



Mechanisms and adaptations that shape division of labour in stingless bees

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Stingless bees are a diverse and ecologically important group of pollinators in the tropics. Division of labour allows bee colonies to meet the various demands of their social life, but has been studied in only ~3% of all described stingless bee species. The available data suggest that division of labour shows both parallels and striking differences compared with other social bees. Worker age is a reliable predictor of worker behaviour in many species, while morphological variation in body size or differences in brain structure are important for specific worker tasks in some species. Stingless bees provide opportunities to confirm general patterns of division of labour, but they also offer prospects to discover and study novel mechanisms underlying the different lifestyles found in eusocial bees.

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Introduction

Division of labour, that is, non-random differences in the tasks that the members of a colony perform, is nearly universal in social insects [1]. The degree and persistence in time of behavioural variation vary among species, worker groups and tasks that are performed [2–6]. A

honeybee (*Apis mellifera*) might spend only a few hours of her life as a nest guard [7], while a leaf-cutter ant minor worker will show a lifelong dedication to fungus gardening and nursing [5]. Division of labour is similarly diverse and complex in stingless bees (Meliponini), the largest group of eusocial bees [8], yet the social, physiological and molecular mechanisms underpinning division of labour in stingless bees remain poorly understood. First steps have been made to explore the links between division of labour and gene expression patterns [9], juvenile hormone titres (JH) [10] or variation in immune defence [11]. These studies indicate that patterns repeatedly found in honeybees might vary in stingless bees. Here, we summarise recent advances in our understanding of the proximate factors linked to division of labour in stingless bees.

Role of age in stingless bee division of labour

Worker age has consistently been found to predict which tasks a worker performs (temporal polyethism or age polyethism). Young worker ants, bees or wasps often perform tasks close to the brood, while older workers defend the colony and forage for resources [1,6,12,13]. Stingless bees largely follow this pattern (reviewed in [8]). In the first few days after emergence, overall activity is low and workers can be seen grooming themselves and receiving food [14–16]. In the next phase, workers start to perform nest building tasks, followed by activities related to the brood provisioning and oviposition process (POP) (approx. week 1–3). Workers increasingly perform tasks away from the brood, such as removing waste or unloading and dehydrating nectar brought back by foragers [4,17]. In the later stages of adult life, workers spend more time outside their nest guarding the entrance and foraging for resources [14–17]. The onset of guarding and foraging coincides with an increase in mortality and workers usually die after 4–10 weeks, depending on the species and the intensity of foraging [8].

Non-random task performance unrelated to worker age

There is some evidence that this pattern of age-related behavioural transitions is not universal among stingless bees. Inoue et al. [18] observed in the Asian *Tetragonula minangkabau* that individual workers seemed to fall into different behavioural categories or clusters. Some workers mainly cared for the brood, whereas others focused on foraging. In the Neotropical *Melipona marginata*, task

performance was linked to age, but there were considerable behavioural differences that were not related to age [4]. Many workers were never seen foraging, while others were not observed to be involved in the POP. These patterns are probably more common in stingless bees, but discovering them will require long-term observations of individually marked workers.

Morphological and physiological correlates of division of labour

In several species of stingless bees, behavioural variation is linked to differences in body size and shape [19–21]. The guards of these species are larger than foragers and, in some species, these two tasks are performed by distinct morphological sub-castes [20]. A larger body size is achieved through increased brood food feeding of certain brood cells by nurse bees [22] and is likely to be beneficial for colonies because a larger body size improves fighting ability [19]. In addition, body size is linked to chemosensory perception and antennal sensitivity, as shown in bumble bees [23]. In the Australian *Tetragonula carbonaria* and the Neotropical *Tetragonisca angustula*, the larger guards have more antennal sensilla than foragers ([21,24], but see [25]), which is likely to be important in enemy detection [24,26]. Body size effects are likely to be more common, including for tasks other than guarding, such as foraging for mud (Figure 1a), where body size is linked to mud load size in *Melipona* [27], or for material-handling tasks. For example, waste-removing bees were found to be larger than foragers, but smaller than guards in *Tetragonisca angustula* [19].

Brain morphology: how is the brain linked to task performance?

As we have seen in the previous section, age and size heterogeneity among workers are often good predictors for task allocation. Each task is associated with an array of sensorial information processed by the brain. Thus, to meet the needs of the colony in an ever-changing and complex environment, the relatively small brain of a bee needs to process multiple modalities of sensory information and integrate them into behavioural outputs, which often involve learning and memory. The sophisticated sensory capacities, complex behavioural repertoire and comparatively simple nervous system has made social bees excellent models to study brain plasticity, that is, synaptic rearrangements in response to intrinsic or extrinsic stimuli that ultimately affect the size of the brain [28,29]. In stingless bees, researchers have only just started to address how brain morphology correlates with differences in behaviour.

In *Melipona quadrifasciata*, a stingless bee species with an age-based division of labour, Tomé et al. [30] found that ageing was associated with a volume increase of brain regions associated with processing of olfactory information

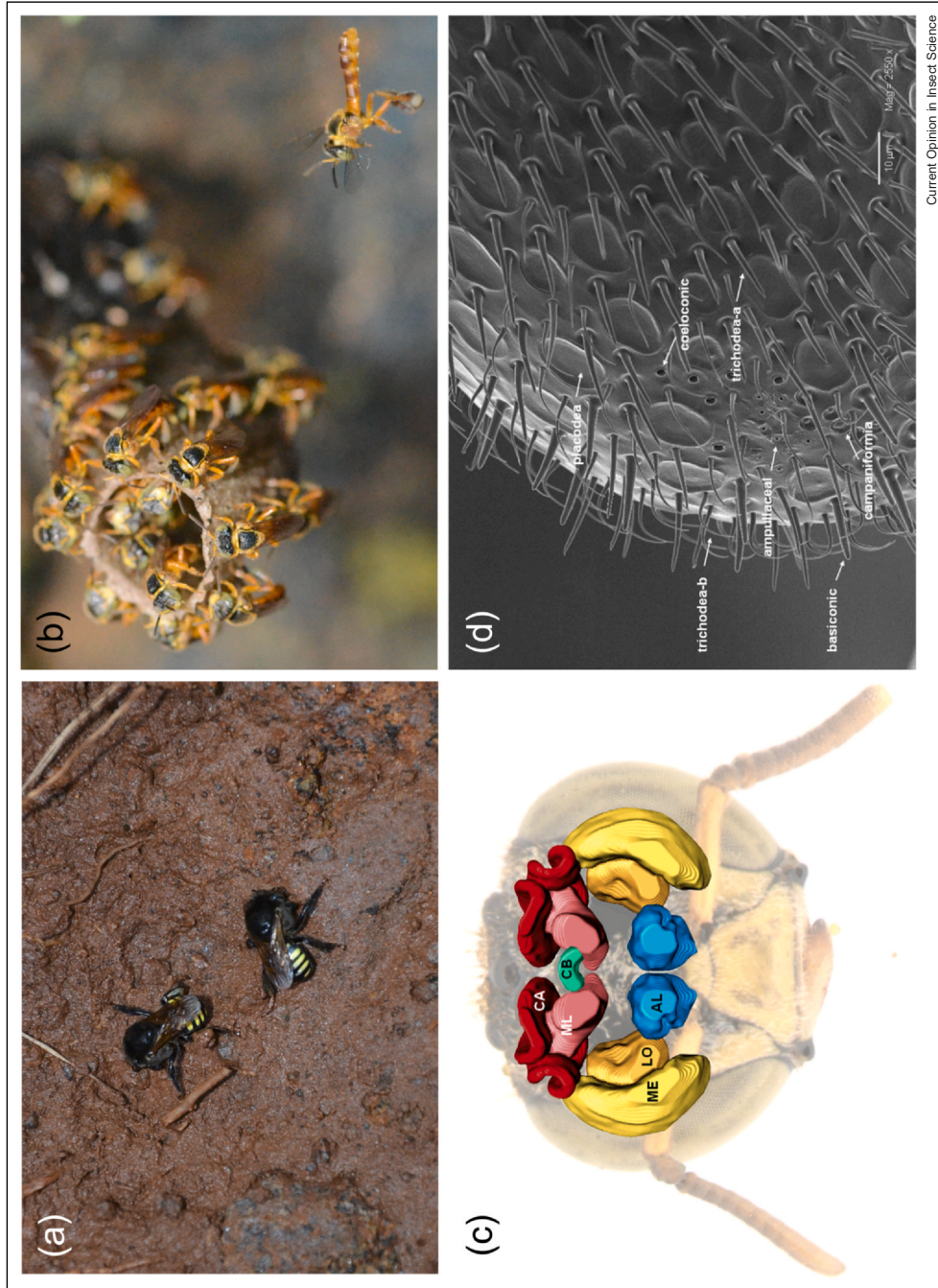
(the antennal lobes (AL)) and with multisensorial integration, memory and learning (the mushroom bodies (MB)). However, the MB size increase was far more pronounced than the AL size increase, especially during the intranidal stage of age polyethism. In contrast, in honeybees (*Apis mellifera*), AL and MB enlargement is associated with switching from intranidal tasks to foraging [31–34]. The different patterns of MB growth in these two bee species could be linked to the fact that, compared with honeybees, *M. quadrifasciata* colonies house a small number of workers (300–600 individuals), which spend longer time periods on intranidal tasks, possibly requiring greater behavioural flexibility. Young *M. quadrifasciata* workers might experience a strong demand of sensory information processing, which in turn would affect the size of their brain at an early age. Alternatively, *M. quadrifasciata* workers might increase MB size in anticipation of the cognitive demands of foraging in a complex tropical environment, a phenomenon referred to as experience-expectant plasticity [31].

In *Tetragonisca angustula*, the larger workers (guards) perform different defensive tasks: (1) hovering near the nest entrance for the detection and interception of heterospecific bees (a task associated with processing of visual information) and (2) standing at the nest entrance tube for the interception of conspecifics at short-range distance (a task that requires assessment of chemosensory information) (Figure 1b) [35–38]. In accordance with the demands of this task, hovering guards were found to have larger brain compartments related to visual information processing, the optic lobes (OL) (see Figure 1c for a brain illustration) [39,40]. Interestingly, between the OL compartments, only the medulla (ME) region was different between the two types of guards [40]. The ME processes information related to shape and colour [41,42], optimisation of spatial resolution [41] and small-field motion detection [43]. Thus, it appears that the ME is tuned to the specific requirements of being a hovering guard. These differences in brain size associated with behavioural specialisation in defence in *T. angustula* workers illustrate a functional neuroplasticity underpinning division of labour.

Response thresholds and chemosensory perception

Division of labour is linked to individual differences in response thresholds for different tasks [44,45]. All else being equal, individuals with lower response thresholds for a particular task are more likely to perform it than workers with a higher response threshold. One well-studied example is division of labour in foraging honeybees, where sucrose response thresholds (SRTs) predict which resource a bee collects [46–48]. Honeybees with lower SRTs are more likely to collect pollen or water, while bees with higher thresholds collect nectar. Balbuena and Farina [25] recently tested for the first time whether SRTs correlate with behavioural roles in a

Figure 1



Links between morphology and task performance in stingless bees. **(a)** Mud-collecting *Melipona quadrifasciata* foragers (Photo by C. Grüter). **(b)** Standing and hovering guards in the species *Tetragonisca angustula* are larger than their foraging nestmates (Photo by C. Grüter). **(c)** 3D reconstruction of a brain of a hovering guard of *T. angustula*; CA = calyx; CB = central body; LO = lobula; ML = mushroom body lobes (pedunculus, vertical lobe and medial lobe). **(d)** Scanning electron microscope image of the tip of the antenna of a *T. fiebrigii* worker showing different types of sensilla. (c) (from [40]). (d) (from [25]).

stingless bee (*Tetragonisca fiebrigi*). Similar to what has been observed in honeybees, they found that nectar foragers were less responsive to sucrose solutions than pollen foragers and guards. The authors also found that the antennal response (electroantennography) to odours that are important in nest defence (citra, a pheromone produced by *Lestrimelitta* robber bees) was stronger in guards than in nectar foragers, which could be linked to their body size differences and/or differences in their roles [23].

In addition, Balbuena and Farina [25] described the sensilla present on the antenna of foragers and guards (Figure 1d) and found that they did not differ in number among bee groups (in contrast to [49]). More work is needed to understand the links between task performance and antennal sensitivity. One interesting question for future research is the role of basiconic sensilla, which were only found on the antennae of *T. fiebrigi* females but not in males [49]. In ants, these sensilla are important for the detection of cuticular hydrocarbons (CHC), allowing individuals to discriminate between nestmates and non-nestmates [50]. Given that workers performing different tasks differ in their CHC profiles [51], the ability to discriminate between different task groups could be important for the regulation of division of labour in stingless bees (e.g. [52]).

Biogenic amines and division of labour

At the molecular level, biogenic amines (e.g. dopamine, octopamine, tyramine or serotonin) have been identified as key neuroactive molecules acting as neurotransmitters, neuromodulators and/or neurohormones in both vertebrates and invertebrates. In honeybees, biogenic amines modulate the behavioural development and division of labour among workers [53–55]. These effects are, at least in part, driven by biogenic amine effects on the responsiveness of workers to various stimuli, such as sucrose [56–58].

In stingless bees, two studies have investigated the role of biogenic amines in behavioural modulation of workers [59,60]. McCabe et al. [59] found that octopamine (OA) ingestion in *Melipona scutellaris* increased sucrose responsiveness of foragers, similar to the effects in honeybees [56]. More recently, Peng et al. [60] investigated whether OA treatment increases individual foraging effort in the neotropical stingless bee *Plebeia droryana*. They found that bees that fed sugar solution with OA showed a significant increase in foraging tempo, which could be explained by OA increasing sucrose sensitivity and foraging motivation, again similar to the effects of OA found in honeybees [61]. These studies in combination with Balbuena & Farina's [25] findings suggest a causal link between biogenic amines, SRTs and division of labour in stingless bees.

Conclusions and open questions

Stingless bees show both similarities and differences in their division of labour compared with other social bees. Research into the mechanisms of division of labour is at an early stage and our understanding of the adaptations for specific tasks is limited. For example, the role of JH or genes that influence division of labour in other social insects (e.g. *foraging*) requires further research [9,10]. To what extent are different roles linked to differences in response thresholds, biogenic amine signalling, variation in morphology and physiology or the composition of gut microbiome? Many avenues for future research exist, but exciting discoveries are already being made and they suggest that stingless bees are a promising group for the discovery of novel and unexpected patterns of division of labour and for the regulation of individual behaviour.

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Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Hölldobler B, Wilson EO: *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies*. W. W. Norton & Company; 2009.
2. Sempo G, Detrain C: **Between-species differences of behavioural repertoire of castes in the ant genus *Pheidole*: a methodological artefact?** *Insectes Sociaux* 2004, **51**:48-54.
3. Merti AL, Traniello JFA: **Behavioral evolution in the major worker subcaste of twig-nesting *Pheidole* (Hymenoptera: Formicidae): does morphological specialization influence task plasticity?** *Behav Ecol Sociobiol* 2009, **63**:1411-1426.
4. Mateus S, Ferreira-Caliman MJ, Menezes C, Grüter C: **Beyond temporal-polyethism: division of labor in the eusocial bee *Melipona marginata***. *Insectes Sociaux* 2019, **66**:317-328.

5. Wilson EO: **Caste and division of labor in leaf-cutting ants (Hymenoptera: Formicidae: Atta). I. The overall pattern in *A. sexdens*.** *Behav Ecol Sociobiol* 1980, **7**:143-156.
 6. Wild B, Dormagen DM, Zachariae A, Smith ML, Traynor KS, Brockmann D, Couzin ID, Landgraf T: **Social networks predict the life and death of honey bees.** *Nat Commun* 2021, **12**:1110.
 7. Moore AJ, Breed MD, Moor MJ: **The guard honey bee: ontogeny and behavioural variability of workers performing a specialized task.** *Anim Behav* 1987, **35**:1159-1167.
 8. Grüter C: **Stingless Bees: Their Behaviour, Ecology and Evolution.** Springer International Publishing; 2020.
 9. Araujo N, de S, Arias MC: **Gene expression and epigenetics reveal species-specific mechanisms acting upon common molecular pathways in the evolution of task division in bees.** *Sci Rep* 2021, **11**:3654.
- This study reveals species-specific differences in gene expression and epigenetics when comparing bumble bees (*Bombus terrestris*) and the stingless bee *Tetragonisca angustula*. This work highlights variation among eusocial bees in how the molecular factors shape division of labour.
10. Cardoso-Júnior CAM, Silva RP, Borges NA, de Carvalho WJ, Walter SL, Simões ZLP, Bitondi MMG, Vieira CU, Bonetti AM, Hartfelder K: **Methyl farnesoate epoxidase (*mfe*) gene expression and juvenile hormone titers in the life cycle of a highly eusocial stingless bee, *Melipona scutellaris*.** *J Insect Physiol* 2017, **101**:185-194.
 11. Ravaiano SV, Barbosa WF, Campos LA, Martins GF: **Variations in circulating hemocytes are affected by age and caste in the stingless bee *Melipona quadrifasciata*.** *Sci Nat* 2018, **105**:48.
 12. Yerushalmi S, Bodenheimer S, Bloch G: **Developmentally determined attenuation in circadian rhythms links chronobiology to social organization in bees.** *J Exp Biol* 2006, **209**:1044-1051.
 13. Shorter JR, Tibbetts EA: **The effect of juvenile hormone on temporal polyethism in the paper wasp *Polistes dominulus*.** *Insectes Sociaux* 2009, **56**:7-13.
 14. Bassindale R: **The biology of the Stingless Bee *Trigona (Hypotrigona) gribodoi* Magretti (Meliponidae).** *Proc Zool Soc Lond* 1955, **125**:49-62.
 15. Kerr WE, dos Santos Neto GR: **Contribuição para o conhecimento da bionomia dos Meliponini. 5. Divisão de trabalho entre as operárias de *Melipona quadrifasciata quadrifasciata*.** *Insectes Sociaux* 1956, **3**:423-430.
 16. Hammel B, Vollet-Neto A, Menezes C, Nascimento FS, Engels W, Grüter C: **Soldiers in a stingless bee: work rate and task repertoire suggest guards are an elite force.** *Am Nat* 2016, **187**:120-129.
 17. Terada Y, Garofalo CA, Sakagami SF: **Age-survival curves for workers of two eusocial bees (*Apis mellifera* and *Plebeia droryana*) in a subtropical climate, with notes on worker polyethism in *P. droryana*.** *J Apic Res* 1975, **14**:161-170.
 18. Inoue T, Salmah S, Sakagami SF: **Individual variations in worker polyethism of the Sumatran stingless bee, *Trigona (Tetragonula) minangkabau* (Apidae, Meliponinae).** *Jpn J Entomol* 1996, **64**:641-668.
 19. Grüter C, Menezes C, Imperatriz-Fonseca VL, Ratnieks FLW: **A morphologically specialized soldier caste improves colony defence in a Neotropical eusocial bee.** *Proc Natl Acad Sci USA* 2012, **109**:1182-1186.
 20. Grüter C, Segers FHID, Menezes C, Vollet-Neto A, Falcon T, von Zuben LG, Bitondi MMG, Nascimento FS, Almeida EAB: **Repeated evolution of soldier sub-castes suggests parasitism drives social complexity in stingless bees.** *Nat Commun* 2017, **8**:4.
 21. Wittwer B, Elgar MA: **Cryptic castes, social context and colony defence in a social bee, *Tetragonula carbonaria*.** *Ethology* 2018, **124**:617-622.
 22. Segers FHID, Menezes C, Vollet-Neto A, Lambert D, Grüter C: **Soldier production in a stingless bee depends on rearing location and nurse behaviour.** *Behav Ecol Sociobiol* 2015, **69**:613-623.
 23. Spaethe J, Brockmann A, Halbig C, Tautz J: **Size determines antennal sensitivity and behavioral threshold to odors in bumblebee workers.** *Naturwissenschaften* 2007, **94**:733-739.
 24. Grüter C, Segers FHID, Santos LLG, Hammel B, Zimmermann U, Nascimento FS: **Enemy recognition is linked to soldier size in a polymorphic stingless bee.** *Biol Lett* 2017, **13**:20170511.
 25. Balbuena MS, Farina WM: **Chemosensory reception in the stingless bee *Tetragonisca angustula*.** *J Insect Physiol* 2020, **125**:104076.
- This study shows for the first time in a stingless bee that workers performing different tasks differ in their sensory thresholds for cues that play important roles for these tasks, sucrose and social odours. Note that this species is likely to be *T. fiebrigi*.
26. Gill KP, Van Wilgenburg E, Macmillan DL, Elgar MA: **Density of antennal sensilla efficacy of communication in a social insect.** *Am Nat* 2013, **182**:834-840.
 27. Costa-Pereira R: **Removal of clay by stingless bees: load size and moisture selection.** *Acad Bras Cienc* 2014, **86**:1287-1294.
 28. Mateos-Aparicio P, Rodríguez-Moreno A: **The impact of studying brain plasticity.** *Front Cell Neurosci* 2019, **13**:66.
 29. Wolff JR, Missler M: **Synaptic reorganization in developing and adult nervous systems.** *Ann Anat Anat Anz* 1992, **174**:393-403.
 30. Tomé HVV, Rosi-Denadai CA, Pimenta JFN, Guedes RNC, Martins GF: **Age-mediated and environmentally mediated brain and behavior plasticity in the stingless bee *Melipona quadrifasciata anthidioides*.** *Apidologie* 2014, **45**:557-567.
 31. Fahrbach SE, Moore D, Capaldi EA, Farris SM, Robinson GE: **Experience-expectant plasticity in the mushroom bodies of the honeybee.** *Learn Mem* 1998, **5**:115-123.
 32. Ismail N, Robinson GE, Fahrbach SE: **Stimulation of muscarinic receptors mimics experience-dependent plasticity in the honey bee brain.** *Proc Natl Acad Sci* 2006, **103**:207-211.
 33. Withers GS, Fahrbach SE, Robinson GE: **Selective neuroanatomical plasticity and division of labour in the honeybee.** *Nature* 1993, **364**:238-240.
 34. Sigg D, Thompson CM, Mercer AR: **Activity-dependent changes to the brain and behavior of the honey bee, *Apis mellifera* (L.).** *J Neurosci* 1997, **17**:7148-7156.
 35. van Zweden JS, Grüter C, Jones SM, Ratnieks FLW: **Hovering guards of the stingless bee *Tetragonisca angustula* increase colony defensive perimeter as shown by intra- and inter-specific comparisons.** *Behav Ecol Sociobiol* 2011, **65**:1277-1282.
 36. Kärcher M, Ratnieks FLW: **Standing and hovering guards of the stingless bee *Tetragonisca angustula* complement each other in entrance guarding and intruder recognition.** *J Apic Res* 2009, **48**:209-214.
 37. Wittmann D: **Aerial defense of the nest by workers of the stingless bee *Trigona (Tetragonisca) angustula*.** *Behav Ecol Sociobiol* 1985, **16**:111-114.
 38. Baudier KM, Ostwald MM, Grüter C, Segers FHID, Roubik DW, Pavlic TP, Pratt SC, Fewell JH: **Changing of the guard: mixed specialization and flexibility in nest defense (*Tetragonisca angustula*).** *Behav Ecol* 2019, **30**:1041-1049.
 39. Baudier KM, Bennett MM, Barrett M, Cossio FJ, Wu RD, O'Donnell S, Pavlic TP, Fewell JH: **Soldier neural architecture is temporarily modality specialized but poorly predicted by repertoire size in the stingless bee *Tetragonisca angustula*.** *J Comp Neurol* 2022, **530**:672-682.
- This study quantifies brain architecture and morphology in stingless bees performing different tasks and reports differences between hovering guards, standing guards and foragers in *Tetragonisca angustula*. Furthermore, they show that these differences are plastic.
40. Valadares L, Vieira BG, Santos do Nascimento F, Sandoz J-C: **Brain size and behavioral specialization in the jataí stingless bee (*Tetragonisca angustula*).** *J Comp Neurol* 2022, **530**:2304-2314, <https://doi.org/10.1002/cne.25333>.

This study reveals how specific parts of the worker brain in *Tetragonisca angustula* differ in ways that are predicted by the tasks performed by guards. Specifically, they show that hovering guards have larger brain compartments associated with visual information and information integration.

41. Bausenwein B, Dittrich APM, Fischbach K-F: **The optic lobe of *Drosophila melanogaster***. *Cell Tissue Res* 1992, **267**:17-28.
42. Jundi B, el, Pfeiffer K, Homberg U, Distinct A: **Layer of the medulla integrates sky compass signals in the brain of an insect**. *PLoS One* 2011, **6**:e27855.
43. Bausenwein B, Fischbach K-F: **Activity labeling patterns in the medulla of *Drosophila melanogaster* caused by motion stimuli**. *Cell Tissue Res* 1992, **270**:25-35.
44. Beshers SN, Fewell JH: **Models of division of labor in social insects**. *Annu Rev Entomol* 2001, **46**:13-40.
45. Duarte A, Weissing FJ, Pen I, Keller L: **An evolutionary perspective on self-organized division of labor in social insects**. *Annu Rev Ecol Syst* 2011, **42**:91-110.
46. Scheiner R, Page RE, Erber J: **Sucrose responsiveness and behavioral plasticity in honey bees (*Apis mellifera*)**. *Apidologie* 2004, **35**:133-142.
47. Page RE Jr, Erber J, Fondrk MK: **The effect of genotype on response thresholds to sucrose and foraging behavior of honey bees (*Apis mellifera* L.)**. *J Comp Physiol A* 1998, **182**:489-500.
48. Pankiw T, Nelson M, Page RE, Fondrk MK: **The communal crop: modulation of sucrose response thresholds of pre-foraging honey bees with incoming nectar quality**. *Behav Ecol Sociobiol* 2004, **55**:286-292.
49. Month-Juris E, Ravaiano SV, Lopes DM, Salomão TMF, Martins GF: **Morphological assessment of the sensilla of the antennal flagellum in different castes of the stingless bee *Tetragonisca fiebrigi***. *J Zool* 2020, **310**:110-125.
50. Sharma KR, Enzmann BL, Schmidt Y, Moore D, Jones GR, Parker J, Berger SL, Reinberg D, Zwiebel LJ, Breit B: **Cuticular hydrocarbon pheromones for social behavior and their coding in the ant antenna**. *Cell Rep* 2015, **12**:1261-1271.
51. Balbuena MS, González A, Farina WM: **Characterization of cuticular hydrocarbons according to colony duties in the stingless bee *Tetragonisca angustula***. *Apidologie* 2018, **49**:185-195.
52. Greene MJ, Gordon DM: **Cuticular hydrocarbons inform task decisions**. *Nature* 2003, **423**:32.
53. Schulz DJ, Sullivan JP, Robinson GE: **Juvenile hormone and octopamine in the regulation of division of labor in honey bee colonies**. *Horm Behav* 2002, **42**:222-231.
54. Arenas A, Lajad R, Peng T, Grüter C, Farina W: **Correlation between octopaminergic signalling and foraging task specialisation in honeybees**. *Genes Brain Behav* 2021, **20**:e12718.
55. Scheiner R, Kulikovskaja L, Thamm M: **The honey bee tyramine receptor AmTYR1 and division of foraging labour**. *J Exp Biol* 2014, **217**:1215-1217.
56. Mercer AR, Menzel R: **The effects of biogenic amines on conditioned and unconditioned responses to olfactory stimuli in the honeybee *Apis mellifera***. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 1982, **145**:363-368.
57. Scheiner R, Reim T, Søvik E, Entler BV, Barron AB, Thamm M: **Learning, gustatory responsiveness and tyramine differences across nurse and forager honeybees**. *J Exp Biol* 2017, **220**:1443-1450.
58. Page RE, Erber J: **Levels of behavioral organization and the evolution of division of labor**. *Naturwissenschaften* 2002, **89**:91-106.
59. • Mc Cabe S, Ferro MWB, Farina WM, Hrnčir M: **Dose- and time-dependent effects of oral octopamine treatments on the sucrose responsiveness in stingless bees (*Melipona scutellaris*)**. *Apidologie* 2017, **48**:1-7.

The authors show for the first time in a stingless bee that biogenic amines affect sucrose responsiveness. A small dose of octopamine fed to *Melipona scutellaris* bees lowered the SRT. The effects were transient and depended on the dose of octopamine used.

60. Peng T, Schroeder M, Grüter C: **Octopamine increases individual and collective foraging in a neotropical stingless bee**. *Biol Lett* 2020, **16**:20200238.
61. Barron AB, Maleszka R, Vander Meer RK, Robinson GE: **Octopamine modulates honey bee dance behavior**. *Proc Natl Acad Sci USA* 2007, **104**:1703-1707.