

1     **Use of waggle dance information in honey bees is linked to gene expression**  
2                     **in the antennae, but not in the brain**

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25 **Abstract**

26 Communication is essential for social animals, but deciding how to utilize information provided  
27 by conspecifics is a complex process that depends on environmental and intrinsic factors.  
28 Honey bees use a unique form of communication, the waggle dance, to inform nestmates about  
29 the location of food sources. However, as in many other animals, experienced individuals often  
30 ignore this social information and prefer to rely on prior experiences, i.e. private information.  
31 The neurosensory factors that drive the decision to use social information are not yet  
32 understood. Here we test whether the decision to use social dance information or private  
33 information is linked to gene expression differences in different parts of the nervous system.  
34 We trained bees to collect food from sugar water feeders and observed whether they utilize  
35 social or private information when exposed to dances for a new food source. We performed  
36 transcriptome analysis of four brain parts critical for cognition: the subesophageal ganglion, the  
37 central brain, the mushroom bodies, and the antennal lobes but, unexpectedly, detected no  
38 differences between social or private information users. In contrast, we found 413 differentially  
39 expressed genes in the antennae, suggesting that variation in sensory perception mediate the  
40 decision to use social information. Social information users were characterized by the  
41 upregulation of dopamine and serotonin genes while private information users upregulated  
42 several genes coding for odor perception. These results highlight that decision making in honey  
43 bees might also depend on peripheral processes of perception rather than higher-order brain  
44 centers of information integration.

45

46 **Keywords**

47 Animal communication, information strategies, waggle dance, foraging, transcriptomics, brain  
48

## 49 **Introduction**

50 Exchanging information is essential in all animal societies. Communicating about  
51 resources, reproductive state, group membership, and threats are vital in ensuring the survival  
52 and success of the group. However, relying on social information is often not the only available  
53 option, e.g. to find a food source, but searching for a resource individually can often be the  
54 better choice (Laland, 2004; Kendal et al., 2009; Hoppitt & Laland, 2013; Dechaume-  
55 Moncharmont et al., 2005; I'Anson Price et al., 2019). Furthermore, an individual can rely on  
56 private information (e.g. spatial memory) about previously visited food source locations  
57 (Rendell et al., 2010; Grüter & Leadbeater, 2014). It is crucial for an organism to assess the  
58 different available options and their consequences to make the best decision in a given  
59 environment. Acquiring information through individual exploration, for instance, provides up-  
60 to-date information, but comes with the cost of trial-and-error learning. Social information  
61 avoids the costs of individual learning and exploration, but can involve the inefficient or  
62 erroneous transmission of information (Giraldeau et al., 2002; Dechaume-Moncharmont et al.,  
63 2005; Rieucou & Giraldeau, 2011; I'Anson Price et al., 2019). Thus, animals often employ  
64 flexible strategies for deciding between social or private information (Laland, 2004; Kendal et  
65 al., 2009; Hoppitt & Laland, 2013; Grüter & Leadbeater, 2014).

66 Social insects employ various methods to send signals to nestmates. Information  
67 exchange regarding resources is particularly well-studied and a wide range of communication  
68 behaviors are used, such as tandem running in ants (Alleman et al., 2019, Möglich et al., 1974;  
69 Glaser and Grüter, 2018) and trail pheromones in ants, and stingless bees (Jarau, 2009;  
70 Hölldobler & Wilson, 2009; Czaczkes et al., 2015). Honey bees (*Apis*) use a unique form of  
71 communication, the waggle dance that gives spatial information to nestmates about both  
72 distance and direction of a food source or a nest site in relation to the sun (von Frisch, 1967).  
73 In foraging, dances are performed by returning foragers as an advertisement for high quality  
74 food sources. Furthermore, waggle dancers emit floral odors and a blend of hydrocarbons that

75 provide additional information and stimulate foraging in unemployed foragers (Gilley et al.,  
76 2018; Thom et al., 2007; Farina et al., 2012). Only a relatively small percentage of waggle  
77 dance followers use dance information to discover new food sources. The majority of waggle  
78 dances trigger experienced foragers to resume foraging at already familiar food sources,  
79 disregarding social dance information for private spatial information (Biesmeijer & Seeley,  
80 2005; Grüter et al., 2008). While various factors, like experience (Richter & Waddington, 1993;  
81 Biesmeijer & Seeley, 2005; Grüter & Ratnieks, 2011; ) and age (Tofilski, 2009; Woyciechowski  
82 & Moroń, 2009) are likely to affect whether a bee uses social information, still little is known  
83 about the neuronal basis of dance communication and its use (Barron & Plath, 2017).

84 Numerous studies have shown that social insect behavior and responses to social  
85 information are linked to brain gene expression (Toth et al., 2010; Robinson et al., 2008; Zayed  
86 & Robinson, 2012; Ingram et al., 2011; Toth & Robinson, 2009). For example, foragers have a  
87 unique pattern of gene expression compared to nurses as they upregulate genes associated with  
88 synaptic plasticity and cognition (i.e spatial learning and memory), whereas nurses upregulate  
89 genes associated with intracellular signaling involved in the transition from nurse to forager  
90 (Whitfield et al., 2003). Even among foragers different gene expression patterns can be found.  
91 For example, pollen and nectar foragers differentially upregulate genes associated with  
92 regulating food intake (Brockmann et al., 2008). Behavioral variation within foragers seems to  
93 be strongly connected to the expression of genes that are important in biogenic amine signaling,  
94 such as dopamine, octopamine, tyramine, glutamate, and serotonin signaling (Liang et al., 2012;  
95 Scheiner et al., 2002; Schulz et al., 2003; Barron et al., 2002; Scheiner et al., 2017a). Indeed,  
96 manipulation of biogenic amine levels can alter foraging behavior (Liang et al., 2012; Peng et  
97 al., 2020; Linn et al., 2020) and perception of food rewards and odors (Mercer & Menzel, 1982;  
98 Barron et al., 2002; Scheiner et al., 2002). Most studies have focused on whole brains to reveal  
99 expression differences between behavioral groups (e.g. Whitfield et al., 2003; Liang et al.,  
100 2012; Alleman et al., 2019). However, different brain parts serve specific functions and are

101 expected to differ in gene expression. For example, the antennal lobes receive input from the  
102 olfactory sensory neurons in the antennae (Paoli et al., 2016) and process olfactory information  
103 (Homborg et al., 1989; MaBouDi et al., 2017; Paoli et al., 2016). Insect mushroom bodies are  
104 key brain areas for multimodal sensory integration, learning and memory (Strausfeld et al.,  
105 2009; Collett & Collett 2018), whereas the central brain supports foraging behavior via motor  
106 control (Hanesch et al., 1989). Barron and Plath (2017) have suggested that the central brain  
107 might play a crucial role in the decoding of waggle dance information. Finally, the  
108 subesophageal ganglion mediates reward and taste perception (Kreissl et al., 1994; Dacks et al.,  
109 2005; Sinakevitch et al., 2005).

110         If and how these different brain parts are involved in dance communication and  
111 information-use is not well understood. Furthermore, we still know little about the role of the  
112 peripheral nervous system for decision making and information processing (see e.g. Ozaki et  
113 al., 2005). The antennae, in particular, play important functions in social insect behavior, both  
114 within and outside the colony, such as mediating pheromone signaling (Nagari & Bloch, 2012;  
115 Vergoz et al., 2009; Grozinger et al., 2003; Pankiw, 2004), nestmate recognition (Ozaki et al.,  
116 2005; van Zweden & D’Ettorre, 2010) and odor learning (Robertson et al., 2006; Rogers &  
117 Vallortigara, 2008). An important role of the antennae in mediating different behaviors is also  
118 likely to explain why foragers and nurses show distinct antennal expression of chemical sensory  
119 and biogenic amine genes (Nie et al., 2018; McQuillan et al., 2012). Chemical stimuli  
120 differentiation and odor perception are not only important for task differentiation (Arenas &  
121 Farina, 2012; Balbuena & Farina, 2020), but could play a role in the decision to use social or  
122 private information (Thom et al., 2007).

123         Here we compared the gene expression of bees that used dance information (social  
124 information, SI) with those that preferred private information (PI) in different brain areas and  
125 the antennae in the honey bee *Apis mellifera*. We trained cohorts of workers to sucrose solution

126 feeders and, subsequently, confronted them with conflicting social information about a new  
127 high-quality food source. As was shown for scouts, *i.e.* foragers that search for new food  
128 sources independently (Liang et al., 2012), we predicted that there are distinct neurogenomic  
129 signatures underlying the decision to use either social or private information. We compared  
130 different brain and peripheral chemosensory areas in both types of bees. We demonstrate that  
131 bees that decode and use waggle dance information differ in gene expression only in the  
132 antennae and provide evidence for roles of biogenic amine signaling and olfactory perception.

133

## 134 **Materials and Methods**

### 135 Colony Set-up

136 A total of six observation hives of *Apis mellifera carnica* were studied from August through  
137 October 2016 (H1 – H3) and 2018 (C1 -C3), each containing approximately 2000-3000 workers  
138 of mixed ages. Colonies were established from the Johannes Gutenberg University apiary in  
139 Mainz, Germany, a few weeks prior to the start of experiments. Each of the observation colonies  
140 contained three frames, brood, food reserves and were headed by a naturally mated queen.

### 141 Training

142 Training was conducted one colony at a time. Workers were trained according to standard  
143 training procedures to collect sucrose solution at one of two artificial feeders (von Frisch, 1967;  
144 Linn et al., 2020). First, a cohort of 50-60 workers was trained to the training feeder (T.F.).  
145 These workers were used as the samples that would later be designated as either social or private  
146 information users on test day. Then, a smaller cohort of ~20 foragers was trained to the dance  
147 feeder (D.F.). These workers would be designated as dancers on test day. Both feeders were  
148 150m from the observation colonies with ca. 160 meters separating the training and dance  
149 feeder (see Linn et al., 2020, their Fig. 1). Workers were trained to their respective feeder with  
150 an unscented 0.8M sucrose solution and were individually marked with a number tag on the  
151 thorax. This spatial arrangement ensured that workers would visit only one feeder and no

152 mixing of individuals between dance and training feeders occurred. The day after training, the  
153 sucrose solution was reduced to 0.3M at both feeders with the addition of an identical scent  
154 (5 $\mu$ L of essential oil /100mL sucrose solution). This concentration made sure that trained  
155 foragers would return to their respective feeder, but not recruit additional bees. Colonies were  
156 trained to a different odor: C1, H1 = sage, C2, H2 = jasmine, C3, H3 = peppermint. During 60  
157 minutes, workers were allowed to visit their feeder repeatedly (2016:  $5.24 \pm 3.79$  visits, N =  
158 191; 2018:  $8.09 \pm 5.17$  visits, N = 102). The 60-minute training with scented solution allowed  
159 workers to associate reward, scent, and location of the respective feeder.

### 160 Sample Collection

161 On the test day, the day after the 60-minute odor training, 2M sucrose solution with the same  
162 scent as used during training was offered only at the dance feeder location, while the training  
163 feeder was empty. The sucrose concentration at the dance feeder was high to induce the  
164 collecting foragers to perform waggle dances. T.F. trained workers could then decide whether  
165 to use social information by following the waggle dances performed by the returning dancers  
166 (fly to the D.F.) or disregard the dance vector information and use private information (return  
167 to the T.F.). The arrival time and capture time of each individual bee was recorded. Dance and  
168 dance following behavior were recorded in the observation colony using a high definition  
169 camera to quantify dance following behavior by T.F. foragers. Workers trained to the T.F. that  
170 arrived at the D.F location were collected in Eppendorf tubes and immediately preserved in  
171 liquid nitrogen; these workers were the social information users. Workers trained to the T.F.  
172 feeder that arrived at the T.F. feeder location were collected at a similar time; these workers  
173 were the private information users.

### 174 Video Analysis

175 Videos were analyzed using VLC Media Player. Dances and dance following behaviors were  
176 analyzed frame by frame. A worker was only counted as following a dance when she was within  
177 one antennal length of a marked dancer during the waggle run phase (Grüter et al., 2013; Linn

178 et al., 2020), which is the component of the waggle dance that encodes the vector information  
179 (von Frisch, 1967). We compared the dance following behavior of private and social  
180 information users with linear mixed-effects models (LME and GLMM's). The nlme-package  
181 and linear mixed-effects models (LMEs) were used when the response variable was normally  
182 distributed (waggles per dance followed). The lme4-package and generalized linear mixed-  
183 effects models (GLMMs) were used when the response variable had a Poisson distribution (total  
184 number of dances followed) (Zuur et al., 2009). Colony-ID and year (2016 and 2018) were  
185 included as hierarchically nested random effects to account for their effects (Zuur et al., 2009).

### 186 Brain Dissection and RNA Extraction

187 In 2016, we dissected the calyxes of the mushroom bodies and antennal lobes from 14 workers  
188 (7 social information users and 7 private information users, 2-3 per colony and type). We  
189 confirmed that all social information users followed dances extensively. In 2018 we dissected  
190 central brains and subesophageal ganglions from 16 workers (8 social information users and 8  
191 private information users, 2-3 per colony and type), and the antennae from 11 different workers  
192 (1-4 per colony and type) (see Fig. 1 in Sen Sarma et al., 2009 for a schematic representation  
193 of the brain areas and cut-off lines). The additional handling of the samples after being flash  
194 frozen in liquid nitrogen caused the antennae of some samples to be brittle and easily break  
195 apart. Different workers were used to ensure that whole antennae could be used for equal  
196 extraction of RNA from all samples.

197 Heads from individual workers were cut from the body and fixed on melted dental wax  
198 in a pre-chilled petri dish over ice. The antennae were cut off and stored in 100 mL of TRIzol™  
199 (Invitrogen, USA). Incisions were made at the antennal base, around the eyes, through the  
200 compound eye, and the ocellus. The cuticles, glands, retina and tissue around the brain were  
201 removed and the exposed tissues of the head were submerged with cooled bee saline (154 mM  
202 NaCl, 2 mM NaH<sub>2</sub>PO<sub>4</sub>, 5.5 mM Na<sub>2</sub>HPO<sub>4</sub>, pH 7.2). Subesophageal ganglion and central brain



203 (which included the mushroom body peduncles, the bundled axons from the Kenyon Cells in  
204 the calyces), were removed by cutting off optic lobes, antennal lobes, and mushroom body  
205 calyces. All tissues called “mushroom body” refer to mushroom body calyces as it is extremely  
206 difficult to remove mushroom body peduncles. The calyces contain the intrinsic Kenyon cells,  
207 where a large part of mushroom body transcription takes place and, therefore, the calyces are  
208 often used to study mushroom body gene expression (Sarma et al., 2009; Reim & Scheiner,  
209 2014; Humphries et al., 2003). Furthermore, the tissue called “central brain” refers to a brain  
210 region that also includes the mushroom body peduncles and putative differences in expression  
211 in this tissue should be interpreted carefully because of the different functions of these tissues.  
212 Each dissection was completed in less than 5 minutes to prevent RNA degradation. Brain parts  
213 were stored in 100 mL of Trizol™ (Invitrogen, USA) in -80 °C for later RNA extraction using  
214 RNAeasy Mini Extraction Kit™ (Qiagen, Germany) according to the manufacturers’ protocol.

### 215 Transcriptome Analysis

216 For sequencing, aliquots of RNA from private and social information users were sent to Beijing  
217 Genomics Institute (BGI) for library construction and sequencing. In 2016, Hiseq 4000 was  
218 used to sequence 100 base pair (bp) paired-end reads, obtaining 40 Mio clean reads per  
219 sample. The total sample size was 28. In 2018, BGISEq was used to sequence 100 base pair  
220 (bp) paired-end reads, obtaining 70 Mio clean reads per sample. The sequencing failed for 1  
221 sample and 1 sample was damaged during the travel (Eppendorf tube burst), decreasing our  
222 total sample size to 41. Raw reads were quality checked using *FastQC* v.0.11.8 (Andrews et  
223 al., 2010) followed by Illumina adapter removal using *Trimmomatic* v.0.38. (Bolger et al.,  
224 2014). Clean reads were aligned using *HiSat2* v.2.1.0 (Kim et al., 2017) to the honey bee  
225 genome HvA3.1 as a reference (Wallberg et al., 2019). To count how many aligned reads  
226 mapped to genes, we used *HtSeq* v.0.11.2 (Anders et al., 2015) to generate count tables. Count  
227 tables for each part were analyzed separately for gene expression differences between social  
228 and private information users using the R package *DESeq2* v.1.24.0 (Love et al., 2014). Before

229 the analysis, an additional filtering step was added to ensure that only genes with counts of at  
230 least 10 reads in at least 6 samples (n-1 of the smallest sample size) were used in the gene  
231 expression analysis. Information strategies were compared using the likelihood ratio test (LRT)  
232 approach whereby a full model with information type (SI or PI) and colony-ID as fixed factors  
233 is compared with a reduced model containing only colony-ID, taking into consideration colony  
234 effects. Genes were considered differentially expressed if the false discovery rate (FDR)  
235 corrected p-value was  $< 0.05$ . To ensure that the number of DEGs calculated by *DESeq2* were  
236 not due to chance and to account for the uneven number of samples across bee types and  
237 colonies for the antennae, we additionally performed permutations by switching samples from  
238 opposite information user groups while maintaining colony structure (see methods in Libbrecht  
239 et al., 2016). For example, a sample from the same colony was switched for a different  
240 information user group and the number and distribution of DEGs was compared to those  
241 calculated from our model in *DESeq2*. We performed 28 permutations (14 times switching two  
242 samples for each group and 14 times switching three samples for each group) and recorded the  
243 number of DEGs in each permutation. We then compared this number to the numbers for all  
244 possible combinations of our samples to assess the number of DEGs that could be expected by  
245 chance.

246 We used the R package *DEGreport* v.1.20.0 (Pantano, 2019) to visualize any patterns  
247 for all genes going into the analyses and to identify clustering patterns across social and private  
248 information users by using the *rlog* function of *DESeq2* to generate normalized count data and  
249 the default settings. PCAs (principal components analysis) based on all genes were performed  
250 for all tissues to visualize variation between samples. All analysis were performed in R v.3.5.0  
251 (R Developmental Core Team, 2019).

252 *Gene Ontology Enrichment*

253 DEGs were loaded in a BLAST search on the NCBI database against the honey bee genome  
254 HVA3.1 to find gene annotations. To further obtain information about Gene Ontology (GO)  
255 (Ashburner et al., 2000) and KEGG pathway (Ogata et al., 1999) enrichment we used  
256 InterProScan v.5.36-75.0 (Jones et al., 2014) on the protein sequences. The R package *topGo*  
257 v.2.36.0 (Alexa & Rahnenfuhrer, 2016) was used to perform an enrichment analysis of GO  
258 terms and a Fisher's exact test was performed on the list of biological processes.

259

## 260 **Results**

### 261 *Dance following of social and private information users*

262 Dance following behavior was analyzed by combining data collected from video analysis for  
263 both years. Using a linear mixed-effects model, we found that SI bees followed fewer dances  
264 than PI bees during the testing period ( $5 \pm 0.7559$  vs.  $7.091 \pm 1.546$  dances) (LME: t-value =  
265 2.218;  $p = 0.0396$ ). However, SI bees followed dances for longer (more waggle runs per dance)  
266 than PI bees ( $27.214 \pm 4.089$  vs.  $30.818 \pm 6.5$ ) (GLMM: z-value = -2.122;  $p = 0.0338$ ).

### 267 *Gene Expression Analysis*

268 The likelihood ratio test (LRT) comparison of information use strategies revealed no differences  
269 in gene expression between the two information user groups in the central brain, antennal lobes,  
270 and subesophageal ganglion (Fig. 1). There was only one differentially expressed gene between  
271 social and private information users from our mushroom body calyxes' samples, which encodes  
272 for an uncharacterized protein ( $p = 0.026$ , gene ID: rna-XR\_003305479.1). However, there  
273 were 413 differentially expressed genes in the antennae, 318 were higher expressed in social  
274 information users and 95 were higher expressed in private information users. To confirm these  
275 substantial differences in gene expression in the antennae, we used permutations of samples to  
276 assess how this affects the number of DEGs in the antennae. The permutations showed that only  
277 very few DEGs were found when 2-3 samples were swapped between the SI and PI groups  
278 within their respective colonies (colony ID as fixed factor:  $11.89 \pm 31.87$ ,  $N = 28$ ; colony ID

279 not included:  $3.25 \pm 7.01$ ,  $N = 28$ ) (Fig. S1). This confirms that the substantial differences in  
280 gene expression in the antennae are linked to whether bees belonged to the SI or the PI group.  
281 PCA plots used transformed data of all genes to further explore whether there is a clustering of  
282 samples based on information use strategies and colony. While a clustering pattern based on  
283 information use and colony can be seen for the antennae (Fig. 1), the other tissues showed no  
284 clear clustering according to information use.

285 Exploring the list of DEGs in the antennae revealed that numerous odorant binding and  
286 chemosensory proteins differed in their expression in social and private information users.  
287 Specifically, we detected five genes for odorant or chemical perception among the upregulated  
288 genes in private information users (*odorant binding protein 5,11, 19,7 and chemosensory*  
289 *protein 1*) and two among the upregulated genes in social information users (*odorant binding*  
290 *protein 7 and chemosensory protein 2*) (Fig. 2). Several genes involved in biogenic amine  
291 production or signaling were also differentially expressed. Social information users had a higher  
292 expression of *tyrosine kinase Btk29A; dopamine N-acetyltransferase, tryptophan 5-*  
293 *hydroxylase 1*, which are involved in the production of dopamine or serotonin (Vavricka et al.,  
294 2014; Coleman et al., 2005; Sasaki et al., 2012), while private information users had a higher  
295 expression of one gene *tyramine receptor, transcript variant XI*, which is associated with  
296 biogenic amine signaling (Mustard et al., 2005; Blenau et al., 2000) (Fig. 3). Social information  
297 users also had higher expression of the egg yolk precursor protein *vitellogenin*, a gene that is  
298 upregulated in nurses and downregulated in foragers fat bodies and brain (Amdam et al., 2002;  
299 Nunes et al., 2013) (Fig. 3).

### 300 Gene function and enrichment analysis

301 Separate GO enrichment analyses of only upregulated genes for each information strategy  
302 showed a small number of enriched functions: 9 biological processes enriched in social  
303 information users connected mainly on *carbohydrate (10 genes) and lipid (7) metabolic*

304 *process* and 18 enriched biological processes in private information users focused on  
305 *oxidation-reduction process (7) and protein catabolic process (11)*.

306

## 307 **Discussion**

308 Information and its use in animals is an important topic in behavior, ecology, and  
309 evolution because information is a critical currency that allows animals to make adaptive  
310 decisions in a given situation (e.g. Danchin et al., 2004; Dall et al., 2005; Rieucan & Giraldu,  
311 2011; Hoppitt & Laland, 2013). The decision of when to utilize social versus private  
312 information to best exploit potential opportunities while avoiding costs is crucial for success  
313 and has been studied within a variety of both social and non-social animals (e.g. Bonnie &  
314 Earley, 2007; Weimerskirch et al., 2010; Grüter & Ratnieks, 2011; Wray et al., 2011; Taborsky  
315 & Oliveira, 2012; Haak et al., 2020). However, it is still unclear if and how molecular and  
316 neurosensory factors determine an individual's preference for social or private information.

317 Here we explore whether gene expression differences between honey bee foragers are  
318 linked to the use of social or private information about food sources to uncover the potential  
319 molecular mechanisms that underlie the decision to decode and use waggle dances in honey  
320 bees. Contrary to our prediction, the transcriptomes of all four analyzed brain parts did not  
321 differ between bees using these two foraging strategies. Strikingly, however, we found  
322 substantial gene expression differences in the antennae. Over 400 genes were differentially  
323 expressed between social and private information users, suggesting that the sensory perception  
324 of these two forager types differs. This is further supported by expression differences related to  
325 odorant binding proteins, chemosensory proteins, and genes associated with biogenic amine  
326 production.

327           The lack of differences in the brain areas was unexpected given that Liang et al. (2012)  
328 found extensive differences in whole-brain gene expression between scouts and non-scout  
329 foragers (in their study, non-scout foragers could have included both private and social  
330 information users). We expected the mushroom bodies to show differences since it has  
331 previously been shown that they are involved in multisensory integration, learning, and place  
332 memory (e.g. Strausfeld et al., 2009; Collett & Collett, 2018). The antennal lobes are involved  
333 in odor recognition and memory through the interconnectivity of neurons with the mushroom  
334 body and were thus selected as another area of interest (Boeckh & Tolbert, 1993). The central  
335 brain has been suggested as an important area for dance communication (Barron & Plath, 2017),  
336 while the subesophageal ganglion plays important roles in reward perception and taste (Galizia  
337 et al., 2011). Together, these brain regions were thought to process reward and odor perception  
338 which could play an important role in the decision to use dance information. Our study indicates  
339 that information use strategies may not primarily depend on integration of information in higher  
340 order centers, but that the antennae play a major role in decision-making when facing  
341 communication signals.

342           The 413 differentially expressed genes in the antennae present an array of gene families  
343 and functions. Of particular interest are genes coding for odorant binding proteins and those  
344 involved in biogenic amine production and signaling due to their potential roles in  
345 chemosensory perception. Thus, differences in the perception of chemosensory information  
346 cues and signals could result in divergent foraging strategies. While our study cannot  
347 disentangle whether gene expression is the cause or the consequence of the information use  
348 strategy, they suggest that chemosensory perception by the antennae could be involved in the  
349 decision to decode waggle dances and use social information. In many social insects, the  
350 antennae play an integral role in social recognition (Ozaki et al., 2005; Sharma et al., 2015;  
351 Balbuena & Farina, 2020). Studies in *Oecophylla smaragdina*, for instance, indicated that the  
352 density of antennal sensilla is important in regulating behavior, particularly in determining the

353 aggression response behavior to non-nestmates (Gill et al., 2013; Chol e et al., 2019). Similar to  
354 other social insects, honey bee foragers first use their antennae to perceive and respond to a  
355 variety of chemical signals for navigation (Menzel & Greggers, 2013), efficient nectar/pollen  
356 collection (Arenas & Farina, 2012), and dance communication (Thom et al., 2007; Reinhard &  
357 Srinivasan, 2009; Gilley et al., 2012).

358 By transporting odorants, e.g. from antennal sensilla to odorant receptors, odorant  
359 binding proteins (OBPs) play important roles for olfactory sensitivity (Leal, 2013). They are  
360 hypothesized to be important in insect communication (Pelosi et al., 2005), including in the  
361 honey bee which use highly complex odors and pheromones to regulate their social activities  
362 (Farina et al., 2012; Baracchi et al., 2020). Of the 21 OBPs found in the honey bee, only 9 are  
363 exclusively expressed in the antennae. The remaining OBPs are active throughout the honey  
364 bee body or specific non-olfactory tissues (For t & Maleszka, 2006). Our analysis revealed that  
365 workers which rely on private information in the form of spatial memory show higher  
366 expression of four odorant binding proteins (*obp5*, *obp11*, *obp19*, and *obp7*), whereas workers  
367 that rely on socially acquired information upregulate one (*obp7*). Thus, ~25% of all OBPs found  
368 in honey bees were differentially expressed. Of the OBPs that were upregulated in private  
369 information users, *obp5* and *obp11* have been previously shown to be exclusively expressed in  
370 the antennae and suggest a chemosensory function (For t & Maleszka, 2006). Interestingly,  
371 *obp11* is mainly expressed in a rare type of antennal sensilla found only in female honey bees,  
372 the *sensilla basiconica*, and is likely to facilitate the function of these sensilla (Kucharski et al.,  
373 2016). While the ligand of *obp11* remains unknown, there is evidence that the *sensilla*  
374 *basiconica* play important roles in the perception of cuticular hydrocarbons (CHCs) in ants  
375 (Sharma et al., 2015) and may play a similar role in honey bees (Kucharski et al., 2016). This  
376 is remarkable because CHCs emitted by dancing bees are known to trigger the use of private  
377 information in honey bees (Thom et al., 2007; Gilley et al., 2012). This raises the possibility  
378 that a higher expression of *obp11* increases the sensitivity of bees towards CHCs emitted by

379 waggle dancers, thereby triggering private information use. The remaining differentially  
380 expressed OBPs (*obp19* and *obp7*) have been shown to be ubiquitously expressed, which  
381 suggests they may have additional molecular functions which we currently do not know.  
382 Overall, these results indicate a difference in perceptual sensitivity where workers which use  
383 private information perceive some chemosensory stimuli more or differently than social  
384 information users. This could have far reaching consequences for their behavior given the role  
385 that odors play in the decision-making and information use of a forager, e.g. in the identification  
386 and learning of floral resources or the perception of cuticular hydrocarbons (von Frisch, 1967;  
387 Johnson, 1967; Reinhard et al., 2004; Grüter et al., 2008; Gilley et al., 2012).

388         Chemosensory proteins serve a similar role as OBPs in transporting chemical stimuli  
389 through mechanisms that are not yet well understood. These proteins are heavily concentrated  
390 in antennal sensilla but are also expressed in non-olfactory tissues (Forêt et al., 2007; Calvello  
391 et al., 2005). Of the six chemosensory proteins found in honey bees (McKenzie et al., 2014),  
392 two were differentially expressed in social and private information users, chemosensory  
393 proteins 1 and 2. Both chemosensory proteins have been shown to be highly expressed in the  
394 antennae (Li et al., 2016), which further supports the view that the differences between the  
395 information strategies may be rooted in chemoreception.

396         Biogenic amines have been associated with regulating learning, foraging behavior, and  
397 the transition from in-hive tasks to foraging (Lehman et al. 2006). Biogenic amine signaling is  
398 known to change with age and tissue location in honey bees (e.g. McQuillan et al., 2012; Perry  
399 & Barron, 2013; Reim & Scheiner, 2014; Thamm et al., 2017). Specifically, dopamine,  
400 serotonin, octopamine, and tyramine titers in the brain were found to be linked to both task and  
401 age (Schulz & Robinson, 1999; Barron et al., 2002; Harris & Woodring, 1991; Kokay & Mercer,  
402 1997). For example, tyramine levels have been linked to novelty seeking in scouting behavior  
403 (Cook et al., 2018; Liang et al. 2012), sucrose responsiveness (Scheiner et al., 2002; 2017a;



404 2017b), and division of labor between nectar and pollen foragers (Hunt et al., 1995; Scheiner  
405 et al., 2001). Dopamine has been shown to modulate sucrose responsiveness (Scheiner et al.,  
406 2002), learning (Vergoz et al., 2007) and dance following (Linn et al., 2020), whereas serotonin  
407 influences foraging activity (Schulz et al., 2003) and regulates feeding in many animals (French  
408 et al., 2014; Blundell & Halford, 1998; Voigt & Fink, 2015). Our findings of an upregulation  
409 of genes associated with biogenic amine production, raise the possibility that social information  
410 users could differ in their sensory perception as well as sucrose response thresholds compared  
411 to private information users. It is noteworthy, however, that the differences we found in relation  
412 to biogenic amine signaling were not in the brain. Instead, higher expression of several genes  
413 associated with dopamine and serotonin production was found in the antennae of social  
414 information users. We did not control for foraging age or experience, which have already been  
415 shown to affect gene biogenic amine expression (Reim & Scheiner, 2014). However, the lack  
416 of differential expression in brain areas suggests that there was no systematic age bias in our  
417 samples.

418 Another interesting differentially expressed gene, *vitellogenin*, is best known as an egg  
419 yolk precursor protein for egg laying organisms. Under normal conditions in social insects, the  
420 queen is the main reproductive member and therefore produces the highest levels of  
421 *vitellogenin*. However, *vitellogenin* serves important roles for other behaviors and functions  
422 outside of reproduction (Nelson et al., 2007; Morandin et al., 2014). For example, nurses  
423 produce the next highest levels of *vitellogenin* in their hypopharyngeal glands to fortify brood  
424 food with protein (Amdam et al., 2003; Amdam et al., 2009; Wegener & Bienefeld, 2009). A  
425 characteristic feature of the transition from nurse to forager is the drop in vitellogenin levels  
426 (Amdam et al., 2003; Messan et al., 2018). Our finding is consistent with evidence that biogenic  
427 amine levels are linked to *vitellogenin* and foraging behavior (Linn et al., 2020; Koywiwattrakul  
428 et al., 2005), where social information have a similar physiological state to nurses.

429           Intrinsic factors such as genetic differences could also affect the decision to decode  
430 waggle dances. Honey bee queens can mate with more than 20 drones (Strassman, 2001), and  
431 the patriline composition of our samples is not known. It is well-known that different patrilines  
432 can differ in foraging behaviors, such as foraging age (Kolmes et al., 1989). Paternal effects  
433 can also impact gustatory responsiveness and learning abilities (Scheiner et al., 1999; 2001;  
434 2005; Behrends et al., 2007; Scheiner & Arnold, 2009). It is unclear whether systematic  
435 patriline differences in the composition of PI and SI bees would lead to differential gene  
436 expression only in the antennae, but future studies should explore whether bees using private  
437 or social information differ in their patrilines.

438           Overall, our results suggest an important role of the antennae in mediating decision-  
439 making and information use. In particular, we suggest a link between chemosensory perception  
440 and the reliance on communication in honey bees. Further studies are needed to disentangle the  
441 potential effects of genetic differences (i.e. different patrilines), differences in foraging  
442 experience, and other factors on gene expression. In addition, we need studies to confirm our  
443 hypothesis that SI and PI bees differ in sensory perception such as sucrose response thresholds,  
444 odor learning, and electroantennograms.

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### **Author Contributions**

458 A.K., T.P., M.L., S.M.G., S.F. and C.G. conceived the study and designed the experiments.  
459 A.K., T.P., M.L. and S.M.G. conducted the field experiments. T.P., M.L. and S.M.G. performed  
460 all honey bee brain dissections and RNA extractions. T.P. and A.K. worked together on gene  
461 expression analysis. Data analysis was supported by S.F. and C.G. A.K. wrote the first draft of  
462 the manuscript, all authors contributed to writing the final version.

### **Data Accessibility**

463 All of the supplemental material and additional data generated and used throughout this  
464 project may be found within the Dryad repository  
465 <https://doi.org/XX.XXXX/dryad.XXXXXXX>, which contains the following: dance following  
466 information for all samples, lists of differentially expressed genes for all brain tissues,  
467 InterProScan annotation of gene lists and GO enrichments from all antenna samples. All  
468 sequencing data will be deposited in the Sequencing Read Archive (SRA) of the NCBI upon  
469 acceptance.  
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### **Conflict of Interest**

472 We declare no conflict of interest for this study.  
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475 **References**

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477 Alexa, A., & Rahnenfuhrer, J. (2018). TOPGO: Enrichment analysis for gene ontology.R  
478 package version 2.28.0.

479 Alleman, A., Stoldt, M., Feldmeyer, B., & Foitzik, S. (2019). Tandem-running and scouting  
480 behaviour are characterized by up-regulation of learning and memory formation genes within  
481 the ant brain. *Molecular Ecology*, 28, 2342-2359. doi: 10.1111/mec.15079

482 Amdam, G. V., Norberg, K., Hagen, A., & Omholt, S. W. (2003). Social exploitation of  
483 vitellogenin. *Proceedings of the National Academy of Sciences*, 100, 1799-1802. doi:  
484 10.1073/pnas.0333979100

485 Amdam, G. V., Rueppell, O., Fondrk, M. K., Page, R. E., & Nelson, C. M. (2009). The  
486 nurse's load: early-life exposure to brood-rearing affects behavior and lifespan in honey bees  
487 (*Apis mellifera*). *Experimental Gerontology*, 44, 467-471. Doi: 10.1016/j.exger.2009.02.013

488 Anders, S., Pyl, P. T., & Huber, W. (2015). HTSeq—a Python framework to work with high-  
489 throughput sequencing data. *Bioinformatics*, 31, 166-169. doi: 10.1093/bioinformatics/btu638

490 Andrews, S. (2010). FastQC: A quality control tool for high throughput sequence data.  
491 Retrieved from <http://www.bioinformatics.babraham.ac.uk/projects/fastqc>

492 Arenas, A., & Farina, W. M. (2012). Learned olfactory cues affect pollen-foraging  
493 preferences in honeybees, *Apis mellifera*. *Animal Behaviour*, 83, 1023-1033. doi:  
494 10.1016/j.anbehav.2012.01.026

495 Ashburner, M., Ball, C. A., Blake, J. A., Botstein, D., Butler, H., Cherry, J. M., ... & Harris,  
496 M. A. (2000). Gene ontology: tool for the unification of biology. *Nature Genetics*, 25, 25-29.  
497 doi: 10.1038/75556

498 Balbuena, M. S., & Farina, W. M. (2020). Chemosensory reception in the stingless bee  
499 *tetragonisca angustula*. *Journal of Insect Physiology*, 125, 104076. doi:  
500 10.1016/j.jinsphys.2020.104076

501 Baracchi, D., Cabirol, A., Devaud, J. M., Haase, A., d’Ettorre, P., & Giurfa, M. (2020).  
502 Pheromone components affect motivation and induce persistent modulation of associative  
503 learning and memory in honey bees. *Communications Biology*, 3, 1-9. doi: 10.1038/s42003-  
504 020-01183-x

505 Barron, A. B., & Plath, J. A. (2017). The evolution of honey bee dance communication: a  
506 mechanistic perspective. *Journal of Experimental Biology*, 220, 4339-4346.  
507 doi:10.1242/jeb.142778

508 Barron, A., Schulz, D., & Robinson, G. (2002). Octopamine modulates responsiveness to  
509 foraging-related stimuli in honey bees (*Apis mellifera*). *Journal of Comparative Physiology*  
510 *A*, 188, 603-610. doi: 10.1007/s00359-002-0335-5

- 511 Behrends, A., Scheiner, R., Baker, N., & Amdam, G. V. (2007). Cognitive aging is linked to  
512 social role in honey bees (*Apis mellifera*). *Experimental Gerontology*, *42*, 1146-1153. doi:  
513 10.1016/j.exger.2007.09.003
- 514 Biesmeijer, J. C., & Seeley, T. D. (2005). The use of waggle dance information by honey bees  
515 throughout their foraging careers. *Behavioral Ecology and Sociobiology*, *59*, 133-142. doi:  
516 10.1007/s00265-005-0019-6
- 517 Blenau, W., Balfanz, S., & Baumann, A. (2000). *Amyr1*: characterization of a gene from  
518 honeybee (*Apis mellifera*) brain encoding a functional tyramine receptor. *Journal of*  
519 *Neurochemistry*, *74*, 900-908. doi: 10.1046/j.1471-4159.2000.0740900.x
- 520 Blundell, J. E., & Halford, J. C. (1998). Serotonin and appetite regulation. *CNS Drugs*, *9*, 473-  
521 495. Doi: 10.2165/00023210-199809060-00005
- 522 Boeckh, J., & Tolbert, L. P. (1993). Synaptic organization and development of the antennal  
523 lobe in insects. *Microscopy Research and Technique*, *24*, 260-280. doi:  
524 10.1002/jemt.1070240305
- 525 Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: a flexible trimmer for Illumina  
526 sequence data. *Bioinformatics*, *30*, 2114-2120. doi: 10.1093/bioinformatics/btu170
- 527 Bonnie, K. E., & Earley, R. L. (2007). Expanding the scope for social information  
528 use. *Animal Behaviour*, *74*, 171-181. doi: 10.1016/j.anbehav.2006.12.009
- 529 Brockmann, A., Annangudi, S. P., Richmond, T. A., Ament, S. A., Xie, F., Southey, B. R., ...  
530 & Sweedler, J. V. (2009). Quantitative peptidomics reveal brain peptide signatures of  
531 behavior. *Proceedings of the National Academy of Sciences*, *106*, 2383-2388. doi:  
532 10.1073/pnas.0813021106
- 533 Calvello, M., Brandazza, A., Navarrini, A., Dani, F. R., Turillazzi, S., Felicioli, A., & Pelosi,  
534 P. (2005). Expression of odorant-binding proteins and chemosensory proteins in some  
535 hymenoptera. *Insect Biochemistry & Molecular Biology*, *35*, 297-307. doi:  
536 10.1016/j.ibmb.2005.01.002
- 537 Cholé, H., Carcaud, J., Mazeau, H., Famié, S., Arnold, G., & Sandoz, J. C. (2019). Social  
538 contact acts as appetitive reinforcement and supports associative learning in  
539 honeybees. *Current Biology*, *29*, 1407-1413. doi: 10.1016/j.cub.2019.03.025
- 540 Coleman, C. M., & Neckameyer, W. S. (2005). Serotonin synthesis by two distinct enzymes  
541 in *Drosophila melanogaster*. *Archives of Insect Biochemistry and Physiology: Published in*  
542 *Collaboration with the Entomological Society of America*, *59*, 12-31. doi: 10.1002/arch.20050
- 543 Collett, M., & Collett, T. S. (2018). How does the insect central complex use mushroom body  
544 output for steering? *Current Biology*, *28*, R733-R734. doi: 10.1016/j.cub.2018.05.060
- 545 Cook, C. N., Mosquero, T., Brent, C. S., Ozturk, C., Gadau, J., & Pinter-Wollman, N., et al.  
546 (2018). Individual differences in learning and biogenic amine levels influence the behavioural  
547 division between foraging honey bee scouts and recruits. *Journal of Animal Ecology*, *88*, 236-  
548 246 doi: 10.1111/1365-2656.12911

- 549 Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. (2015). Trail pheromones: an integrative view of  
550 their role in social insect colony organization. *Annual review of entomology*, *60*, 581-599.  
551 doi:10.1146/annurev-ento-010814-020627
- 552 Dacks, A. M., Christensen, T. A., Agricola, H. J., Wollweber, L., & Hildebrand, J. G. (2005).  
553 Octopamine-immunoreactive neurons in the brain and subesophageal ganglion of the  
554 hawkmoth *Manduca sexta*. *Journal of Comparative Neurology*, *488*, 255-268. doi:  
555 10.1002/cne.20556
- 556 Dall, S. R., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005).  
557 Information and its use by animals in evolutionary ecology. *Trends in Ecology &*  
558 *Evolution*, *20*, 187-193. doi: 10.1016/j.tree.2005.01.010
- 559 Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information:  
560 from nosy neighbors to cultural evolution. *Science*, *305*, 487-491. doi:  
561 10.1126/science.1098254
- 562 Dechaume-Moncharmont, F. X., Dornhaus, A., Houston, A. I., McNamara, J. M., Collins, E.  
563 J., & Franks, N. R. (2005). The hidden cost of information in collective foraging. *Proceedings*  
564 *of the Royal Society B: Biological Sciences*, *272*, 1689-1695. doi: 10.1098/rspb.2005.3137
- 565 Farina, W. M., Grüter, C., & Arenas, A. (2012). Olfactory information transfer during  
566 recruitment in honey bees. In G.C. Galizia, D. Eisenhardt & M. Giurfa (Eds.), *Honeybee*  
567 *Neurobiology and Behavior* (pp. 89-101). Dordrecht: Springer.
- 568 Forêt, S., & Maleszka, R. (2006). Function and evolution of a gene family encoding odorant  
569 binding-like proteins in a social insect, the honey bee (*Apis mellifera*). *Genome Research*, *16*,  
570 1404-1413. doi: 10.1101/gr.5075706
- 571 Forêt, S., Wanner, K. W., & Maleszka, R. (2007). Chemosensory proteins in the honey bee:  
572 insights from the annotated genome, comparative analyses and expressional profiling. *Insect*  
573 *Biochemistry & Molecular Biology*, *37*, 19-28. doi: 10.1016/j.ibmb.2006.09.009
- 574 French, A. S., Simcock, K. L., Rolke, D., Gartside, S. E., Blenau, W., & Wright, G. A.  
575 (2014). The role of serotonin in feeding and gut contractions in the honeybee. *Journal of*  
576 *insect physiology*, *61*, 8-15. doi: 10.1016/j.jinsphys.2013.12.005
- 577 Galizia, C. G., Eisenhardt, D., & Giurfa, M. (2011). *Honeybee Neurobiology and Behavior: A*  
578 *Tribute to Randolph Menzel*. Heidelberg: Springer.
- 579 Gill, K. P., van Wilgenburg, E., Macmillan, D. L., & Elgar, M. A. (2013). Density of antennal  
580 sensilla influences efficacy of communication in a social insect. *The American*  
581 *Naturalist*, *182*, 834-840. doi: 10.1086/673712
- 582 Gilley, D. C., Kuzora, J. M., & Thom, C. (2012). Hydrocarbons emitted by waggle-dancing  
583 honey bees stimulate colony foraging activity by causing experienced foragers to exploit  
584 known food sources. *Apidologie*, *43*, 85-94. doi: 10.1007/s13592-011-0080-2
- 585 Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using  
586 socially acquired information. *Philosophical Transactions of the Royal Society of London.*  
587 *Series B: Biological Sciences*, *357*, 1559-1566. doi: 10.1098/rstb.2002.1065

- 588 Glaser, S. M., & Grüter, C. (2018). Ants (*Temnothorax nylanderi*) adjust tandem running  
589 when food source distance exposes them to greater risks. *Behavioral Ecology and*  
590 *Sociobiology*, *72*, 40. doi: 10.1007/s00265-018-2453-2
- 591 Grozinger, C. M., Sharabash, N. M., Whitfield, C. W., & Robinson, G. E. (2003). Pheromone-  
592 mediated gene expression in the honey bee brain. *Proceedings of the National Academy of*  
593 *Sciences*, *100*, 14519-14525. doi: 10.1073/pnas.2335884100
- 594 Grüter, C., & Leadbeater, E. (2014). Insights from insects about adaptive social information  
595 use. *Trends in Ecology & Evolution*, *29*, 177-184. doi: 10.1016/j.tree.2014.01.004
- 596 Grüter, C., & Ratnieks, F. L. (2011). Honeybee foragers increase the use of waggle dance  
597 information when private information becomes unrewarding. *Animal Behaviour*, *81*, 949-954.  
598 doi: 10.1016/j.anbehav.2011.01.014
- 599 Grüter, C., Balbuena, M. S., & Farina, W. M. (2008). Informational conflicts created by the  
600 waggle dance. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 1321-1327. doi:  
601 10.1098/rspb.2008.0186
- 602 Haak, C. R., Hui, F. K., Cowles, G. W., & Danylchuk, A. J. (2020). Positive interspecific  
603 associations consistent with social information use shape juvenile fish  
604 assemblages. *Ecology*, *101*, e02920. doi: 10.1002/ecy.2920
- 605 Hanesch, U., Fischbach, K. F., & Heisenberg, M. (1989). Neuronal architecture of the central  
606 complex in *Drosophila melanogaster*. *Cell and Tissue Research*, *257*, 343-366. doi:  
607 10.1007/BF00261838
- 608 Harris, J. W., & Woodring, J. (1992). Effects of stress, age, season, and source colony on  
609 levels of octopamine, dopamine and serotonin in the honey bee (*Apis mellifera* L.)  
610 brain. *Journal of Insect Physiology*, *38*, 29-35. doi: 10.1016/0022-1910(92)90019-A
- 611 Hölldobler, B., & Wilson, E. O. (2009). *The Superorganism: the Beauty, Elegance, and*  
612 *Strangeness of Insect Societies*. New York: WW Norton & Company.
- 613 Homberg, U., Christensen, T. A., & Hildebrand, J. G. (1989). Structure and function of the  
614 deutocerebrum in insects. *Annual Review of Entomology*, *34*, 477-501. doi:  
615 10.1146/annurev.en.34.010189.002401
- 616 Hoppitt, W., & Laland, K. N. (2013). *Social Learning: An Introduction to Mechanisms,*  
617 *Methods, and Models*. Princeton: Princeton University Press.
- 618 Humphries, M. A., Mustard, J. A., Hunter, S. J., Mercer, A., Ward, V., & Ebert, P. R. (2003).  
619 Invertebrate D2 type dopamine receptor exhibits age-based plasticity of expression in the  
620 mushroom bodies of the honeybee brain. *Journal of Neurobiology*, *55*, 315-330. doi:  
621 10.1002/neu.10209
- 622 Hunt, G. J., Page, R. E., Fondrk, M. K., & Dullum, C. J. (1995). Major quantitative trait loci  
623 affecting honey bee foraging behavior. *Genetics*, *141*, 1537-1545. doi:  
624 10.1002/gcc.2870140411

- 625 I'Anson Price, R., Dulex, N., Vial, N., Vincent, C., & Grüter, C. (2019). Honeybees forage  
626 more successfully without the “dance language” in challenging environments. *Science*  
627 *Advances*, 5, eaat0450. doi: 10.1126/sciadv.aat0450
- 628 Ingram, K. K., Kleeman, L., & Peteru, S. (2011). Differential regulation of the foraging gene  
629 associated with task behaviors in harvester ants. *BMC Ecology*, 11, 1-9. doi: 10.1186/1472-  
630 6785-11-19
- 631 Jarau, S. (2009) Chemical communication during food exploitation in stingless bees. In S.  
632 Jarau & M. Hrncir (Eds.), *Food Exploitation by Social Insects: Ecological, Behavioral, and*  
633 *Theoretical Approaches* (pp. 223-249). Boca Raton: CRC Press.
- 634 Johnson, D. L. (1967). Communication among honey bees with field experience. *Animal*  
635 *behaviour*, 15, 487-492. doi: 10.1016/0003-3472(67)90048-6
- 636 Jones, P., Binns, D., Chang, H. Y., Fraser, M., Li, W., McAnulla, C., ... & Pesseat, S. (2014).  
637 InterProScan 5: genome-scale protein function classification. *Bioinformatics*, 30, 1236-1240.  
638 doi: 10.1093/bioinformatics/btu031
- 639 Kendal, J., Giraldeau, L. A., & Laland, K. (2009). The evolution of social learning rules:  
640 payoff-biased and frequency-dependent biased transmission. *Journal of Theoretical*  
641 *Biology*, 260, 210-219. doi: 10.1016/j.jtbi.2009.05.029
- 642 Kim, D., Langmead, B., & Salzberg, S. (2017). HISAT2: graph-based alignment of next-  
643 generation sequencing reads to a population of genomes. Baltimore, MD: Johns Hopkins  
644 University. *Center for Computational Biology*. doi: 10.1101/012591
- 645 Kokay, I. C., & Mercer, A. R. (1997). Age-related changes in dopamine receptor densities in  
646 the brain of the honey bee, *Apis mellifera*. *Journal of Comparative Physiology A*, 181, 415-  
647 423. doi: 10.1007/s003590050125
- 648 Kolmes, S. A., Winston, M. L., & Fergusson, L. A. (1989). The division of labor among  
649 worker honey bees (Hymenoptera: Apidae): the effects of multiple patriline. *Journal of the*  
650 *Kansas Entomological Society*, 62, 80-95. doi: 10.1016/0022-1910(89)90027-9
- 651 Koywiwattrakul, P., Thompson, G. J., Sitthipraneed, S., Oldroyd B. P., Maleszka, R. (2005).  
652 Effects of carbon dioxide narcosis on ovary activation and gene expression in worker  
653 honeybees, *Apis mellifera*. *Journal of Insect Science*, 5, 1-10. doi: 10.1093/jis/5.1.36
- 654 Kreissl, S., Eichmüller, S., Bicker, G., Rapus, J., & Eckert, M. (1994). Octopamine-like  
655 immunoreactivity in the brain and subesophageal ganglion of the honeybee. *Journal of*  
656 *Comparative Neurology*, 348, 583-595. doi: 10.1002/cne.903480408
- 657 Kucharski, R., Maleszka, J., & Maleszka, R. (2016). A possible role of DNA methylation in  
658 functional divergence of a fast evolving duplicate gene encoding odorant binding protein 11  
659 in the honeybee. *Proceedings Biological Sciences*, 283, 20160558. doi:  
660 10.1098/rspb.2016.0558
- 661 Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, 32, 4-14. doi:  
662 [10.3758/BF03196002](https://doi.org/10.3758/BF03196002)



- 663 Leal, W. S. (2013). Odorant reception in insects: roles of receptors, binding proteins, and  
664 degrading enzymes. *Annual Review of Entomology*, *58*, 373-391. doi: 10.1146/annurev-ento-  
665 120811-153635
- 666 Lehman, H. K., Schulz, D. J., Barron, A. B., Wraight, L., Hardison, C., Whitney, S., ...  
667 Robinson, G. E. (2006). Division of labor in the honey bee (*Apis mellifera*): the role of  
668 tyramine  $\beta$ -hydroxylase. *Journal of Experimental Biology*, *209*, 2774-2784. doi:  
669 10.1242/jeb.02296
- 670 Li, H. L., Ni, C. X., Tan, J., Zhang, L. Y., & Hu, F. L. (2016). Chemosensory proteins of the  
671 eastern honeybee, *Apis cerana*: identification, tissue distribution and olfactory related  
672 functional characterization. *Comparative Biochemistry and Physiology Part B: Biochemistry  
673 and Molecular Biology*, *194*, 11-19. doi: 10.1016/j.cbpb.2015.11.014
- 674 Liang, Z. S., Nguyen, T., Mattila, H. R., Rodriguez-Zas, S. L., Seeley, T. D., & Robinson, G.  
675 E. (2012). Molecular determinants of scouting behavior in honey bees. *Science*, *335*, 1225-  
676 1228. doi: 10.1126/science.1213962
- 677 Libbrecht, R., Oxley, P. R., Keller, L., & Kronauer, D. J. C. (2016). Robust DNA methylation  
678 in the clonal raider ant brain. *Current Biology*, *26*, 391-395. Doi: 10.1016/j.cub.2015.12.040
- 679 Linn, M., Glaser, S. M., Peng, T., & Grüter, C. (2020). Octopamine and dopamine mediate  
680 waggle dance following and information use in honeybees. *Proceedings of the Royal Society  
681 B*, *287*, 20201950. doi: 10.1098/rspb.2020.1950
- 682 Love, M., Huber, W., & Anders, S. (2014). Moderated estimation of fold change and  
683 dispersion for RNA-seq data with DESeq2. *Genome Biology*, *15*, 1165-1186. doi:  
684 10.1186/s13059-014-0550-8
- 685 Maboudi, M., Amini, J., Hahn, M., & Saati, M. (2017). Object-based road extraction from  
686 satellite images using ant colony optimization. *International Journal of Remote Sensing*, *38*,  
687 179-198. doi: 10.1080/01431161.2016.1264026
- 688 McKenzie, S. K., Oxley, P. R., & Kronauer, D. J. (2014). Comparative genomics and  
689 transcriptomics in ants provide new insights into the evolution and function of odorant  
690 binding and chemosensory proteins. *BMC Genomics*, *15*, 718. doi: 10.1186/1471-2164-15-  
691 718
- 692 McQuillan, H. J., Barron, A. B., & Mercer, A. R. (2012). Age-and behaviour-related changes  
693 in the expression of biogenic amine receptor genes in the antennae of honey bees (*Apis  
694 mellifera*). *Journal of Comparative Physiology A*, *198*, 753-761. doi: 10.1007/s00359-012-  
695 0745-y
- 696 Menzel, R., & Greggers, U. (2013). Guidance by odors in honeybee navigation. *Journal of  
697 Comparative Physiology A Neuroethology Sensory Neural and Behavioral physiology*, *199*,  
698 867-873. doi: 10.1007/s00359-013-0850-6
- 699 Mercer, A. R. & Menzel, R. (1982). The effects of biogenic amines on conditioned and  
700 unconditioned responses to olfactory stimuli in the honeybee *Apis mellifera*. *Journal of  
701 Comparative Physiology*, *145*, 363-368. doi: 10.1007/BF00619340

- 702 Messan, M. R., Page Jr, R. E., & Kang, Y. (2018). Effects of vitellogenin in age polyethism  
703 and population dynamics of honeybees. *Ecological Modelling*, 388, 88-107. doi:  
704 10.1016/j.ecolmodel.2018.09.011
- 705 Möglich, M., Maschwitz, U., & Hölldobler, B. (1974). Tandem calling: a new kind of signal  
706 in ant communication. *Science*, 186, 1046-1047. doi: 10.1126/science.186.4168.1046
- 707 Morandin, C., Havukainen, H., Kulmuni, J., Dhaygude, K., Trontti, K., & Helanterä, H.  
708 (2014). Not only for egg yolk—functional and evolutionary insights from expression,  
709 selection, and structural analyses of Formica ant vitellogenins. *Molecular Biology and*  
710 *Evolution*, 31, 2181-2193. doi: 10.1093/molbev/msu171
- 711 Mustard, J. A., Kurshan, P. T., Hamilton, I. S., Blenau, W., & Mercer, A. R. (2005).  
712 Developmental expression of a tyramine receptor gene in the brain of the honey bee, *Apis*  
713 *mellifera*. *Journal of Comparative Neurology*, 483, 66-75. doi: 10.1002/cne.20420
- 714 Nagari, M., & Bloch, G. (2012). The involvement of the antennae in mediating the brood  
715 influence on circadian rhythms in “nurse” honey bee (*Apis mellifera*) workers. *Journal of*  
716 *Insect Physiology*, 58, 1096-1103. doi: 10.1016/j.jinsphys.2012.05.007
- 717 Nelson, C. M., Ihle, K. E., Fondrk, M. K., Page, R. E., & Amdam, G. V. (2007). The gene  
718 *vitellogenin* has multiple coordinating effects on social organization. *PLoS Biology*, 5, e86.  
719 doi: 10.1371/journal.pbio.0050062
- 720 Nie, H., Xu, S., Xie, C., Geng, H., Zhao, Y., Li, J., ... & Su, S. (2018). Comparative  
721 transcriptome analysis of *Apis mellifera* antennae of workers performing different  
722 tasks. *Molecular Genetics and Genomics*, 293, 237-248. doi: 10.1007/s00438-017-1382-5
- 723 Nunes, F. M. F., Ihle, K. E., Mutti, N. S., Simoes, Z. L. P., & Amdam, G. V. (2013). The gene  
724 vitellogenin affects microrna regulation in honey bee (*Apis mellifera*) fat body and  
725 brain. *Journal of Experimental Biology*, 216, 3724-3732. doi: 10.1242/jeb.089243
- 726 Ogata, H., Goto, S., Sato, K., Fujibuchi, W., Bono, H., & Kanehisa, M. (1999). KEGG: Kyoto  
727 encyclopedia of genes and genomes. *Nucleic Acids Research*, 27(1), 29-34. doi:  
728 10.1093/nar/27.1.29
- 729 Ozaki, M., Wada-Katsumata, A., Fujikawa, K., Iwasaki, M., Yokohari, F., Satoji, Y., ... &  
730 Yamaoka, R. (2005). Ant nestmate and non-nestmate discrimination by a chemosensory  
731 sensillum. *Science*, 309, 311-314. doi: 10.1126/science.1105244
- 732 Pankiw, T., Roman, R., Sagili, R. R., & Zhu-Salzman, K. (2004). Pheromone-modulated  
733 behavioral suites influence colony growth in the honey bee (*Apis*  
734 *mellifera*). *Naturwissenschaften*, 91(12), 575-578. doi: 10.1007/s00114-004-0568-y
- 735 Pantano Lorena. DEGREport: Report of DEG analysis. (2019)
- 736 Paoli, M., Weisz, N., Antolini, R., & Haase, A. (2016). Spatially resolved time-frequency  
737 analysis of odour coding in the insect antennal lobe. *European Journal of Neuroscience*, 44,  
738 2387-2395. doi: [10.1111/ejn.13344](https://doi.org/10.1111/ejn.13344)

- 739 Paoli, M., Weisz, N., Antolini, R., & Haase, A. (2016). Spatially resolved time-frequency  
740 analysis of odour coding in the insect antennal lobe. *European Journal of Neuroscience*, *44*,  
741 2387-2395. doi: 10.1111/ejn.13344
- 742 Pelosi, P., Calvello, M., & Ban, L. (2005). Diversity of odorant-binding proteins and  
743 chemosensory proteins in insects. *Chemical Senses*, *30*, i291-i292. doi:  
744 10.1093/chemse/bjh229
- 745 Peng, T., Schroeder, M., & Grüter, C. (2020). Octopamine increases individual and collective  
746 foraging in a neotropical stingless bee. *Biology Letters*, *16*, 20200238. doi:  
747 10.1098/rsbl.2020.0238
- 748 Perry, C. J., & Barron, A. B. (2013). Neural mechanisms of reward in insects. *Annual Review*  
749 *of Entomology*, *58*, 543-562. doi: 10.1146/annurev-ento-120811-153631
- 750 R Core Team. (2018). R: *A language and environment for statistical computing*. Vienna,  
751 Austria: R Foundation for Statistical Computing. [https:// www.R-project.org/](https://www.R-project.org/)
- 752 Reim, T., & Scheiner, R. (2014). Division of labour in honey bees: age-and task-related  
753 changes in the expression of octopamine receptor genes. *Insect Molecular Biology*, *23*, 833-  
754 841. doi: 10.1111/imb.12130
- 755 Reinhard, J., & Srinivasan, M. V. (2009). The role of scents in honey bee foraging and  
756 recruitment. In S. Jarau & M. Hrncir (Eds.), *Food Exploitation by Social Insects: Ecological,*  
757 *Behavioral, and Theoretical Approaches* (pp. 165-182). Boca Raton: CRC Press.
- 758 Reinhard, J., Srinivasan, M. V., & Zhang, S. (2004). Scent-triggered navigation in  
759 honeybees. *Nature*, *427*, 411-411. doi: 10.1038/427411a
- 760 Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., ... & Laland,  
761 K. N. (2010). Why copy others? Insights from the social learning strategies  
762 tournament. *Science*, *328*, 208-213. doi: 10.1126/science.1184719
- 763 Richter, M. R., & Waddington, K. D. (1993). Past foraging experience influences honey bee  
764 dance behaviour. *Animal Behaviour*, *46*, 123-128. doi: 10.1006/anbe.1993.1167
- 765 Rieucan, G., & Giraldeau, L. A. (2011). Exploring the costs and benefits of social information  
766 use: an appraisal of current experimental evidence. *Philosophical Transactions of the Royal*  
767 *Society B: Biological Sciences*, *366*, 949-957. doi: 10.1098/rstb.2010.0325
- 768 Robertson, H. M., & Wanner, K. W. (2006). The chemoreceptor superfamily in the honey  
769 bee, *Apis mellifera*: expansion of the odorant, but not gustatory, receptor family. *Genome*  
770 *Research*, *16*, 1395-1403. doi: 10.1101/gr.5057506
- 771 Robinson, G. E., Fernald, R. D., & Clayton, D. F. (2008). Genes and social  
772 behavior. *Science*, *322*, 896-900. doi: 10.1126/science.1159277
- 773 Rogers, L. J., & Vallortigara, G. (2008). From antenna to antenna: lateral shift of olfactory  
774 memory recall by honeybees. *PLoS One*, *3*, e2340. doi: 10.1371/journal.pone.0002340
- 775 Sarma, M. S., Rodriguez-Zas, S. L., Hong, F., Zhong, S., & Robinson, G. E. (2009).  
776 Transcriptomic profiling of central nervous system regions in three species of honey bee

- 777 during dance communication behavior. *PLoS One*, 4, e6408. doi:  
778 10.1371/journal.pone.0006408
- 779 Sasaki, K., Matsuyama, S., Harano, K. I., & Nagao, T. (2012). Caste differences in dopamine-  
780 related substances and dopamine supply in the brains of honeybees (*Apis mellifera*  
781 L.). *General and Comparative Endocrinology*, 178, 46-53. doi: 10.1016/j.ygcen.2012.04.006
- 782 Scheiner, R., & Arnold, G. (2010). Effects of patriline on gustatory responsiveness and  
783 olfactory learning in honey bees. *Apidologie*, 41, 29-37. doi: 10.1051/apido/2009040
- 784 Scheiner, R., Entler, B. V., Barron, A. B., Scholl, C., & Thamm, M. (2017a). The effects of  
785 fat body tyramine level on gustatory responsiveness of honeybees (*Apis mellifera*) differ  
786 between behavioral castes. *Frontiers in Systems Neuroscience*, 11, 55. doi:  
787 10.3389/fnsys.2017.00055
- 788 Scheiner, R., Erber, J., & Page Jr, R. E. (1999). Tactile learning and the individual evaluation  
789 of the reward in honey bees (*Apis mellifera* L.). *Journal of Comparative Physiology A*, 185, 1-  
790 10. doi: 10.1007/s003590050360
- 791 Scheiner, R., Kuritz-Kaiser, A., Menzel, R., & Erber, J. (2005). Sensory responsiveness and  
792 the effects of equal subjective rewards on tactile learning and memory of  
793 honeybees. *Learning & Memory*, 12, 626-635. doi: 10.1101/lm.98105
- 794 Scheiner, R., Page Jr, R. E., & Erber, J. (2001). The effects of genotype, foraging role, and  
795 sucrose responsiveness on the tactile learning performance of honey bees (*Apis mellifera*  
796 L.). *Neurobiology of Learning and Memory*, 76, 138-150. doi: 10.1006/nlme.2000.3996
- 797 Scheiner, R., Plückerhahn, S., Öney, B., Blenau, W., & Erber, J. (2002). Behavioural  
798 pharmacology of octopamine, tyramine and dopamine in honey bees. *Behavioural Brain*  
799 *Research*, 136, 545-553. doi: 10.1016/S0166-4328(02)00205-X
- 800 Scheiner, R., Reim, T., Sjøvik, E., Entler, B. V., Barron, A. B., & Thamm, M. (2017b).  
801 Learning, gustatory responsiveness and tyramine differences across nurse and forager  
802 honeybees. *Journal of Experimental Biology*, 220(8), 1443-1450. doi: 10.1242/jeb.152496
- 803 Schulz, D. J., & Robinson, G. E. (1999). Biogenic amines and division of labor in honey bee  
804 colonies: behaviorally related changes in the antennal lobes and age-related changes in the  
805 mushroom bodies. *Journal of Comparative Physiology A*, 184, 481-488. doi:  
806 10.1007/s003590050348
- 807 Schulz, D. J., Elekonich, M. M., & Robinson, G. E. (2003). Biogenic amines in the antennal  
808 lobes and the initiation and maintenance of foraging behavior in honey bees. *Journal of*  
809 *Neurobiology*, 54, 406-416. doi: 10.1002/neu.10138
- 810 Sharma, K. R., Enzmann, B. L., Schmidt, Y., Moore, D., Jones, G. R., Parker, J., ... & Liebig,  
811 J. (2015). Cuticular hydrocarbon pheromones for social behavior and their coding in the ant  
812 antenna. *Cell Reports*, 12, 1261-1271. doi: 10.1016/j.celrep.2015.07.031
- 813 Sinakevitch, I., Niwa, M., & Strausfeld, N. J. (2005). Octopamine-like immunoreactivity in  
814 the honey bee and cockroach: Comparable organization in the brain and subesophageal  
815 ganglion. *Journal of Comparative Neurology*, 488, 233-254. doi: 10.1002/cne.20572

- 816 Strassmann, J. (2001). The rarity of multiple mating by females in the social  
817 Hymenoptera. *Insectes Sociaux*, 48, 1-13. doi: 10.1007/PL00001737
- 818 Strausfeld, N. J., Sinakevitch, I., Brown, S. M., & Farris, S. M. (2009). Ground plan of the  
819 insect mushroom body: functional and evolutionary implications. *Journal of Comparative*  
820 *Neurology*, 513, 265-291. doi: 10.1002/cne.21948
- 821 Taborsky, B., & Oliveira, R. F. (2012). Social competence: an evolutionary approach. *Trends*  
822 *in Ecology & Evolution*, 27, 679-688. doi: 10.1016/j.tree.2012.09.003
- 823 Thamm, M., Scholl, C., Reim, T., Grübel, K., Möller, K., Rössler, W., & Scheiner, R. (2017).  
824 Neuronal distribution of tyramine and the tyramine receptor AmTAR1 in the honeybee  
825 brain. *Journal of Comparative Neurology*, 525, 2615-2631. doi: 10.1002/cne.24228
- 826 Thom, C., Gilley, D. C., Hooper, J., & Esch, H. E. (2007). The scent of the waggle  
827 dance. *PLoS Biology*, 5, e228. doi: 10.1371/journal.pbio.0050228
- 828 Tofilski, A. (2009). Shorter-lived workers start foraging earlier. *Insectes Sociaux*, 56, 359-  
829 366. doi: 10.1007/s00040-009-0031-3
- 830 Toth, A. L., & Robinson, G. E. (2009). Evo-devo and the evolution of social behavior: brain  
831 gene expression analyses in social insects. *Cold Spring Harbor Symposia on Quantitative*  
832 *Biology*, 74, 419-426. doi: 10.1101/sqb.2009.74.026
- 833 Toth, A. L., Varala, K., Henshaw, M. T., Rodriguez-Zas, S. L., Hudson, M. E., & Robinson,  
834 G. E. (2010). Brain transcriptomic analysis in paper wasps identifies genes associated with  
835 behaviour across social insect lineages. *Proceedings of the Royal Society B: Biological*  
836 *Sciences*, 277, 2139-2148. doi: 10.1098/rspb.2010.0090
- 837 van Zweden, J. S., & d'Etterre, P. (2010). Nestmate recognition in social insects and the role  
838 of hydrocarbons. In G. J. Blomquist (Eds.), *Insect Hydrocarbons: Biology, Biochemistry and*  
839 *Chemical Ecology* (pp. 222-243). Cambridge: Cambridge University Press.
- 840 Vavricka, C. J., Han, Q., Mehere, P., Ding, H., Christensen, B. M., & Li, J. (2014). Tyrosine  
841 metabolic enzymes from insects and mammals: a comparative perspective. *Insect Science*, 21,  
842 13-19. doi: 10.1111/1744-7917.12038
- 843 Vergoz, V., McQuillan, H. J., Geddes, L. H., Pullar, K., Nicholson, B. J., Paulin, M. G., &  
844 Mercer, A. R. (2009). Peripheral modulation of worker bee responses to queen mandibular  
845 pheromone. *Proceedings of the National Academy of Sciences*, 106, 20930-20935. doi:  
846 10.1073/pnas.0907563106
- 847 Vergoz, V., Roussel, E., Sandoz, J. C., & Giurfa, M. (2007). Aversive learning in honeybees  
848 revealed by the olfactory conditioning of the sting extension reflex. *PloS One*, 2, e288. doi:  
849 10.1371/journal.pone.0000288
- 850 Voigt, J. P., & Fink, H. (2015). Serotonin controlling feeding and satiety. *Behavioural Brain*  
851 *Research*, 277, 14-31. doi: 10.1016/j.bbr.2014.08.065
- 852 Von Frisch, K. (1967) *The Dance Language and Orientation of Bees*. Cambridge: Harvard  
853 University Press.

- 854 Wallberg, A., Bunikis, I., Pettersson, O. V., Mosbech, M. B., Childers, A. K., Evans, J. D., ...  
855 & Webster, M. T. (2019). A hybrid de novo genome assembly of the honeybee, *Apis*  
856 *mellifera*, with chromosome-length scaffolds. *BMC Genomics*, *20*, 275. doi: 10.1186/s12864-  
857 019-5642-0
- 858 Wegener, J., Lorenz, M. W., & Bienefeld, K. (2009). Physiological consequences of  
859 prolonged nursing in the honey bee. *Insectes Sociaux*, *56*, 85-93. doi: 10.1007/s00040-008-  
860 1042-1
- 861 Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C., & Goya, E. (2010). Use of social  
862 information in seabirds: compass rafts indicate the heading of food patches. *PloS One*, *5*,  
863 e9928. doi: 10.1371/journal.pone.0009928
- 864 Whitfield, C. W., Cziko, A. M., & Robinson, G. E. (2003). Gene expression profiles in the  
865 brain predict behavior in individual honey bees. *Science*, *302*, 296-299. doi:  
866 10.1126/science.1086807
- 867 Woyciechowski, M., & Moroń, D. (2009). Life expectancy and onset of foraging in the  
868 honeybee (*Apis mellifera*). *Insectes Sociaux*, *56*, 193-201. doi: 10.1007/s00040-009-0012-6
- 869 Wray, M. K., Klein, B. A., & Seeley, T. D. (2012). Honey bees use social information in  
870 waggle dances more fully when foraging errors are more costly. *Behavioral Ecology*, *23*, 125-  
871 131. doi: 10.1093/beheco/arr165
- 872 Zayed, A., & Robinson, G. E. (2012). Understanding the relationship between brain gene  
873 expression and social behavior: lessons from the honey bee. *Annual Review of Genetics*, *46*,  
874 591-615. doi: 10.1146/annurev-genet-110711-155517
- 875 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects*  
876 *Models and Extensions in Ecology with R*. New York: Springer.
- 877

878

879 **Figure 1:** Principal Component Analysis (PCA) plots displaying variance between individual  
880 samples based on all genes for each tissue type. Samples are organized by color according to  
881 information use strategy (blue = social, red = private) and shapes by colony ID (circles = colony  
882 1, triangles = colony 2, squares = colony 3).

883

884 **Figure 2:** Plots of individual odorant binding protein (OBP) and chemosensory protein (CSP)  
885 genes. Black dots show counts for individual samples and shapes correspond to the colony ID  
886 (circle = colony1, triangle = colony 2, square = colony 3). Colored circles are representative  
887 of the average for the respective information strategy (red = private, blue = social) with  
888 confidence intervals. A) OBP11 ( $p < 0.001$ ) B) OBP19 ( $p = 0.001$ ) C) OBP5 ( $p = 0.03$ ) D) OBP7  
889 ( $p < 0.001$ ) E) CSP1 ( $p = 0.009$ ) F) CSP2 ( $p = 0.007$ ). P-values shown are after FDR correction.

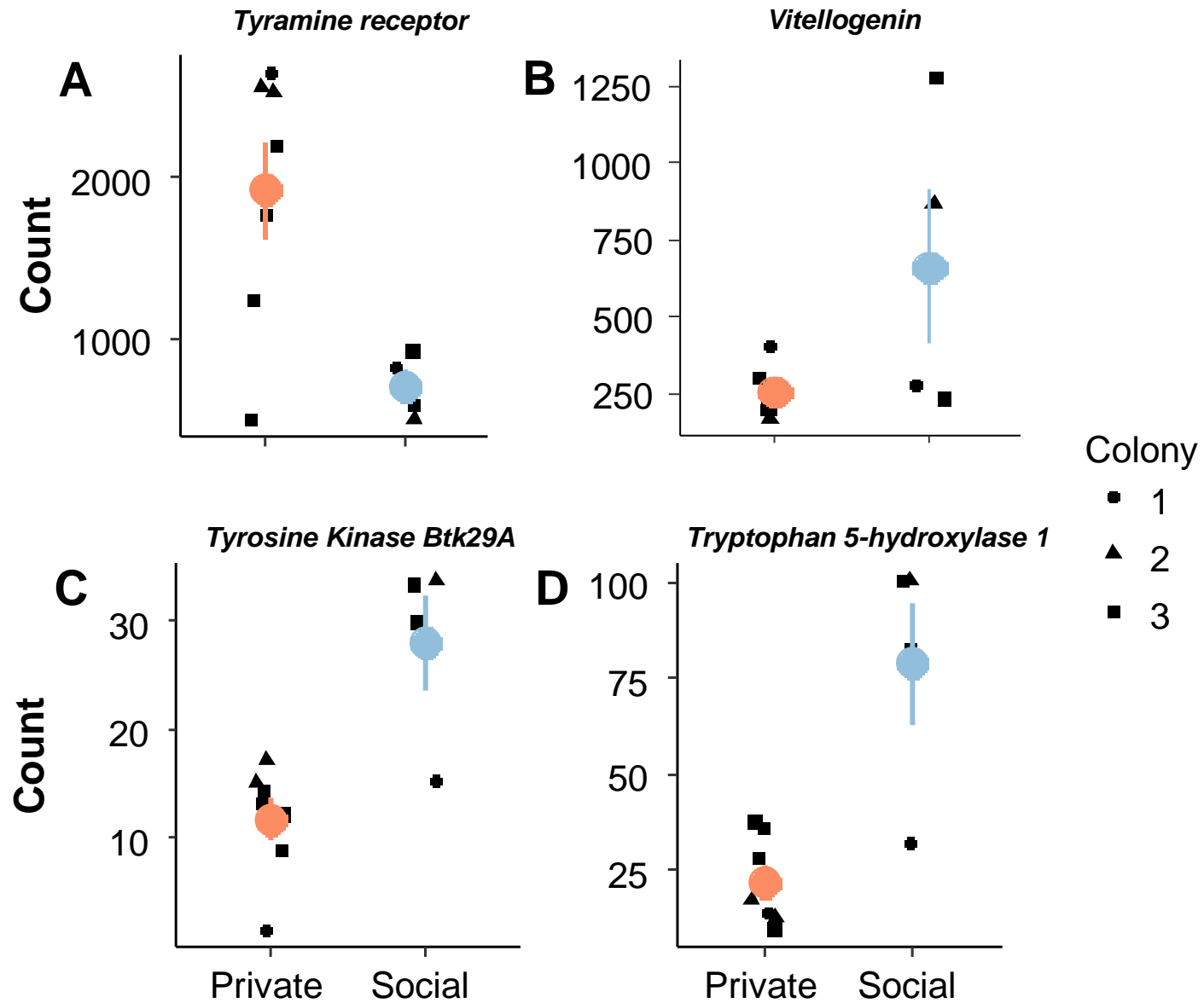
890

891 **Figure 3:** Plots of individual genes associated with biogenic amine production and  
892 reproduction. Black dots show counts for individual samples and shapes correspond to the  
893 colony ID (circle = colony1, triangle = colony 2, square = colony 3). Colored circles are  
894 representative of the average for the respective information strategy (red = private, blue =  
895 social) with confidence intervals. A) Tyramine receptor ( $p = 0.018$ ) B) Vitellogenin ( $p = 0.045$ )  
896 C) Tyrosine Kinase Btk29A ( $p = 0.006$ ) D) Tryptophan 5-hydroxylase 1 ( $p < 0.001$ ). p-values  
897 shown are after FDR correction.

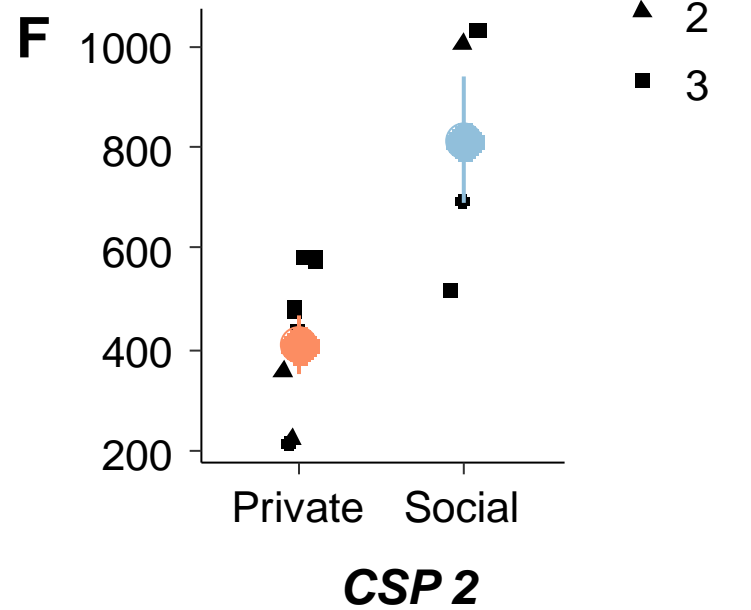
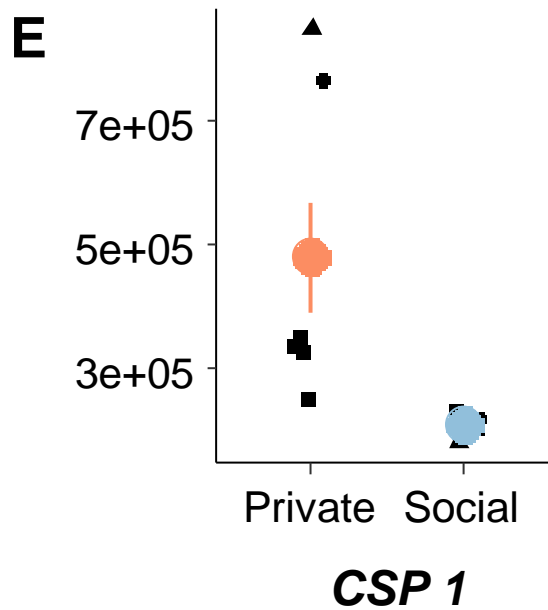
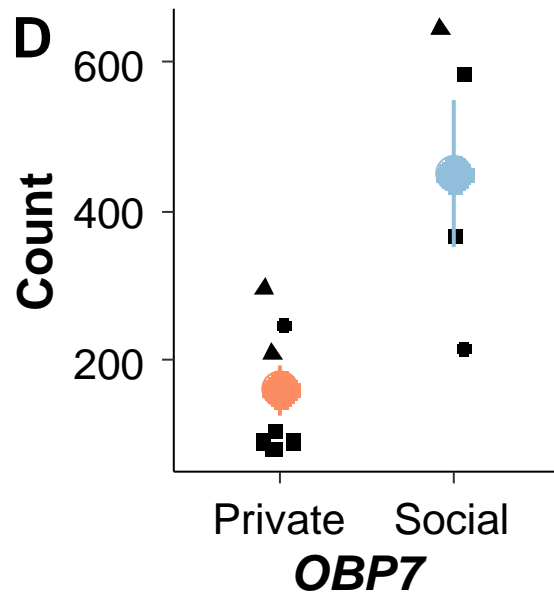
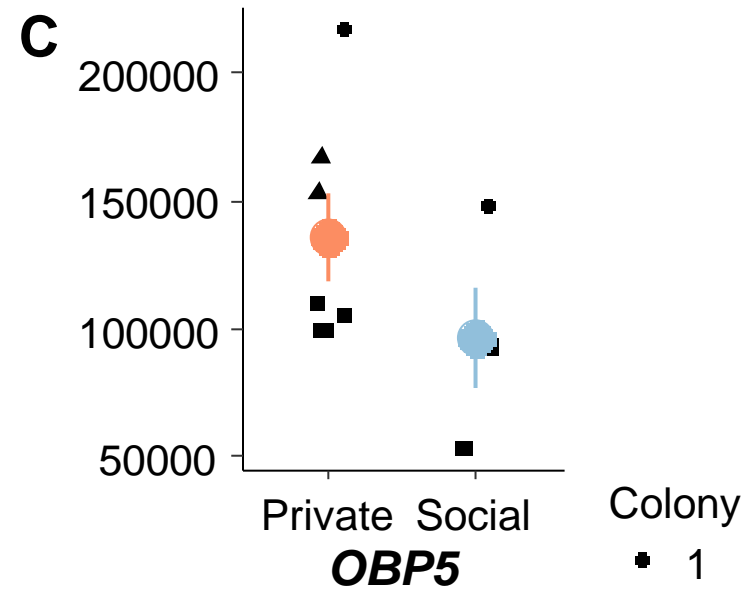
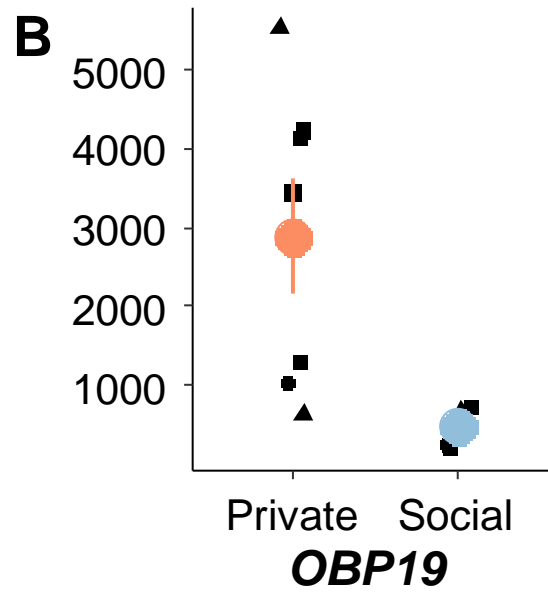
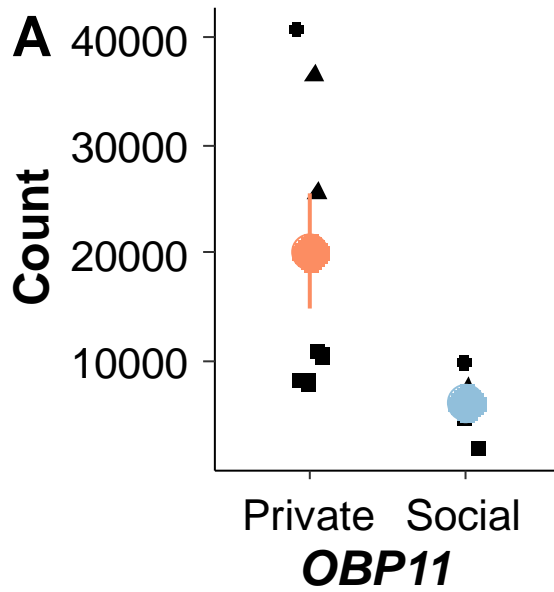
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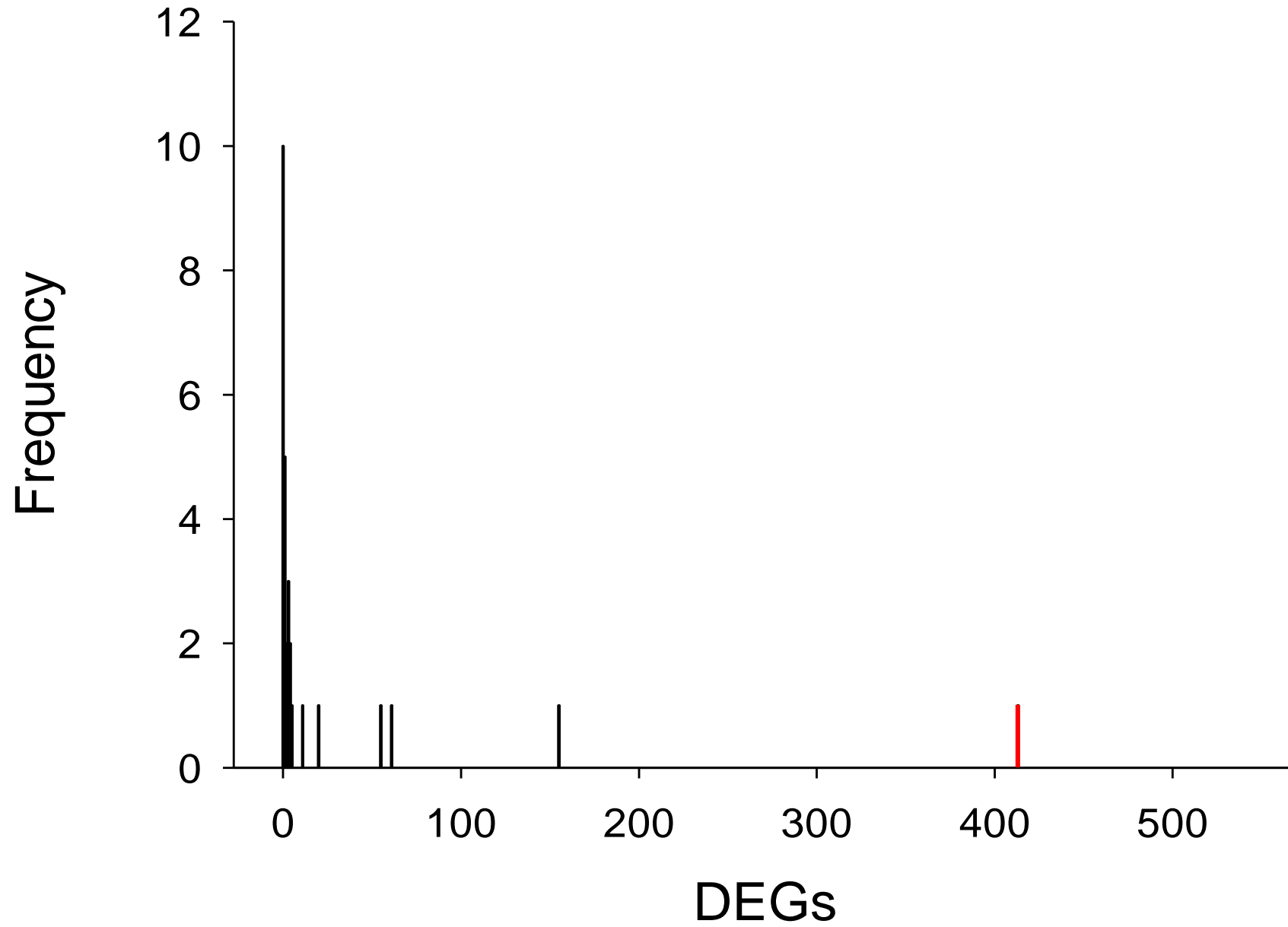
899 **Supplemental Figure 1:** Distribution of differentially expressed genes (DEGs) expected by  
900 chance after permutation results ( $N = 28$ ). The x-axis indicates the number of DEGs and the  
901 y-axis indicates the frequency of occurrences. Black bars indicate the results from the  
902 permutations, the red bar indicates our results.

903

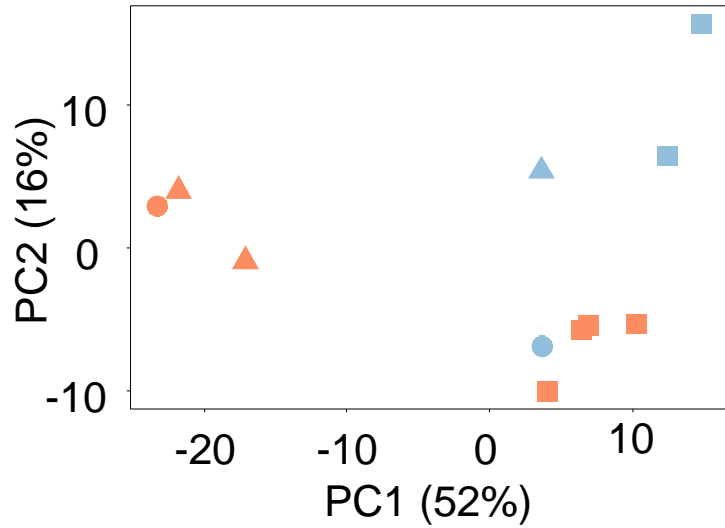




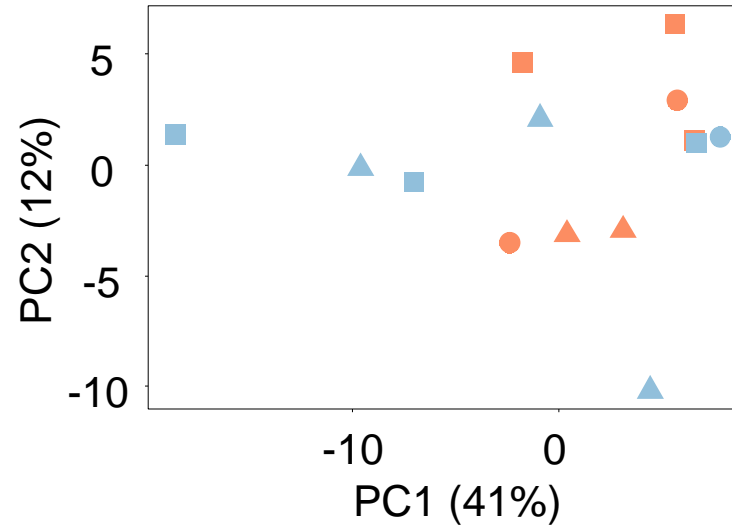




Antennae



Antennae lobes



Colony

● 1

▲ 2

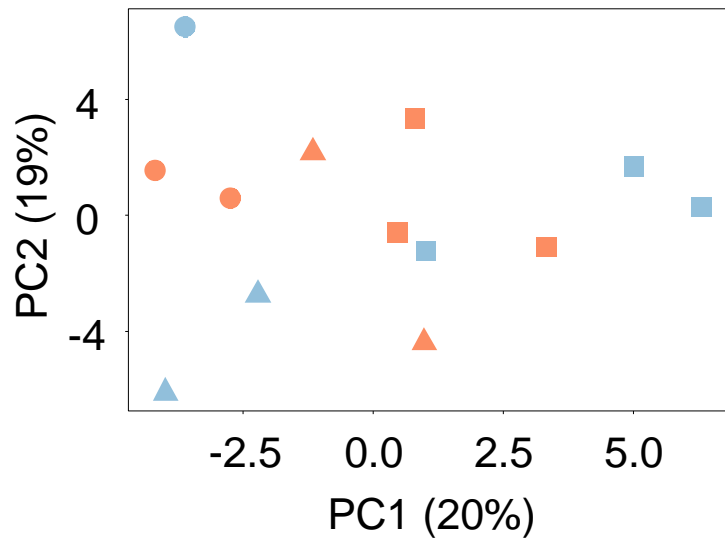
■ 3

Information use

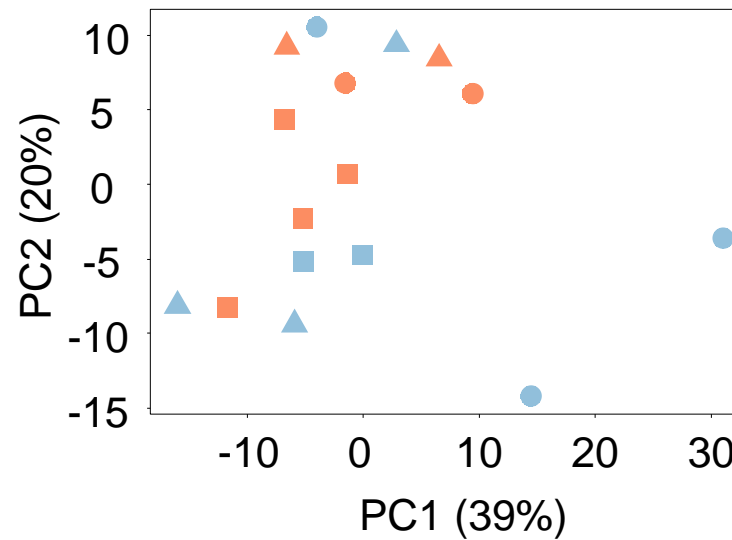
● Private

● Social

Mushroom bodies



Central brain



Subesophageal ganglion

