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Peripheral sensory organs vary among ant workers but variation does not predict division of labor

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ABSTRACT

The neural mechanisms underlying behavioral variation among individuals are not well understood. Differences among individuals in sensory sensitivity could limit the environmental stimuli to which an individual is capable of responding and have, indeed, been shown to relate to behavioral differences in different species. Here, we show that ant workers in *Temnothorax rugatulus* differ considerably in the number of antennal sensory structures, or sensilla (by 45% in density and over 100% in estimated total number). A larger quantity of sensilla may reflect a larger quantity of underlying sensory neurons. This would increase the probability that a given set of neurons in the antenna detects an environmental stimulus and becomes excited, thereby eliciting the expression of a behavior downstream at lower stimulus levels than an individual with comparatively fewer sensilla. Individual differences in antennal sensilla density, however, did not predict worker activity level or performance of any task, suggesting either that variation in sensilla density does not, in fact, reflect variation in sensory sensitivity or that individual sensory response thresholds to task-associated stimuli do not determine task allocation as is commonly assumed, at least in this social insect. More broadly, our finding that even closely related individuals can differ strongly in peripheral sensory organ elaboration suggests that such variation in sensory organs could underlie other cases of intraspecific behavioral variation.

1. Introduction

Consistent inter-individual behavioral differences are nearly ubiquitous in animals (e.g. in arthropods (Pruitt et al., 2008), fish (Bell and Sih, 2007), mammals (Gosling, 1998)). Still, little is known about the fundamental neural mechanisms underlying them. Social insects provide a convenient model system for this question because nestmates exhibit stable, inter-individual differences in behavior by specializing on particular tasks. Often, nestmates vary considerably in overall activity level as well (e.g. Charbonneau et al., 2014; Jandt et al., 2012). Such division of labor (in both task and activity level) emerges without any leader and may rely on intrinsic variation in task preference among workers (Beshers and Fewell, 2001), learned differences (e.g. Ravary et al., 2007), or social signals (e.g. Greene and Gordon, 2007; Pinter-Wollman et al., 2011).

Here, we investigate whether fixed differences at the level of the peripheral nervous system, specifically in the number of antennal sensory structures, contribute to behavioral variation among social insect workers. We base this idea on a widely accepted hypothesis explaining division of labor in social insects (both task specialization and overall activity level), which invokes variable response thresholds to task-related stimuli: if workers differ in the levels of task-related stimuli they respond to, this may lead to differences in how often a task is performed (Beshers and Fewell, 2001). Most studies have assumed these 'thresholds' generally arise in the central nervous system (CNS) and therefore limit their scope to the brain (reviewed in Kamhi and Traniello, 2013; Page and Robinson, 1991). However, variation in sensory organ size, development, or innervation could also directly lead to different response thresholds by limiting or biasing sensory information before it even reaches the brain.

A possible role for the peripheral nervous system in worker behavioral differences is supported by findings that differences in olfactory receptor expression, for example, are associated with behavioral receptivity to odor stimuli in honeybees (Villar et al., 2015). In addition, variation in the number of antennal sensory organs (sensilla) is linked to olfactory acuity in bumblebees (Spaethe et al., 2007), forager

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Table 1
Different behavioral states used to determine task allocation. No other tasks were observed.

Behavior	Description
Inactive	Completely immobile
Brood care	Feeding, grooming or moving brood
Foraging	Outside the nest in the foraging arena
Grooming	Worker grooming itself or nestmate
Wandering inside	Moving inside nest but not performing a discernable task
Trophallaxis	Receiving or giving liquid food to/from another worker

resource preferences in honeybees (Riveros and Gronenberg, 2010) and aggression level in weaver ants (Gill et al., 2013). Whether such peripheral mechanisms underlie social insect response thresholds that drive division of labor in a broader context (i.e. across all tasks) is unclear. Here, we use the brown rock ant *Temnothorax rugatulus* to quantify inter-individual variation in the number of particular functional types of antennal sensilla and test the hypothesis that differences in sensilla number predict activity level and/or task allocation. *T. rugatulus* workers show pronounced differences in activity level and are weakly specialized in different tasks (Charbonneau and Dornhaus, 2015; Charbonneau et al., 2017; Pinter-Wollman et al., 2012). If sensilla number corresponds to higher sensory sensitivity, and thus affects task-associated response thresholds, we expect that ants with more sensilla will be (1) more active overall and/or (2) more active or specialized in particular tasks that are likely to depend on chemical sensitivity, such as foraging (an outside task conducted in a complex sensory environment) and brood care (Vander Meer and Alonso, 1998; Conte and Hefetz, 2008).

2. Methods

Six queen-right *T. rugatulus* colonies were collected November 2014–October 2016 from the Santa Catalina Mountains, Tucson, AZ, at an elevation of 2134 m. Colony sizes ranged from 14 to 55 workers. Each colony was housed in an artificial nest consisting of a cardboard nest chamber between two glass slides and kept inside a fluon-coated container, as described by (Charbonneau et al., 2014). Ants were provided freeze-killed fruit flies, honey solution and water *ad libitum* and kept on a 12 h light cycle at 21 °C. Each ant was individually marked using Testor's Pactra® paint.

We measured worker behavior using one of two protocols: (1) filming whole colonies for five minutes at arbitrary timepoints between 8 a.m. and 5 p.m. on three days within a two-week period, or (2) filming whole colonies for 10 min at arbitrary times between 8 a.m. and 5 pm on four days in a one week period. The behavioral state (see Table 1) of each ant was recorded every second by an observer analyzing all three videos. Therefore, for each colony 3 sessions were filmed and analyzed. Activity level for each worker was measured as the proportion of time each ant was not 'inactive' (motionless and apparently not working). Task specialization was measured in two ways: as (1) proportion of *total* time and (2) proportion of *active* time each ant spent in the focal behavioral state. Immediately following the final filming session for each colony, ants were fixed in alcoholic Bouin's fixative (formaldehyde, picric acid, acetic acid) then washed with 70% ethanol. We quantified elaboration of the peripheral sensory organs by counting the number of sensillum insertions ('sockets', hereafter also referred to as 'sensilla') on the distal-most segment of the right antenna of each worker. *T. rugatulus* ants have club-shaped antennae in which the distal-most segment comprises by far the highest number of sensilla (Ramirez-Esquivel et al., 2017). If the right antenna was damaged, we instead used the left antenna since sensilla number is bilaterally symmetrical (Online Resource 1). To visualize under the light microscope, antennae were incubated in 100% ethanol at 25° C for ten minutes and then in methyl salicylate for sixty minutes. Antennae were then mounted onto slides using methyl salicylate, sealed under a cover slip with nail polish and viewed under a 63 × /1.25 Plan-Neofluoar oil objective using a Zeiss Axioplan bright-field microscope. We used SPOTbasic software to capture images of the dorsal and ventral surfaces of the distal-most segment and the GNU image manipulation program GIMP 2.8 to count sensilla sockets within a defined area (100 μm × 50 μm) covering most of the segment and aligned with the base of the segment on both surfaces. We approximated total sensilla number by estimating the distal-most segment surface area using the equation of a cylinder ($2\pi rh$) for 70% of the segment's length and a circular cone (πrl) for 30% of its length (resembling the approximate shape of the antennal segment). Ants with missing or damaged antennae were discarded, leaving us with a total sample size of 150 ants.

Socket size was used to differentiate between thinner sensilla with smaller sockets and thicker sensilla with larger sockets. The "small-socket" group broadly included sensilla chaetica (mechanoreceptors, Dumpert, 1972a), coeloconica (responsive to temperature change, Ruchty et al., 2009), trichoidea (putative contact chemoreceptors, Hashimoto, 1990) and trichoidea-II (unknown function, previously described in ants by Nakanishi et al., 2009; Ramirez-Esquivel et al., 2014) (Fig. 1a, white arrows). The "large-socket" group included two chemosensitive sensilla types: sensilla basiconica (contact

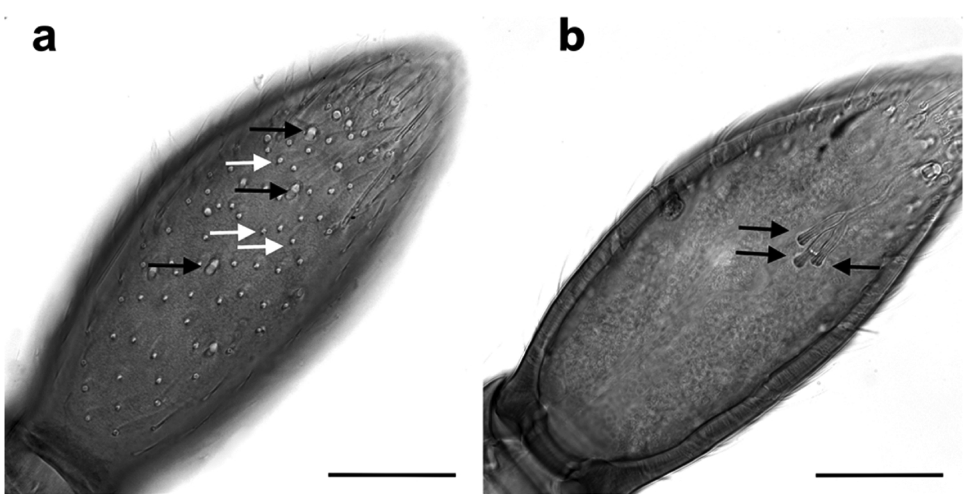

Fig. 1. The distal-most antennal segment of a *T. rugatulus* worker showing (a) sensilla sockets (black arrows: large sockets, white arrows: small sockets); and (b) invaginated sensilla ampullacea (black arrows). Scale bar: 100 μm.

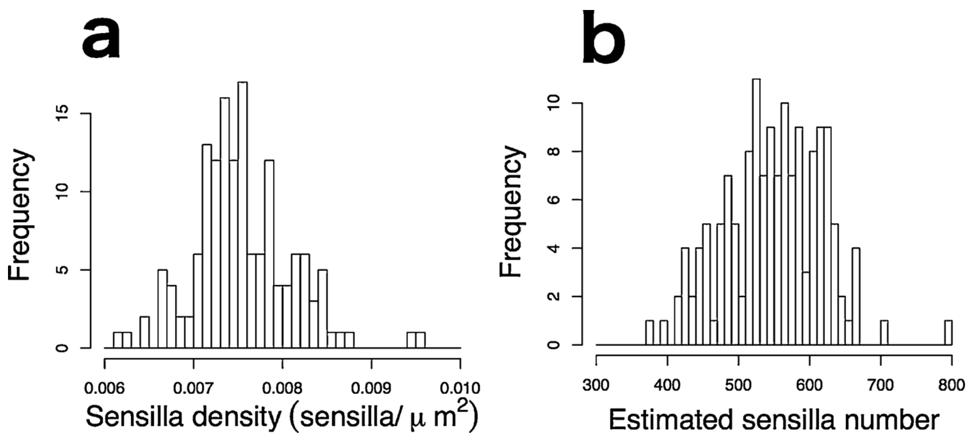

Fig. 2. Sensilla density (a) and absolute sensilla number (b) varies among *T. rugatulus* workers (density: min = 0.0062 sensilla/μm^2, max = 0.0096 sensilla/μm^2; absolute number: min = 377 sensilla, max = 798 sensilla, n = 150 ants, 6 colonies).

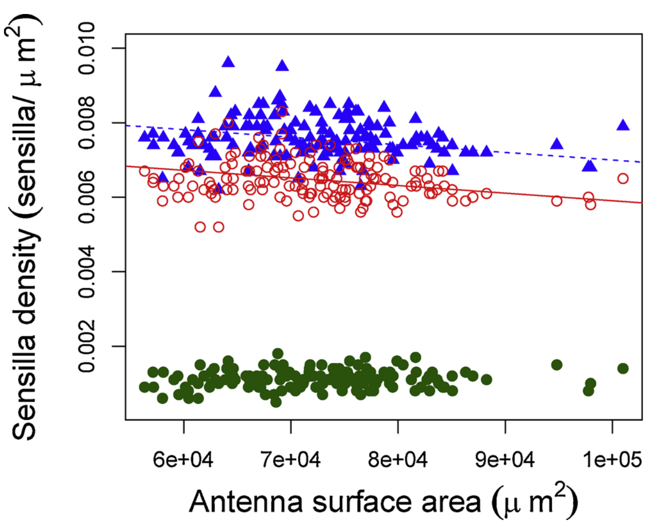

Fig. 3. Both total and small-socket sensilla density decrease with increasing surface area of the distal-most antennal segment. Large-socket sensilla density, however, varies independently of surface area. Blue triangles: total sensilla socket density (linear mixed effects model p-value < 0.0001, random effect: colony, fixed effect: sensilla density, slope = -2.04 × 10^{-8}); Red open circles: small sensilla socket density (linear mixed effects model p-value < 0.0001, random effect: colony, fixed effect: sensilla density, slope = -2.07 × 10^{-8}); Green: large sensilla socket density (linear mixed effects model p-value = 0.18, random effect: colony, fixed effect: sensilla density, n = 150 ants, 6 colonies).

chemoreceptors, thought to be involved in nestmate recognition, Renthal et al., 2003; Sharma et al., 2015) and trichoidea curvata (detection of volatile compounds, e.g. pheromones, Dumpert, 1972b) (Fig. 1a, black arrows). Sensilla ampullacea, sensitive to carbon dioxide (Kleineidam et al., 2000) were quantified by counting the distinctive peg-like structures located within the lumen of the distal-most antennal segment (Fig. 1b). Absolute number was used instead of density in this case because sensilla ampullacea are clustered in one area of the segment. For 32 samples, air bubbles that remained in the lumen made counting of the internal sensilla impossible. For this analysis, therefore, we had a total sample size of 118 ants. Antenna size was assessed by measuring the length of the distal-most antennal segment using a stage micrometer and Image J ® software.

2.1. Statistical analyses

We used a linear model to test the hypothesis that sensilla density is associated with task allocation, specifically the proportion of time spent performing different tasks. A linear model was also used to assess the relationship between different (i.e. small and large-socket) sensillum types and their association with the surface area of the distal-most antennal segment. Colony was incorporated as a random factor for all linear models. We used a non-parametric Kruskal-Wallis test for determining the relationship between the surface area of the distal-most antennal segment and number of sensilla ampullacea, which had discrete values of 3, 4, 5 or 6 sensilla and was not normally distributed. All statistical analyses were performed in R 2.15.1, using lme4 and base 'stats' packages.

3. Results

3.1. Variation across workers

Antennal sensilla density and absolute sensilla number varied considerably among workers across colonies (Fig. 2a, b). Within colonies sensilla density and total sensilla number also varied among nestmates (average coefficient of variation in sensilla density = 0.064, absolute number = 0.100).

3.2. Variation in sensilla types and total sensilla number

Small and total sensilla density decreased with increasing surface area of the distal-most antennal segment (Fig. 3), indicating that ants with larger antennae do not have proportionately more (small) sensilla. The shallow slope of the trend lines, however, suggests that larger ants, on average, still have more sensilla than smaller ants. In addition, as total sensilla density increased, both small-socket sensilla (on average 85% of total) and large-socket sensilla (15% of total) increased (Fig. 4). Ants with more small-socket sensilla, however, had fewer large-socket sensilla (Fig. 5). Though contributing less to overall number, large-socket sensilla density varied more than small-socket sensilla (coefficient of variation: small-socket sensilla = 0.084 and large-socket sensilla = 0.22). The number of CO_2-sensitive sensilla ampullacea was much lower than that of the other two types and did not correlate with surface area of the distal-most antennal segment (coefficient of variation = 0.14; Fig. 6). There was no relationship between the number of sensilla ampullacea and total sensilla density (Online Resource 2).

3.3. Sensilla density and worker behavior

The quantitative differences we observed in the number of sensory units (presumably reflecting the number of underlying sensory neurons) should be associated with differences in sensory sensitivity and, according to the response threshold hypothesis, response thresholds and worker behavior (Chapman, 1982; Spaethe et al., 2007). However, we

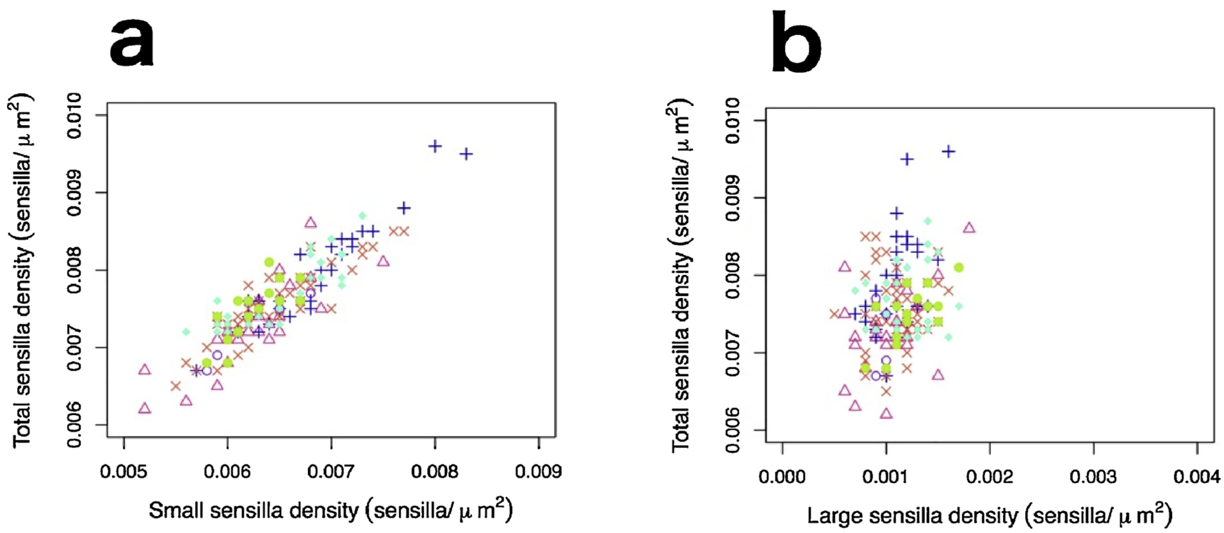

Fig. 4. As total sensilla density increases, (a) small-socket and (b) large-socket sensilla increase. No statistics are reported here because variables are not independent of one another. Graphs serve to simply illustrate the relationship between different sensilla types and total sensilla density. Each colony is represented by a different color and shape, n = 150 ants, 6 colonies.

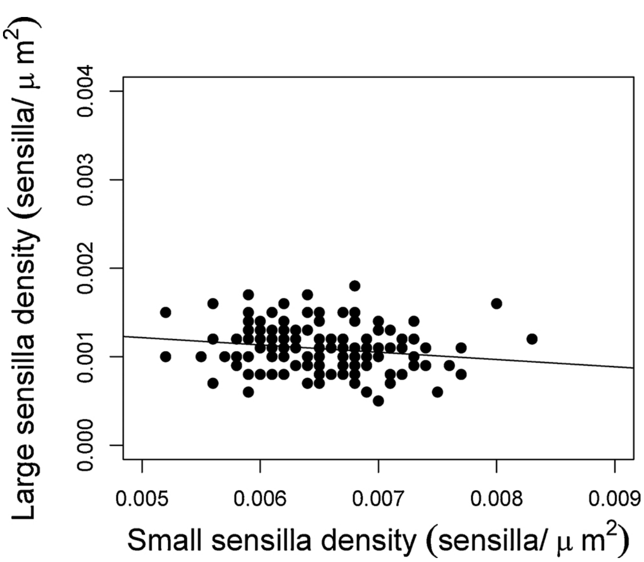

Fig. 5. Ants with a higher density of small-socket have a lower density of large-socket sensilla, suggesting that these two sensilla types trade off against one another (Linear mixed effects model p-value = 0.03, random effect: colony, fixed effect: large sensilla density, slope = -0.07, n = 150 ants, 6 colonies.

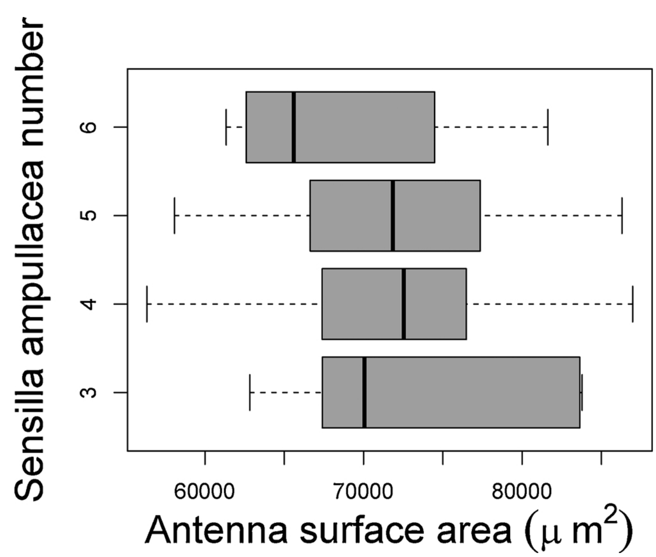

Fig. 6. The number of sensilla ampullacea (CO_2-sensitive sensilla) on the distal-most antennal segment is not associated with the surface area of that segment. Kruskal-Wallis p-value = 0.48, n = 118 ants, 6 colonies. Boxplot shows the lower and upper quartiles (box), median (horizontal line in box), and extremes (whiskers) for antennal surface area associated with each number of sensilla ampullacea.

found no relationship between individual worker sensilla density and activity level (Fig. 7a). Sensilla density was also not associated with any specific tasks, whether calculated as proportion of *total* time (Fig. 7; Table 2) or *active* time (Table 2; Online Resource 3). No relationship was found when using any of the specific sensilla types (Online Resource 4). Similarly, antennal surface area (i.e. antenna size) did not predict worker performance in any task (Table 2; Online Resource 5). None of these analyses changed qualitatively if only ants from the first or second filming protocol were used.

4. Discussion

We find considerable variation across workers in the density and total number of sensory structures on the antenna. Total sensilla density and small-socket sensilla density decrease slightly with increasing antenna size, while variation in large-socket sensilla density is not associated with antenna size. Interestingly, ants with higher small-socket sensilla density tend to have lower large-socket sensilla density, suggesting the possibility that these two sensilla types might trade off against each other. The number of sensilla ampullacea is much smaller (between 3–6) and appears to stay constant across antennal surface areas and sensilla densities. This result supports earlier findings in other ant species in which the number of ampullacea is stable across workers. In the very large ant *Atta sexdens,* workers have about 10 sensilla ampullacea within the distal-most antennal segment (Kleineidam et al., 2000), while the moderately sized *Myrmecia pyriformis* workers have far more ampullacea, between 21–24 (Ramirez-Esquivel et al., 2014). Apparently, then, ampullacea number does not covary with worker size either within or across species. This raises interesting questions about how differences in these species' natural histories (e.g. nesting habits) has led to different stabilizing selection pressures on CO_2 -sensitive

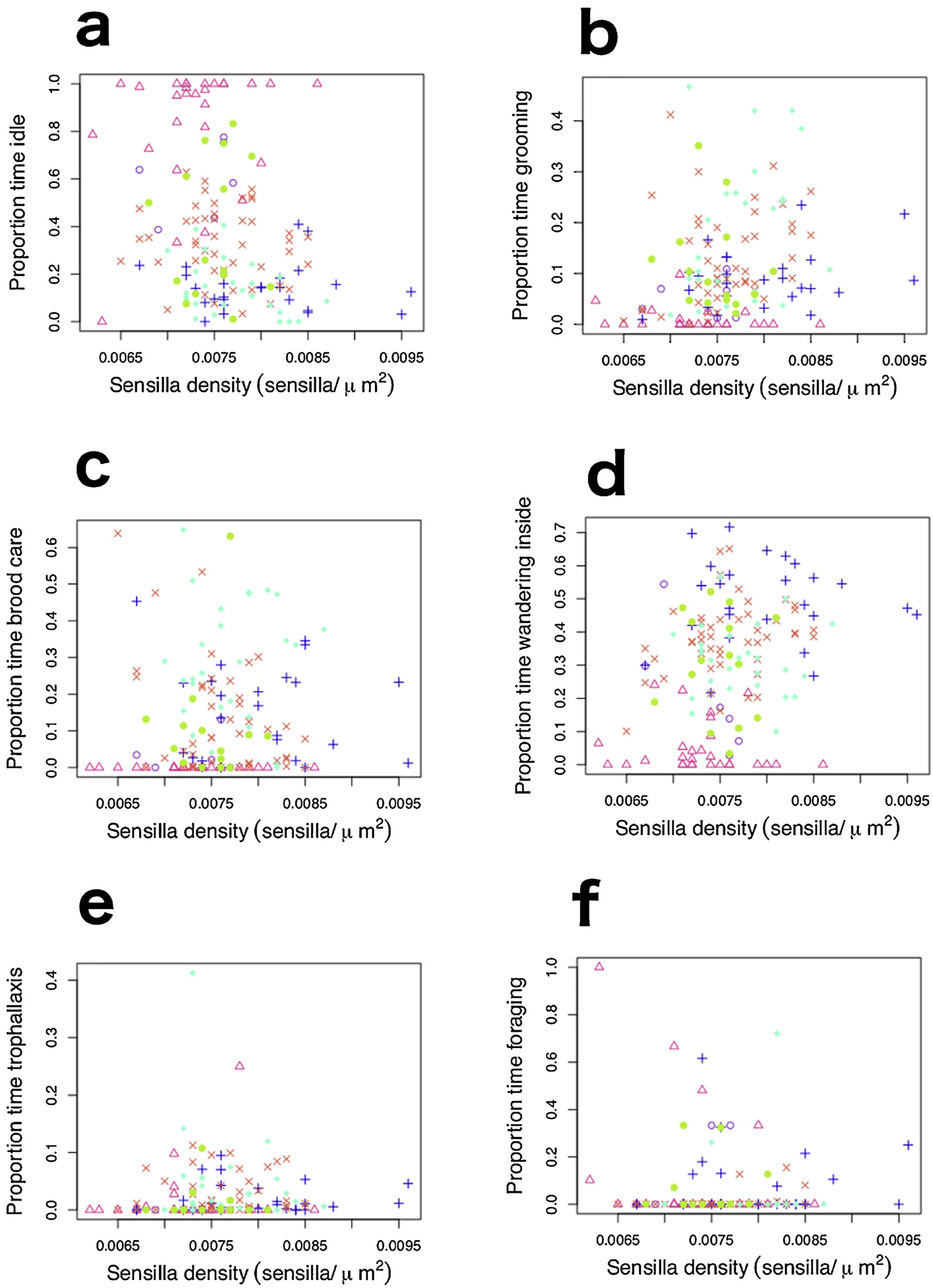

Fig. 7. Individual worker sensilla density does not predict proportion of total time spent performing any task (a–e). Different colors/shapes represent different colonies. Statistics summarized in Table 2, n = 150 ants, 6 colonies.

Table 2
Sensilla socket density does not predict time spent performing any tasks after Bonferroni correction for multiple comparisons (adjusted α ≤ 0.008). Similarly, the surface area of the distal-most antennal segment does not predict task specialization. Shown above are the results of linear mixed effects models based on proportion of *total* time spent performing each focal task and proportion of *active* time spent performing each focal task. Random effect: colony, n = 150 ants, 6 colonies.

		Proportion of total time		Proportion of active time	
Behavior	Fixed effect	F-value	p-value	F-value	p-value
Activity level	Sensilla density	0.23	0.63	n/a	n/a
	Antennal surface area	3.01	0.08	n/a	n/a
Grooming	Sensilla density	7.03	0.009	4.15	0.04
	Antennal surface area	2.08	0.15	1.71	0.19
Brood care	Sensilla density	2.44	0.12	3.44	0.07
	Antennal surface area	6.85	0.009	5.63	0.02
Wandering inside	Sensilla density	0.08	0.77	0.71	0.4
	Antennal surface area	0.91	0.34	0.07	0.79
Trophallaxis	Sensilla density	0.11	0.74	0.55	0.46
	Antennal surface area	0.22	0.64	0.0004	0.98
Foraging	Sensilla density	0.76	0.38	0.42	0.52
	Antennal surface area	0.1	0.75	0.13	0.72

sensilla.

Despite the large variation in total sensilla density across individual workers, this was not associated with task allocation or activity level in *T. rugatulus*. Given our result, variation in sensilla density must either (1) not significantly affect sensory sensitivity or (2) performance in most tasks must not be predicted by sensory sensitivity, at least in *T. rugatulus*. The lack of a relationship between sensilla density and any of the tasks we measured is puzzling given that earlier work had established a link between sensilla number and differences in behavior, sensitivity and even learning in some social insects (Gill et al., 2013; Riveros and Gronenberg, 2010). Larger bumblebee workers, for example, have more sensilla and lower response thresholds to a conditioned olfactory stimulus (Spaethe et al., 2007). However, it appears that the functional consequence of sensory organ variation is far from obvious and perhaps cannot be generalized across species, or even across tasks within the same species. Recent work in *Pheidole* ants, for example, demonstrates that unilateral antennal ablation (i.e. resulting in the loss of roughly half of their sensilla) does not prevent workers from carrying out most of their normal task repertoire (Waxman et al., 2017). In contrast, antennal removal has significant effects on behavior in *Tetragonula* bees (though this was not associated with sensilla number), and in honeybees the right antenna is both more enriched with olfactory sensilla and better at recalling olfactory memories than the left. Yet, in this same species, the peripheral nervous system is not associated with worker differences in responsiveness to alarm pheromone (Robinson, 1987). Though we do find variation in *T. rugatulus* sensory organs, our results are consistent with those of (Waxman et al., 2017), which suggest that sensory organ differences may not have significant effects on behavior and task allocation. Rather than variation in density, variation in the size of individual sensilla or differences across individual sensilla in the number of underlying sensory neurons might affect sensory sensitivity and therefore behavior. If this were the case, quantifying sensilla number or density would not capture the true functional variation in sensory organs among workers, a possibility that deserves further investigation. Alternatively, our results might indicate that the central nervous system, alone, drives response thresholds. In this case, the central nervous system would have to impose a great enough amount of variation to override the considerably large differences we observed in the periphery.

A second possibility is that differences sensitivity (i.e. response thresholds) are *not* the driving force for division of labor as is commonly thought for social insects. Though response thresholds are very well established in honeybees (e.g. Page et al., 1998; Pankiw and Page, 2000) empirical evidence for their existence and role in division of labor in other social species is sparse and sometimes conflicting. In bumblebees, for example, workers differ in fanning thresholds for temperature and CO_2, however these thresholds do not predict the probability that a worker will fan or how long it will fan (Weidenmüller, 2004). If our assumption that sensilla density variation reflects sensitivity variation is correct, then our results would suggest that response thresholds are not governing division of labor in *T. rugatulus* ants and are therefore not a universal driver of social insect division of labor. In summary, a 45% difference in individual sensory organ elaboration that has no effect on task performance suggests one of two possible conclusions: (1) either sensory organ elaboration is not associated with sensory sensitivity, in which case sensilla may not be costly to produce and/or maintain and are therefore under low selection pressure to eliminate unnecessary variation; or (2) differences in sensitivity to task-relevant stimuli (i.e. response thresholds) may not be a driver of task allocation in this social insect. To better understand mechanisms by which division of labor specifically, and inter-individual behavioral variation in general, is created further investigations should attempt to distinguish between these two alternatives.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2018.10.016.

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