouse and Jaffe 1995; Wenseleers et al. 2002), experimental design (van Wilgenburg and Elgar 2013), and the number (Gordon et al. 1993; Roulston et al. 2003; Sorrells et al. 2011), age (Nowbahari and Lenoir 1989; van Wilgenburg et al. 2005), and size (Nowbahari et al. 1999) of the workers. In contrast, Newey et al. (2010) propose that the variation in worker response may derive from differences in signal perception, which they suggest is the result of adaptive differences in individual odor templates. An alternative explanation, not favored by Newey et al. (2010), is that the variation derives from recognition “error.”

The antennae of ants are covered by numerous chemosensory sensilla (Hashimoto 1990; Kleineidam et al. 2000; Renthal et al. 2003; Babu et al. 2011; Barsagade et al. 2013) that detect specific odors, including those associated with nestmate recognition (Ozaki et al. 2005). The abundance and diversity of these sensilla begs the question of whether the number or density of intact sensilla on the antennae influences the capacity of ants to acquire chemical information and respond as expected—in other words, whether the observed variation in aggressive behavior is influenced by the condition of the antennae.

The weaver ant *Oecophylla smaragdina* occurs in tropical North Australia, equatorial Asia, and India (Schlüens et al. 2009; Crozier et al. 2010). Colonies of *O. smaragdina* comprise up to 500,000 workers that inhabit numerous leaf nests located on several neighboring trees. Weaver ants may be polyandrous, with resulting relatively low levels of relatedness within colonies (Schlüens et al. 2009). There are two morphologically distinct worker castes: smaller minor workers that typically remain within the nest, tending the brood and queen, and larger, more aggressive major workers that forage outside the nest (Crozier et al. 2010). The major workers of *O. smaragdina* use chemical signals to distinguish between nestmates and conspecific non-colonymates and other enemies, and they typically respond aggressively to the latter (Hölldobler 1983; Elgar and Allan 2006; Gill et al. 2012). The smaller, minor workers remain within the nest, tending to the queen and brood. Interestingly, the antennae of minor workers have both fewer

antennomeres and fewer sensilla basiconica and sensilla trichoidea curvata per antennomere than do major workers; these differences may be linked to differences in the behavior of the two castes (Babu et al. 2011).

We address two specific questions. First, we ask whether the condition of a worker’s antennae, as reflected by the density of sensilla, explain the variation in the level of aggression directed toward conspecific workers from another colony. Second, we ask whether any differences in the condition of the antennae or the individual’s behavior are related to the age of the worker.

Material and Methods

Behavioral Assays

We conducted standard nestmate recognition bioassays (Dreier et al. 2007) and compared the observed level of aggression with measures of the condition of both antennae and mandibles, using the latter as an estimate of worker age (Smeeton 1982; van Wilgenburg et al. 2005; Massey and Hartley 2009).

We selected, at random, 24 colonies of *Oecophylla smaragdina* located on the campus of James Cook University (Townsville, Australia), and each was individually identified. Numerous workers were removed from the nests of each colony with forceps and held in 1-L plastic containers lined with polytetrafluoroethylene (Fluon). Nests on neighboring trees were deemed to be from different colonies if aggressive behavior was observed between major workers (see Gill et al. 2012).

We conducted standard one-on-one nestmate recognition bioassays between workers from pairs of colonies, following Gill et al. (2012). These assays took place in plastic containers (8 cm diameter × 3 cm high). One ant, deemed the focal ant, was marked on her gaster with a small dot of acrylic fluorescent paint 15 min before the assay. The other ant remained unmarked and was gently introduced into the container, and the pair was observed for 3 min. We marked only the focal ant because we did not want the paint to interfere with any chemical signals produced by the other ant. We recorded the frequency of four behaviors that are typical of interactions between workers: grooming and trophallaxis, recoil and mandible flare, nipping and gaster flexion, and biting and grappling. Each of these four behaviors was weighted from 1 to 4, respectively, providing a comparative, numerical aggression score (modified from Thomas et al. 1999). We calculated an aggression index for each trial (following Dreier et al. 2007; Gill et al. 2012):

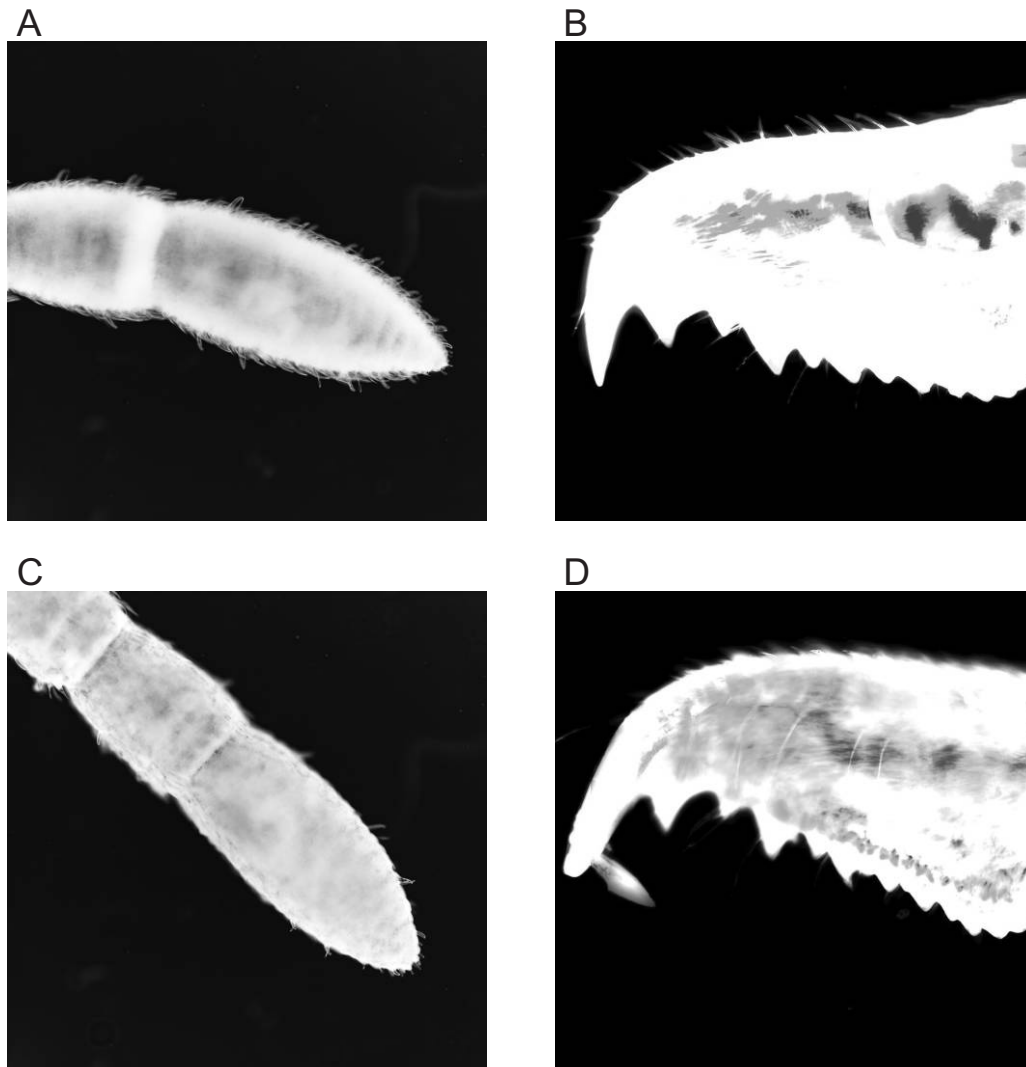


Figure 1: Wear and tear on the antennae and mandibles of *Oecophylla smaragdina* and their effects on behavior: the distal funiculus of the antennae illustrating limited (A) and extensive (C) wear and tear to the sensory hairs on the antennae and limited (B) and extensive (D; with a broken first incisor) wear and tear of the mandibles.

$$\frac{\sum_i^4 (A_i \times f_i)}{N}, \quad (1)$$

where A_i is the aggression score for each behavior i , f_i is the frequency of that behavior, and N is the sum of the frequencies of all behaviors in the 3-min trial.

We conducted four aggression bioassays for each randomly allocated colony pair. The trials took place in the field to minimize the time ants were removed from the colony, and no ant was used more than once. At the end of the trial, each worker was preserved in an individually labeled vial for subsequent morphological measurements, ensuring that the observer had no a priori knowledge of

the density of sensilla on the antennae of the observed worker.

Morphological Measurements

The antennae of each marked worker were cut at the proximal end from the head, laid flat on a clean slide, and viewed under an Olympus BX51 light microscope attached to a camera with $\times 100$ magnification. Several images of the antennae were taken using SPOT (ver. 4.7.0) to obtain a full segment length in focus, and Image-Pro Plus (ver. 6.3) was used to overlay the images and invert the final image. We recorded the number of all types of sensilla

Table 1: Summary statistics of worker traits across 12 colonies of *Oecophylla smaragdina*

Colony	Antennae length (μm)	Total sensilla per μm	Mandible wear	Aggression index
130	367.0 \pm 31.0	6.3 \pm 3.6	3.3 \pm .3	1.6 \pm .7
132	368.6 \pm 33.0	10.2 \pm 4.4	6.0 \pm 3.3	2.2 \pm 1.1
136	365.2 \pm 9.1	9.5 \pm 2.8	4.2 \pm 1.1	2.1 \pm .2
145	355.5 \pm 14.8	6.1 \pm 2.1	4.1 \pm .9	2.7 \pm 1.7
152	364.9 \pm 19.4	6.5 \pm 1.0	3.4 \pm .2	1.4 \pm .6
159	372.7 \pm 12.7	6.1 \pm 1.5	4.4 \pm .9	2.3 \pm 1.0
166	363.3 \pm 12.7	8.0 \pm 1.2	4.2 \pm 1.1	2.1 \pm .1
173	337.7 \pm 19.7	5.5 \pm .6	3.6 \pm .5	2.3 \pm 1.2
182	340.0 \pm 13.7	6.6 \pm 2.1	6.5 \pm 3.7	1.7 \pm .6
185	389.3 \pm 11.0	5.9 \pm 2.4	4.9 \pm 1.5	1.4 \pm .6
186	386.3 \pm 22.4	6.5 \pm 2.5	3.3 \pm .3	1.6 \pm .5
190	342.6 \pm 20.7	8.1 \pm 2.3	3.8 \pm .8	1.9 \pm 1.2

Note: Values are mean \pm SD for four ants per colony (except only two measures of mandible wear were obtained for colony 186).

that were discernible (i.e., in focus) along the perimeter of the most distal antennomere (segment) of the antennae. The length of the segment to the most distal tip was also measured (fig. 1A, 1C). The number of sensilla was then corrected for the length of the antennomere.

We used mandible wear as an estimate of worker age (Smeeton 1982; Acosta et al. 1984; Gibb and Hochuli 2003; van Wilgenburg et al. 2005; Massey and Hartley 2009). The mandibles were dissected from the head of each ant, placed on a slide so that the first incisor pointed upward, and viewed under the light microscope (as described above). Several images of the mandibles were taken using SPOT (ver. 4.7.0) to obtain a full segment length in focus, and Image-Pro Plus (ver. 6.3) was used to overlay the images and invert the final image. We recorded the perpendicular distances of the first incisor and the total length of the mandible from the outer edge of the first incisor to the outer edge of the last incisor (fig. 1B, 1D). Mandible wear was calculated as the inverse of the ratio of incisor length to mandible length (following Acosta et al. 1984; van Wilgenburg et al. 2005).

Morphological measures of both antennae and mandibles were made blind to the individual's aggression score (see van Wilgenburg and Elgar 2013).

Statistical Procedures

The mean number of sensilla per antennal segment, the mean mandible wear, and the mean aggression index score were calculated for each colony. Residual scores were obtained for each individual within a colony by subtracting its raw score from the mean score for their respective colony. We used regression analysis with JMP (ver. 7; SAS Institute) to explore the impact of both residual antennal and mandible wear on residual aggression index.

Results

In general, the ants behaved aggressively toward each other, with a mean aggression index across all trials of 1.9 (SD = 0.86, $n = 48$), although the entire range of behaviors was observed. There was variation in both the number of sensilla per micrometer of antennae and the degree of mandible wear. The number of sensilla per micrometer of antennae ranged from 3.1 to 14.9 (mean = 7.1, SD = 2.6, $n = 48$), while the mandible wear index ranged from 2.9 to 12.0 (mean = 4.3, SD = 1.8, $n = 46$). There was significant variation between colonies in the number of sensilla per micrometer of antennae but not in the level of aggression or mandible wear (table 1).

The capacity of workers to respond aggressively to nonnestmates was significantly affected by the condition of their signal receptor organ. The condition of the antennae of workers varied (fig. 1A, 1B), and workers whose antennae had relatively fewer sensilla reacted less aggressively to nonnestmates than did workers whose antennae had relatively more sensilla (fig. 2A). This crucial behavioral response does not appear to be age specific because the level of aggressive behavior was not correlated with mandible wear (fig. 2B).

The data underlying table 1 and figure 2 are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.7c9q7> (Gill et al. 2013).

Discussion

Our results highlight the largely unappreciated significance of receptor organ condition for animal communication: the level of aggression that ants direct toward nonnestmate workers depended upon the condition of their antennae, and ants with relatively fewer sensilla on their antennae reacted less aggressively to nonnestmate enemies than did

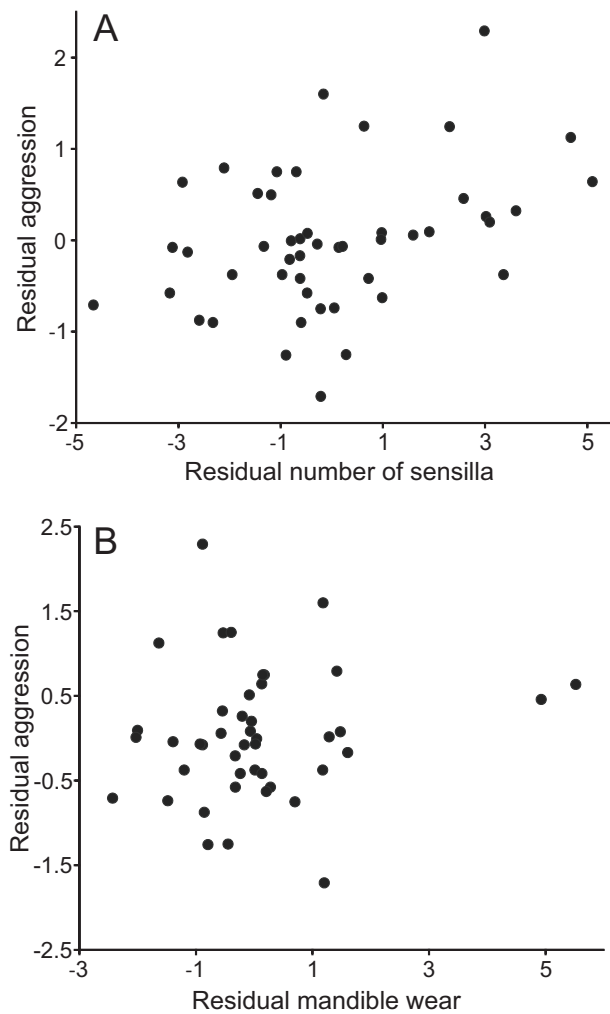


Figure 2: Residual level of aggression toward nonnestmates is positively correlated with the residual number of sensilla per micrometer of antennae (A; $r^2 = 0.137$, $F_{1,47} = 7.298$, $P < 0.01$) but not with the residual condition of the mandible (B; $F_{1,45} = 0.877$, $P > 0.3$).

those with more sensilla. The sources of variation in sensilla density may be due to intrinsic natural variation, accumulated damage through age, or damage that may derive from engagement in a major conflict independent of worker age.

It is perhaps surprising that the correlation between antennal condition and functional behavior in *Oecophylla smaragdina* is not influenced by our estimate of worker age. Neurophysiological studies have reported age-related changes in sensitivity to chemical social signals or environmental cues (Seabrook et al. 1979; Blaney et al. 1986; Vetter and Visscher 1997), although these studies compared the response of very recently eclosed adults with those that are a few days older. Older workers might be

expected to have antennae in poorer condition, simply through ongoing wear and tear. Nevertheless, while it is possible that our estimate of worker age is unreliable, any potential influence of age is unlikely to be straightforward. In theory, older workers might be more likely to engage in defensive activities and react more aggressively to enemies because they are less valuable to the colony (van Wilgenburg et al. 2005; see also Hölldobler 1983). To be effective in defense, these older workers should also have superior sensory capabilities, enabling them to distinguish accurately between nestmates and other enemies. However, such superior sensory capabilities may be more likely found in younger workers, whose receptor organs have had less exposure to the environment and thus may be in better condition. If maintaining colony integrity is at a premium, workers with antennae in good condition should preferentially engage in nest defense, irrespective of their age.

It seems likely that the pattern we observed would be much stronger had we been able to identify and count individual types of sensilla (e.g., using scanning electron micrographs). Our present sample would have mostly included the long and wispy sensilla *trichoidea curvata*, together with the shorter sensilla *basiconica* (see Babu et al. 2011). In the hymenoptera, both of these sensilla are sensitive to olfactory cues, including pheromones (Hashimoto 1990). Both types of sensilla are especially numerous at the distal end of the antennae in *O. smaragdina* (Babu et al. 2011), with the numbers of each being broadly positively correlated across antennomeres 8–11 (Babu et al. 2011). Intriguingly, the number and density of olfactory pore plate sensilla increases with body size in bumblebees, and larger bumblebee workers respond correctly to much lower odor concentrations than do small workers (Spaethe et al. 2007).

Our results could have broader implications for animal signaling. Animal communication reflects coevolutionary processes involving both the signaler and the receiver, yet theoretical and empirical studies rarely take into account variation in the sensitivity or capacity of individuals to detect signals (Johnstone 1994; Broom and Ruxton 2011). This variation may derive from the quality of the receptor organ, reflected in the number and density of intact sensilla that may be due to either natural variation or environmentally induced wear and tear. For example, variation in receiver sensitivity arising from exposure to the environment might partly explain the maintenance of variation in secondary sexual signals under intense sexual selection. Some individuals may simply incorrectly judge a signal as optimal and thus choose a mate of poorer quality. Additionally, selection is thought to favor multiple signaling across different modalities if it improves the capacity of the receiver to discern accurate information (Bro-

Jørgensen 2010). Perhaps multiple signaling is also more common in species in which the receptor organs of one modality are especially prone to damage from the environment—in other words, olfactory and other signal modalities may be favored in species in which the antennae is likely to be damaged during the life of the adult.

Acknowledgments

We thank the late R. Crozier, S. Robson, E. Schlüens, and H. Schlüens for their hospitality at James Cook University; J. Ratcliffe for help with fieldwork; R. Day for statistical advice; A. Barron, K. P. Rajashekhar, and an anonymous referee for helpful comments on the manuscript; and the Australian Research Council (DP0879610) for financial support.

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