

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; Rieucan & 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 (*Apini*) 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 μ 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 ± 3.79 visits, N =
158 191; 2018: 8.09 ± 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 NaH₂PO₄, 5.5 mM Na₂HPO₄, 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 ± 0.7559 vs. 7.091 ± 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 ± 4.089 vs. 30.818 ± 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 ± 31.87 , $N = 28$; colony ID

279 not included: 3.25 ± 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.
470

471

Conflict of Interest

472 We declare no conflict of interest for this study.

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475 **References**

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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.

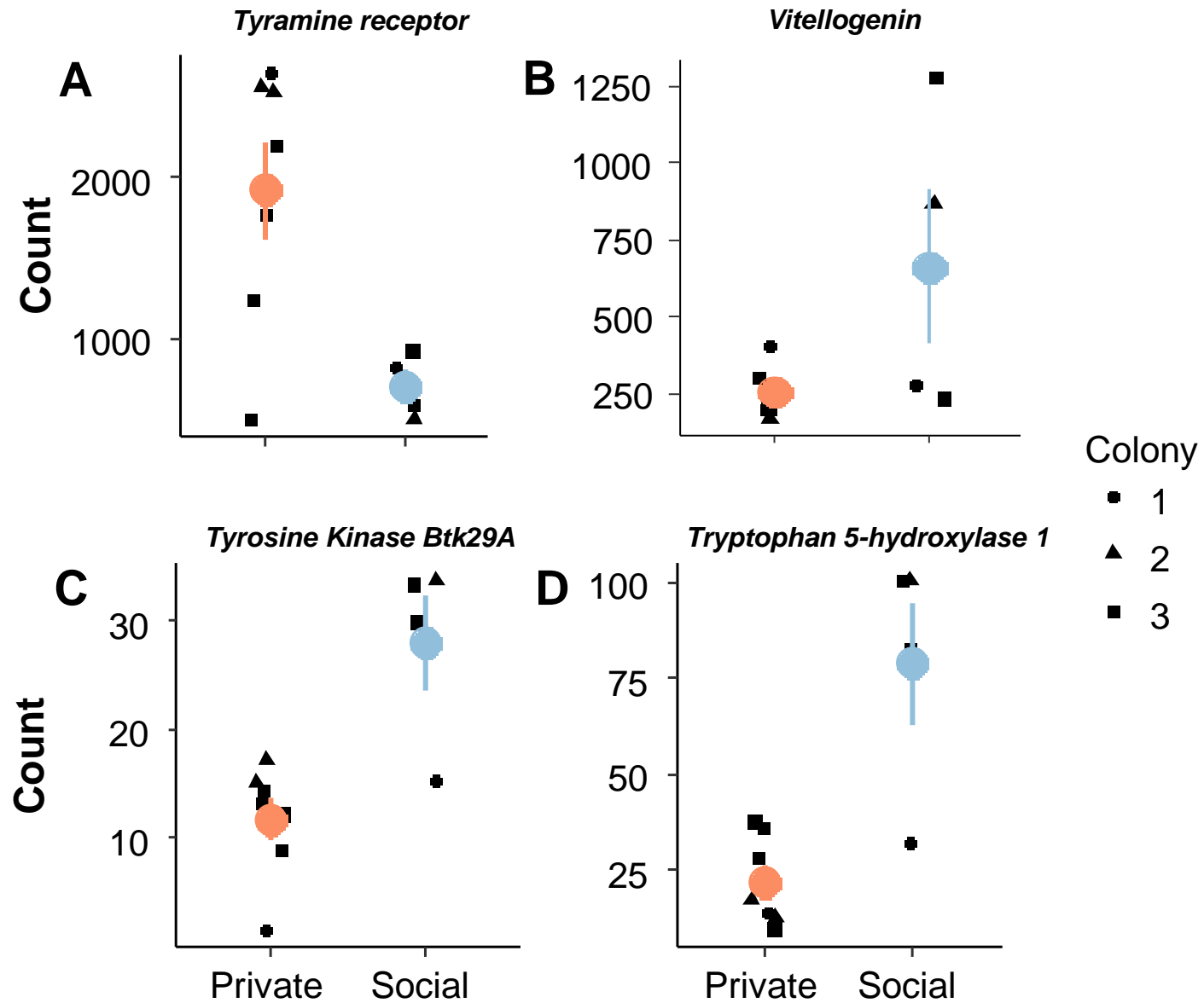
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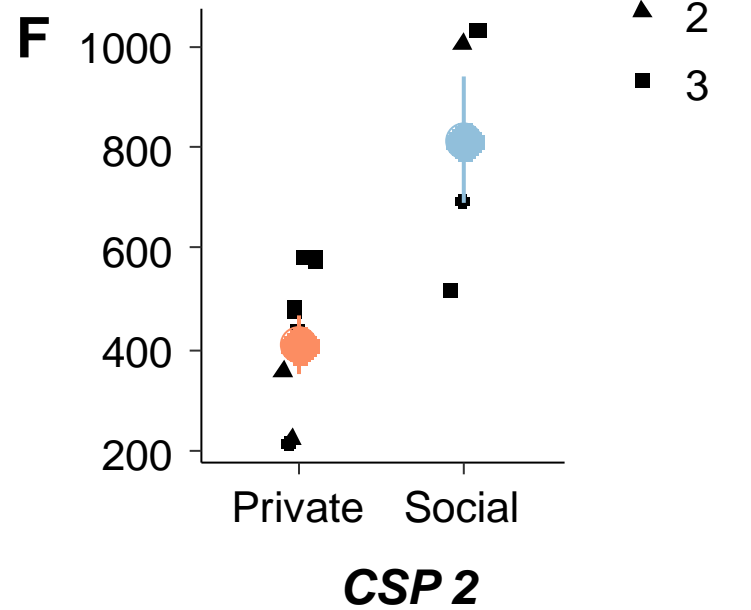
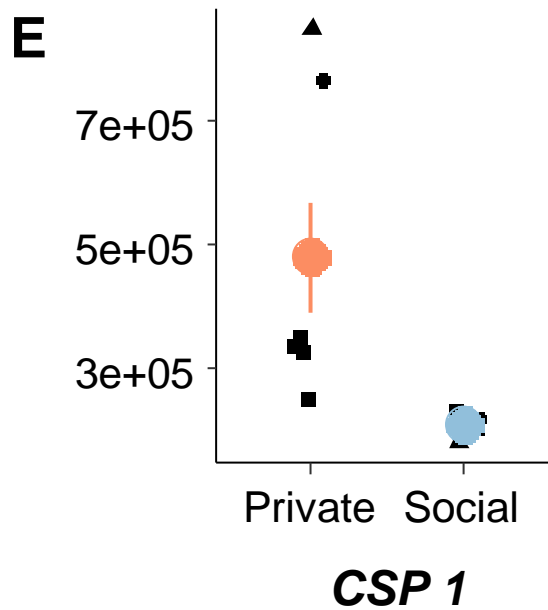
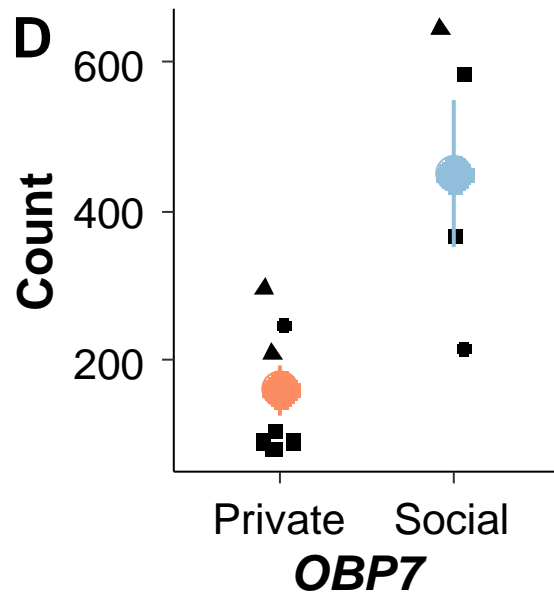
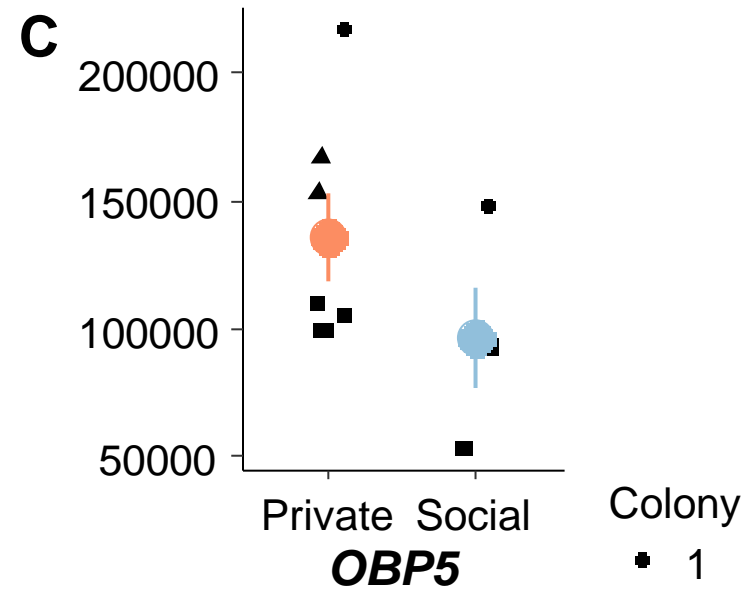
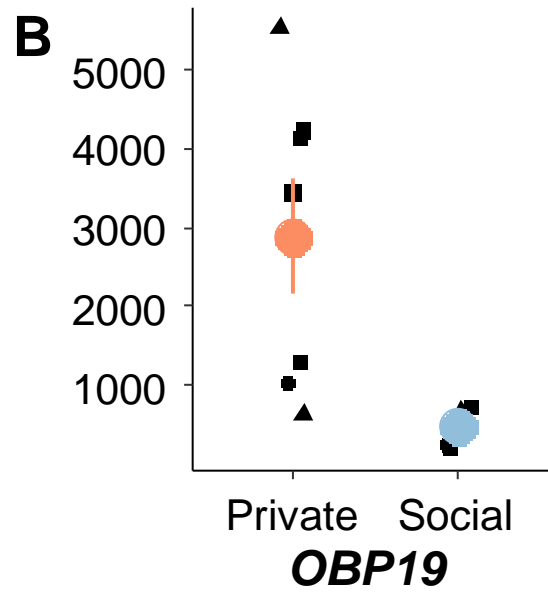
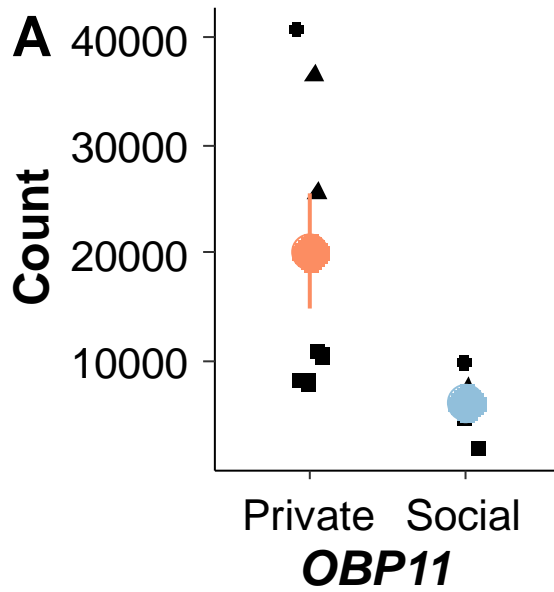
891 **Figure 3:** Plots of individual genes associated with biogenic amine production and
892 reproduction. Black dots show counts for individual samples and shapes correspond to the
893 colony ID (circle = colony1, triangle = colony 2, square = colony 3). Colored circles are
894 representative of the 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.

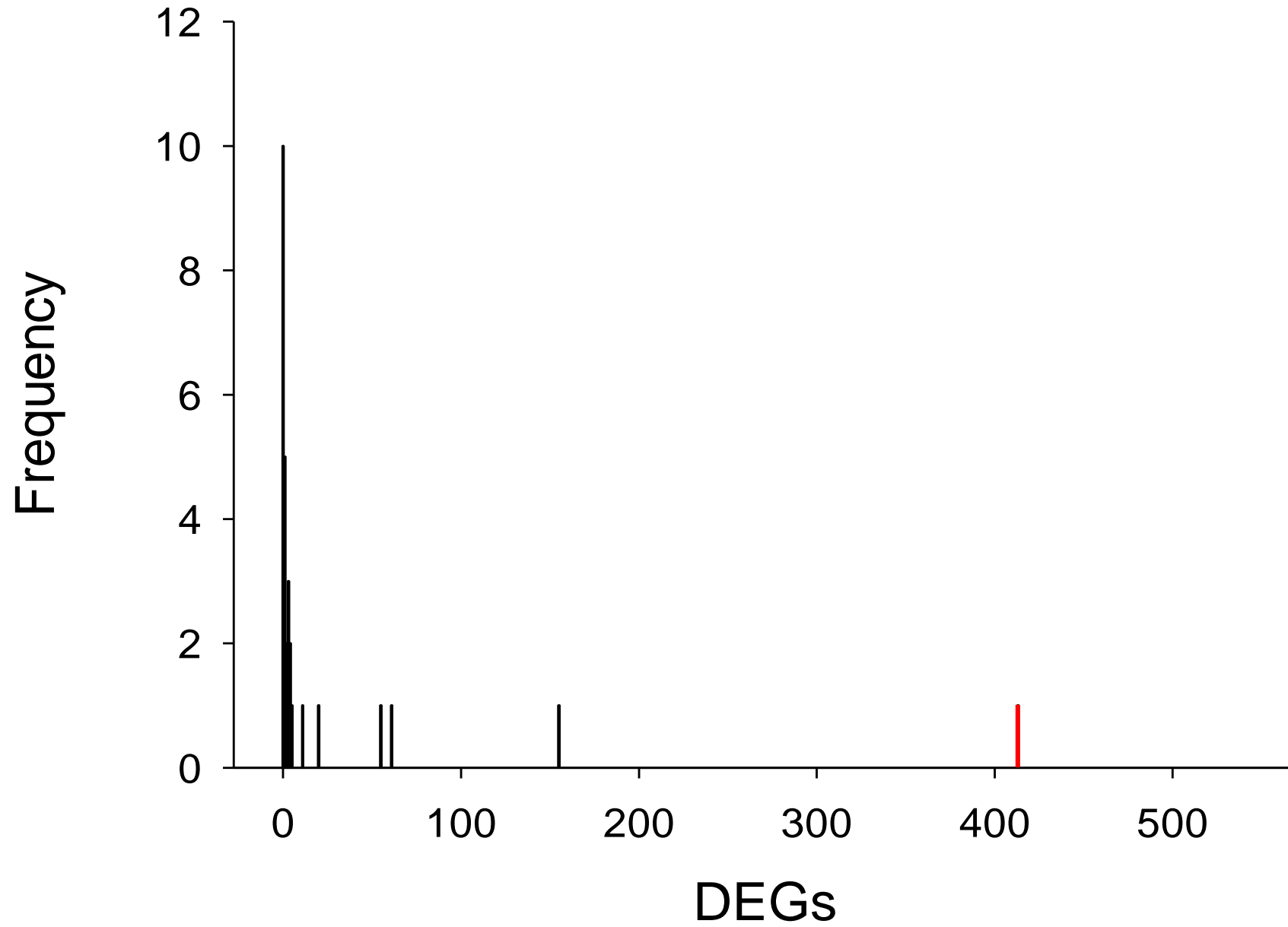
898

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.

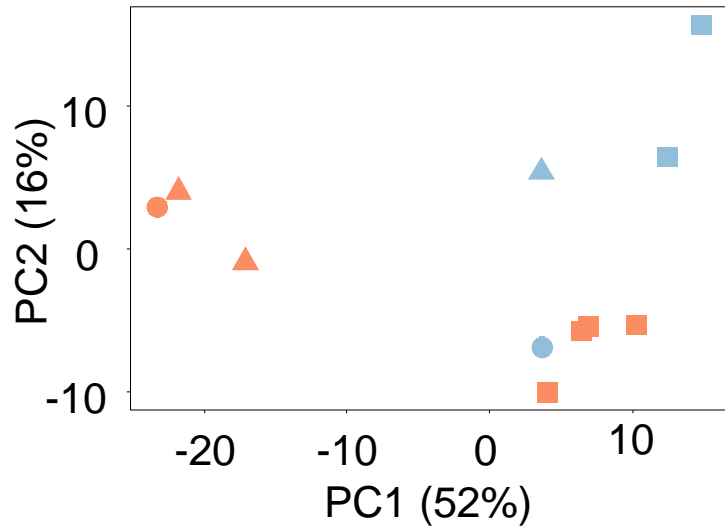
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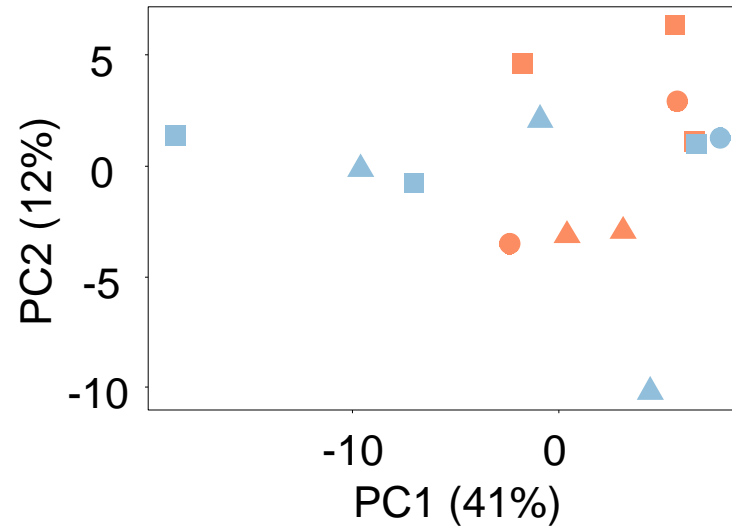




Antennae



Antennae lobes



Colony

● 1

▲ 2

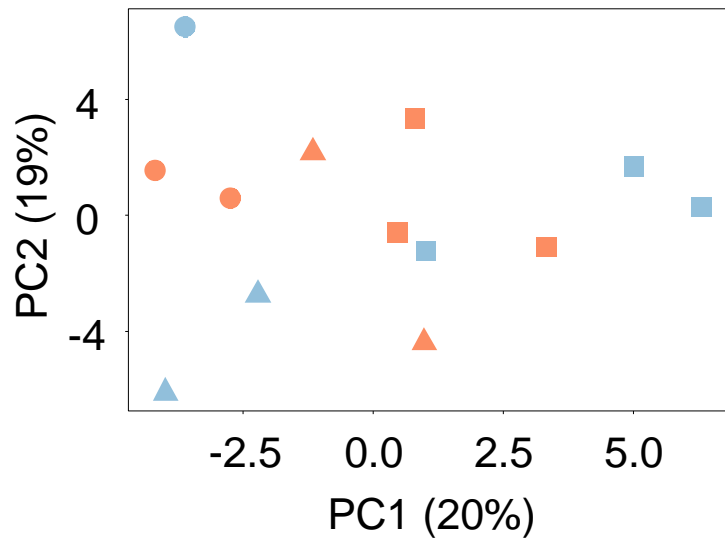
■ 3

Information use

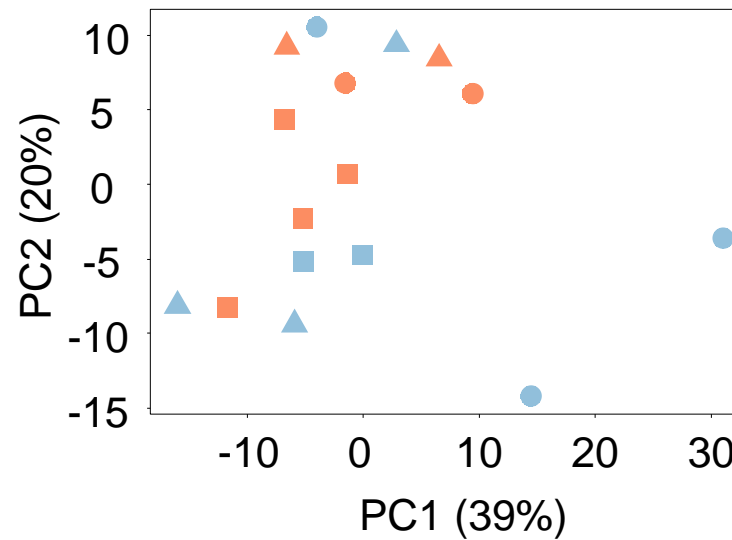
● Private

● Social

Mushroom bodies



Central brain



Subesophageal ganglion

