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1 **Coarse topographic organization of pheromone-sensitive afferents**
2 **from different antennal surfaces in the American cockroach**

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21 **Abstract**

22 In contrast to visual, auditory, taste, and mechanosensory neuropils, in which sensory
23 afferents are topographically organized on the basis of their peripheral soma locations,
24 axons of cognate sensory neurons from different locations of the olfactory sense organ
25 converge onto a small spherical neuropil (glomerulus) in the first-order olfactory center.
26 In the cockroach *Periplaneta americana*, sex pheromone-sensitive afferents with
27 somata in the antero-dorsal and postero-ventral surfaces of a long whip-like antenna are
28 biased toward the anterior and posterior regions of a macroglomerulus, respectively. In
29 each region, afferents with somata in the more proximal antenna project to more
30 proximal region, relative to the axonal entry points. However, precise topography of
31 afferents in the macroglomerulus has remained unknown. Using single and multiple
32 neuronal stainings, we showed that afferents arising from anterior, dorsal, ventral and
33 posterior surfaces of the proximal regions of an antenna were biased progressively from
34 the anterior to posterior region of the macroglomerulus, reflecting chiasmatic axonal
35 re-arrangements that occur immediately before entering the antennal lobe.
36 Morphologies of individual afferents originating from the proximal antenna matched
37 results of mass neuronal stainings, but their three-dimensional origins in the antenna
38 were hardly predictable on the basis of the projection patterns. Such projection biases
39 made by neuronal populations differ from strict somatotopic projections of antennal
40 mechanosensory neurons in the same species, suggesting a unique sensory mechanism
41 to process information about odor location and direction on a single antenna.

42

43 Keywords: insects; olfactory afferents; glomerulus; topographic map; sex pheromone;
44 antenna

45

46 Accurate representation of the stimulus source is fundamental in sensory processing.
47 The key neuroanatomical feature is the topographic sensory map seen in the central
48 nervous system, where axon terminals are organized on the basis of cellular
49 arrangements in the peripheral sense organ [1]. This topographic map, therefore, allows
50 animals to localize the stimulus source, discriminate stimuli of different locations, and
51 further reconstruct the object shape by integrating multiple stimulus sources. The most
52 well-known examples are the “homunculus” in the somatosensory cortex of humans, in
53 which peripheral arrangements of mechanosensory neurons from different body regions
54 are conserved in the brain [1]. A similar topographic organization of afferents is also
55 seen in the visual, taste, and auditory systems [1].

56 In contrast, cognate sensory neurons, generally scattered throughout the olfactory
57 epithelium, converge axons onto a small spherical neuropilar unit, the glomerulus [2].
58 Each glomerulus consists of a large number of incoming sensory afferents and dendrites
59 of a smaller number of second-order (projection) neurons and local interneurons [2].
60 This unique glomerular organization is important for detecting and differentiating
61 minute quantities of volatile chemicals [3,4]. On the other hand, several studies have
62 shown that odor plumes emitted from an odor source are not smooth and continuous
63 with a clear concentration gradient but, rather, are composed of filaments of various
64 sizes (> mm) and concentrations interspersed with regions of clean air, suggesting that
65 fine-scale topographic structures exist within odor plumes [5,6].

66 We have found that an elaborate topographic organization of sensory afferents exists
67 in the sex pheromone-receptive macroglomerulus (B-glomerulus) of the American
68 cockroach [7]. The B-glomerulus is the largest in the male antennal lobe and is
69 specialized for processing periplanone-B (a major pheromone component) [8].
70 Periplanone-B is especially important for attracting conspecific males from long
71 distances [9]. The B-glomerulus receives convergent projections from single sensory
72 neurons housed by approximately 36,000 *single-walled* B (*s-w* B) sensilla distributed
73 throughout the antennal flagellum (the third antennal segment) [10,11]. Firstly, afferents
74 arising from the sensilla on the antero-dorsal half surface of the flagellum and those on
75 the postero-ventral half surface of the flagellum are biased toward the anterior half and
76 the posterior half of the B-glomerulus [7]. A similar topographic organization of
77 afferents based on anterior and posterior surfaces of the flagellum has been detected in
78 pheromone-sensitive glomeruli of several moth species [12-14]. Secondly, afferents

79 arising from sensilla on the more proximal region of the flagellum tend to project
80 progressively to the more proximal region of the glomerulus, relative to axonal entry
81 points [7]. According to these features, three-dimensional locations of
82 pheromone-sensitive neurons are roughly mapped in the B-glomerulus.

83 Now the question arises as to how precisely this topographic sensory map
84 represents the stimulus location. So far, no attempts have been made to characterize
85 projection patterns of cognate olfactory sensory neurons arising from different antennal
86 surfaces in any insects. We used nerve section stainings and single sensillum stainings
87 and evaluated the topography of sensory afferents in the B-glomerulus.

88 Adult male cockroaches (*Periplaneta americana*) with intact antennae (Fig. 1a),
89 reared in a 12:12-hour light–dark cycle at 27 °C, were used. The anterior and posterior
90 nerves, two parallel antennal nerves, contain sensory axons arising from various types
91 of sensilla on the flagellar surface (Fig. 1b-d). Three sets of anterograde stainings of
92 sensory neuronal axons were achieved as follows: 1) differential stainings of a bisection
93 of each antennal nerve, 2) stainings of a small section of each nerve, and 3) single
94 sensillum stainings. The dissection procedures were the same as those in our previous
95 studies [7,11]. In the first experiment, either of the two nerves was split into bisection
96 by an electrolytically tapered tungsten rod and cut with microscissors at the fifth
97 flagellar annulus; their distal cut-ends were then placed separately into two tapered
98 glass electrodes containing either 10% microruby (D-7162, Invitrogen, USA) or 10%
99 microemerald (D-7156, Invitrogen, USA). The preparation was incubated in a humid
100 chamber at 5 °C for 48 h for diffusion of the dye. In the second experiment, about a 1/4
101 section of axonal bundles was separated from each nerve and the cut-end was immersed
102 in a low molecular weight dye (6% nickel chloride hexahydrate). The preparation was
103 incubated in a humid chamber at 5°C up to 36 h. The specimens were subsequently
104 intensified with silver [15]. In the third experiment, the *sw-B* sensillum was clipped and
105 then covered with an electrode containing 10% microruby (Fig. 1e). The preparation
106 was incubated at 10 °C for 2 days and consecutively at 4 °C for 2 days in a humid
107 chamber (see [11] for details).

108 After the incubation, the brain and the antenna were dissected free from the head
109 capsule, fixed in a 4% formaldehyde solution, dehydrated in an ascending ethanol series,
110 and then cleared in methyl salicylate. The cleared brain and the antenna were viewed
111 anteriorly using a confocal laser-scanning microscope, LSM 5 Pascal or LSM 510 (Carl

112 Zeiss, Jena, Germany). The three-dimensional location of a sensillum was identified
113 using hair plates on the pedicel as landmarks and its axons were traced by removing part
114 of the cuticle (Fig. 1f and g). Afferents labeled by microemerald were visualized by
115 confocal microscopy using an argon laser (Lasos Lasertechnik GmbH, Jena, Germany)
116 with a band-pass filter (505–530 nm), whereas those labeled by microruby were
117 visualized using a helium–neon laser (Lasos Lasertechnik GmbH) with a long-pass filter
118 (560 nm). The outline of the B-glomerulus was imaged by autofluorescence using the
119 argon laser. Optical sections made at 1.0–1.2 μm were reconstructed
120 three-dimensionally with Amira 5.33 software (Mercury Computer Systems, Berlin,
121 Germany).

122 For quantitative analysis, tips of afferent terminals derived from different individuals
123 were detected by the “seeded region growing” and “skeletonized” functions in Amira.
124 The shortest distances between afferent tips and the lateral margin of the B-glomerulus
125 outline were calculated using Microsoft Excel 2010. After the coordinated values
126 derived from different individuals had been normalized according to the longitudinal
127 length of the B-glomerulus, the distances, the locations along the lateral edge of the
128 glomerular outline, and the locations along the anterior-posterior axis were plotted on X,
129 Y, and Z axes in three-dimensional plots using Amira (see Fig. 3o). The cross-sectional
130 area of axons immediately before entering the B-glomerulus was measured by Amira.
131 Observations of the surface structure of the antenna were made with a scanning electron
132 microscope (S-4800; Hitachi, Tokyo, Japan). The body axis was used as the reference
133 against which position and direction were defined.

134 The antennal flagellum of the cockroach is composed of repeating segments called
135 annuli, and it tapers distally, its diameter being approximately 400 μm in the most
136 proximal region and 130 μm in the most distal region (Fig. 1a). Each *s-w* B sensillum
137 generally houses four sensory neurons, two of which are sensitive to periplanone-A (a
138 minor sex pheromone component) and periplanone-B, respectively, and the other two of
139 which are sensitive to other monoterpenoid odors. [16]. Sensory neurons arising from
140 sensilla on the antero-dorsal half surface (magenta) and the postero-ventral half surface
141 of the flagellum (green) send axons to the anterior and posterior nerves, respectively [7]
142 (Fig. 1c and d). Axons of sensory neurons from the *s-w* B sensillum form a thin nerve
143 bundle together with axons from nearby olfactory, mechano and contact-chemo sensilla,
144 which joins in the peripheral region of the primary nerve (Fig. 1g).

145 Differential anterograde stainings of a bisection of each nerve revealed detailed
146 axonal entry patterns into the B-glomerulus. The anterior and posterior nerves crossed at
147 the base of the antenna (blue arrow, Fig. 1b) so that axons arising from the anterior,
148 dorsal, ventral and posterior antennal surfaces (Fig. 2o and p) were re-arranged from
149 antero-ventral to postero-dorsal (Fig. 2q). Due to the close apposition of the
150 B-glomerulus to the antennal nerves (Fig. 2 a and b), axonal bundles diverging from the
151 anterior, dorsal, ventral and posterior nerve sections tended to progressively enter from
152 ventral to lateral along the anterior-posterior axis of the glomerulus (Fig. 2c-j and
153 Supplementary data file A).

154 The axonal entries along the antero-posterior axis of the B-glomerulus were reflected
155 in the distribution of afferents within the B-glomerulus. Afferents arising from each of
156 the four antennal surfaces were distributed throughout the B-glomerulus
157 (Supplementary data files B and C), but the relative amounts of them differed along the
158 anterior-posterior axis (Fig. 2r). Afferents arising from the anterior surface (green) and
159 dorsal surface (magenta) were predominantly seen in the anteriormost and
160 anterior-central regions of the B-glomerulus (Fig. 2c-f; n=6), while those arising from
161 the ventral surface (magenta) and the posterior surface (green) were more
162 predominantly seen in the posterior-central and posteriormost regions (Fig. 2g-j; n=6).
163 Small nerve section stainings using heavy metal and subsequent intensification revealed
164 that axons from the anteriormost, dorsalmost, ventralmost, and posteriormost antennal
165 surfaces anticlockwisely entered antero-ventrally to postero-laterally and their afferents
166 were more profusely distributed in the same anterior-posterior focal plane (Fig. 2k-n).
167 These results were in good agreement with those of fluorescent-dye labelings.

168 Next, we performed single sensillum stainings to evaluate axonal projection patterns
169 of individual neurons (Fig. 3a and b). It was found that 82% of the stained afferents
170 diverged into several axons after entering the antennal lobe, providing multiple axonal
171 entry points at the B-glomerulus (red arrows, Fig. 3c-f, h, i, k, l and n; Supplementary
172 data file D). Individual afferents showed diverse morphologies. Most of the stained
173 afferents had localized branches (Fig. 3e-h, j, and k) or those with a few collaterals (Fig.
174 3d,l, and m). A few afferents had rather dispersed branches (Fig. 3c,i and n). Branches
175 of each afferent tended to be more abundant close to the axonal entry points (Fig. 3c-n).
176 Accordingly, three-dimensional plots of the terminal tips of 22 afferents in the
177 normalized B-glomerulus revealed that presumed varicosities of afferents from the

178 antero-dorsal surface (reddish) and postero-ventral surface (greenish) of proximal annuli
179 are biased toward the antero-ventral and postero-lateral regions of the B-glomerulus,
180 respectively (Fig. 3p and q; Supplementary data file E). However, sensilla arising from
181 similar three-dimensional locations but from different individuals tended to have
182 distinct branching patterns (Fig. 3i-k). Thus, at the single neuronal level,
183 three-dimensional origins of somata on the circumference of the flagellum were not
184 predictable based solely on projection profiles.

185 We observed that sex pheromone-sensitive afferents arising from the four surfaces of
186 the antenna exhibit biased distributions in the B-glomerulus, creating projection waves
187 along its anterior-posterior axis. Such projection profiles were blurred at single sensory
188 neurons due to their varied morphologies and individual variation. This was in contrast
189 to antennal mechanosensory projections in the same species, in which sensory neurons
190 on different circumferences of the flagellum project to different sets of neuropilar layers
191 in the deutocerebrum [17].

192 Although morphologies of single neuronal afferents were too diverse to characterize
193 unique projection patterns based on three-dimensional origins, the possibility that finer
194 projection biases based on different antennal surfaces exist can not be ruled out.
195 Obtaining more samples, ideally with differential labelings of two closely located
196 sensilla in the same individual, is necessary to evaluate this possibility.

197 It is tempting to speculate that the coarse topographic organization of olfactory
198 afferents is an evolutionary trade-off to enable both amplification of weak stimuli [3] and
199 topographical representation of stimuli, because more localized projections of
200 individual afferents result in lower convergence rates on the input sites of dendrites of
201 projection neurons, losing the structural advantage as a “glomerulus”. Some
202 arthropod-specific features may promote detection of spatial odor distribution in early
203 odor processing. For example, insect odor receptors have been suggested to be
204 ligand-gated ion channels [18], allowing faster (i.e., biologically more meaningful)
205 representation of odor distribution, than that by vertebrate G protein-coupled receptors
206 [19]. If the flicking cockroach antenna has a fluid filtering system comparable to the
207 lobster antennule [20], odor retention in sensilla on a particular antennal surface could
208 be facilitated, because the fluid in contact with the surface of a moving object does not
209 slip relative to the object and a velocity gradient develops in the flow around the object
210 [20].

211 The two organizational rules of afferents may be related to topographic odor
212 representation in projection neurons. Firstly, according to the developmental rule that
213 newly emerged olfactory afferents arising from the proximal annuli are added to the
214 pre-existing glomerulus [21], afferents arising from proximal annuli tended to have
215 more branches close to the axonal entry points. Therefore, afferents from the proximal
216 (thicker) region of the flagellum are more broadly distributed along the
217 anterior-posterior axis of the glomerulus than are those from the distal (thinner) region,
218 possibly facilitating discrimination of odors on different antennal surfaces by projection
219 neurons in the proximal antenna. Secondly, afferents from the anterior/posterior
220 surfaces were spatially more segregated than were those from dorsal/ventral surfaces of
221 the flagellum in the B-glomerulus. This may be related to the directional preference of
222 odors across the longitudinal antenna. Neurophysiological and ultrastructural studies are
223 needed to understand how the topography of afferents is exploited by projection
224 neurons.

225

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227

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230

231 **References**

232

233 [1] E.R. Kandel, J.H. Schwartz, T.M. Jessell, S. Siegelbaum, A.J. Hudspeth, Principles
234 of Neural Science, Fifth edition (2012).

235

236 [2] L.M. Kay, M. Stopfer, Information processing in the olfactory systems of insects
237 and vertebrates. *Semin. Cell Dev. Biol.* 17 (2006) 433-442.

238

239 [3] R. Tabuchi, T. Sakurai, H. Mitsuno, S. Namiki, R. Minegishi, T. Shiotsuki, K.
240 Uchino, H. Sezutsu, T. Tamura, S.S. Haupt, K. Nakatani, R. Kanzaki, Pheromone
241 responsiveness threshold depends on temporal integration by antennal lobe projection
242 neurons. *Proc. Nat. Acad. Sci USA* 110 (2013) 15455–15460.

243

244 [4] R. Wilson Early olfactory processing in *Drosophila*: mechanisms and principles.
245 *Ann. Rev. Neurosci.* 36 (2013) 217-241.

246

247 [5] J.P. Crimaldi, J.R. Koseff, High-resolution measurements of the spatial and
248 temporal scalar structure of a turbulent plume. *Experiments in Fluids* 31 (2001) 90-102.

249

250 [6] R.T. Carde, M.A. Willis, Navigational strategies used by insects to find distant,
251 wind-borne sources of odor. *J. Chem. Ecol.* 34 (2008) 854-866.

252

253 [7] H. Nishino, M. Mizunami, Sensilla position on antennae influences afferent terminal
254 location in glomeruli. *NeuroReport* 18 (2007) 1765-1769.

255

256 [8] M. Burrows, J. Boeckh, J. Esslen, Physiological and morphological properties of
257 interneurons in the deutocerebrum of male cockroaches which respond to female
258 pheromone. *J. Comp. Physiol.* 145 (1982) 447-457.

259

260 [9] G. Seelinger, Behavioural responses to female sex pheromone components in
261 *Periplaneta americana*. *Anim. Behav.* 33 (1985) 591–598.

262

263 [10] D. Schaller, Antennal sensory system of *Periplaneta americana* L. Distribution and

264 frequency of morphologic types of sensilla and their sex-specific changes during
265 postembryonic development. *Cell Tissue Res.* 191 (1978) 121-139.
266

267 [11] H. Watanabe, S.S. Haupt, H. Nishino, M. Nishikawa, F. Yokohari,
268 Sensilla-specific, topographic projection patterns of olfactory receptor neurons in the
269 antennal lobe of the cockroach *Periplaneta americana*. *J. Comp. Neurol.* 520 (2012)
270 1687-1701.
271

272 [12] T.A. Christensen, I.D. Harrow, C. Cuzzocrea, P. Randolph, J.G. Hildebrand,
273 Distinct projections of two populations of olfactory receptor axons in the antennal lobe
274 of the sphinx moth *Manduca sexta*. *Chem. Senses* 20 (1994) 313–323.
275

276 [13] H. Ai, R. Kanzaki, Modular organization of the silkmoth antennal lobe
277 macroglomerular complex revealed by voltatge-sensitive dye imaging. *J. Exp. Biol.* 207
278 (2004) 633–644.
279

280 [14] B.G. Berg, T.J. Almaas, J.G. Bjaalie, H. Mustaparta, Projections of male-specific
281 receptor neurons in the antennal lobe of the oriental tobacco budworm moth,
282 *Helicoverpa assulta*: a unique glomerular organization among related species. *J. Comp.*
283 *Neurol.* 486 (2005) 209 –220.
284

285 [15] J.P. Bacon, J.S. Altman, A silver intensification method for cobalt-filled neurons in
286 wholemout preparations. *Brain Res.* 138 (1977) 359–363.
287

288 [16] H. Sass, Production, release and effectiveness of two female sex pheromone
289 components of *Periplaneta americana*. *J. Comp. Physiol.* 152 (1983) 309-317.
290

291 [17] H. Nishino, M. Nishikawa, F. Yokohari, M. Mizunami, Dual, multi-layered
292 somatosensory maps formed by antennal tactile and contact chemosensory afferents in
293 an insect brain. *J. Comp. Neurol.* 493 (2005) 291–308.
294

295 [18] K. Sato, M. Pellegrino, T. Nakagawa, T. Nakagawa, L.B. Vosshall, K. Touhara,
296 Insect olfactory receptors are heteromeric ligand-gated ion channels. *Nature* 452 (2008)

297 1002-1006.

298

299 [19] U.B. Kaupp, Olfactory signaling in vertebrates and insects: differences and
300 commonalities. *Nat. Rev. Neurosci.* 11 (2010) 188-200.

301

302 [20] M.A.R. Koehl, J.R. Koseff, J.P. Crimaldi, M.G. McCay, T. Cooper, M. B. Wiley,
303 P.A. Moore, Lobster sniffing: antennule design and hydrodynamic filtering of
304 information in an odor plume. *Science* 294 (2001) 1948-1951.

305

306 [21] H. Nishino, A. Yoritsune, M. Mizunami, Different growth patterns of two adjacent
307 glomeruli responsible for sex-pheromone processing during postembryonic
308 development of the cockroach *Periplaneta americana*. *Neurosci. Lett.* 462 (2009)
309 219-224.

310

311

312 **Figure Legends**

313

314 **Fig. 1.** Two parallel antennal nerves in the antennal flagellum. (a) Semi-schematic
315 diagram of the tapered antenna segmented into more than 140 annuli. (b) Proximal
316 region of the flagellum, showing chiasmatic re-arrangements of two antennal nerves
317 (blue arrow). (c) Two antennal nerves running in parallel in the 26-29 annuli. (d) Cross
318 section of the flagellum at the 1st annulus, showing two equal-sized antennal nerves
319 attached to the inside of the antennal cuticle. Note slight shrinkage of the nerve due to
320 the fixation process. (e) An electrode filled with microruby covering a single sensillum.
321 (f) Single *s-w* B sensillum on the 11th annulus marked by microruby (magenta). (g) A
322 single axon from a single sensillum on the 4th annulus runs in the periphery of the
323 posterior nerve. Scale bars = 5 mm in (a), 1 mm in (b), 100 μ m in (c,d), 50 μ m in (e-g).

324

325 **Fig. 2.** Projection patterns of antennal nerve sections, viewed anteriorly (a-n) and
326 laterally (o-r). (a and b) Antennal lobes in which bisections of the anterior nerve (a) and
327 posterior nerve (b) were differentially stained. (c-j) Confocal stacks at different
328 antero-posterior regions showing afferents from anterior (green), dorsal (magenta),
329 ventral (magenta) and posterior (green) surfaces are biased toward the anterior-most,

330 antero-central, postero-central, and posteriormost regions of the B-glomerulus,
331 reflecting axonal entries (white arrows). Sensory tracts (T I- T IV) progressively enter
332 from antero-ventral to posterior-lateral of the B-glomerulus (see Supplementary data
333 file A for details). Numbers indicate distances from the anterior margin of the
334 B-glomerulus. (k-h) About 1/4 nerve section stainings and subsequent silver
335 intensification, showing anticlockwise axon entries (red arrows) from ventral to lateral
336 along the antero-posterior axis of the B-glomerulus. (o-r) Schematic representation of
337 antennal nerve topography (p), chiasmatic nerve crossing (q), and afferents in the
338 B-glomerulus (r) viewed laterally (o). Scale bars = 100 μm in (a,b and k-n), 50 μm in
339 (c-j), 1 mm in (o).

340

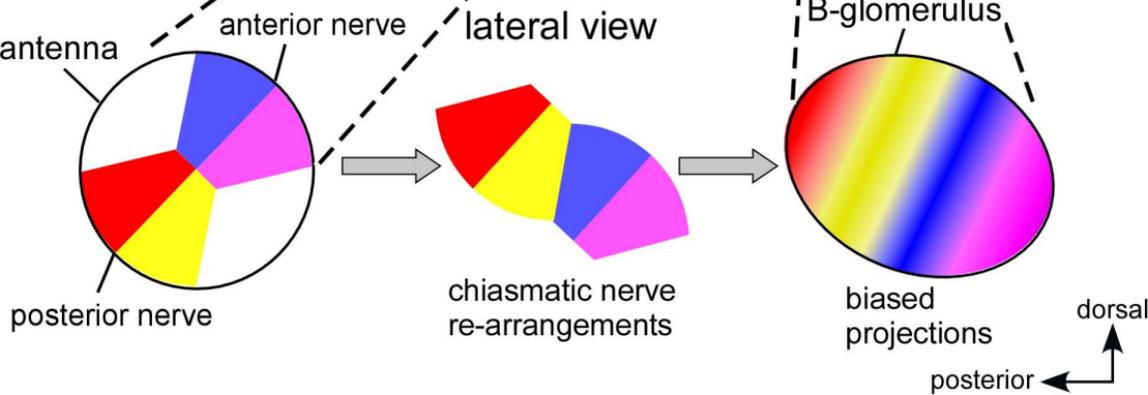
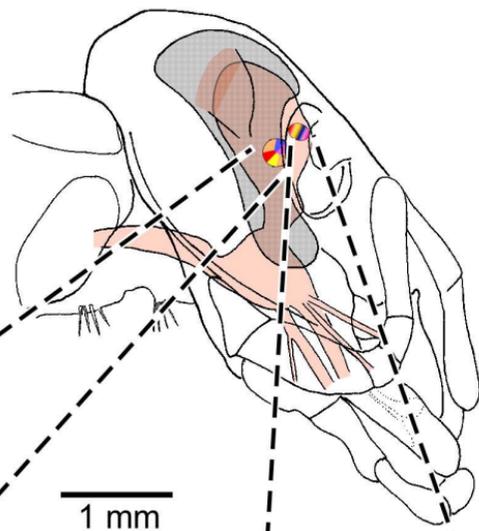
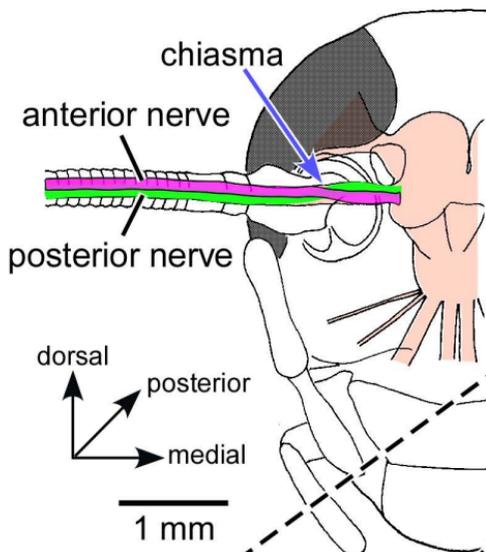
341 **Fig. 3.** Single sensory afferents innervating the B-glomerulus. (a and b) Locations of
342 individual sensilla stained in the flagellum. (c-n) Axon terminals of single afferents
343 from the antero-dorsal half (c-h) and the postero-ventral half surfaces (i-n) of the
344 flagellum, viewed anteriorly (upper column) and dorsally (lower column). Red arrows
345 indicate axonal entries to the B-glomerulus (green). (o-q) 3D mapping procedures of
346 tips of afferents in the normalized B-glomerulus (o) showing distribution patterns of 22
347 afferents viewed anteriorly (p) and dorsally (q). Presumed varicosities of different
348 afferents belonging to the antero-dorsal surface (reddish) and postero-ventral surface
349 (greenish) are generally segregated. Different shapes and color density represent
350 different afferents (See supplementary figure D). Scale bars = 500 μm in (a,b) and 50
351 μm in (c-n and o).

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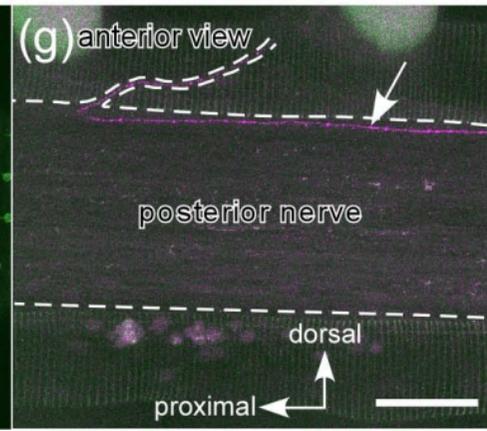
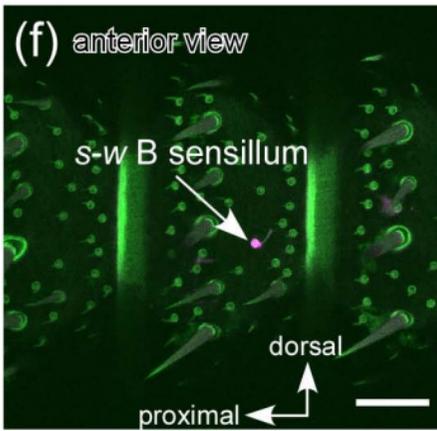
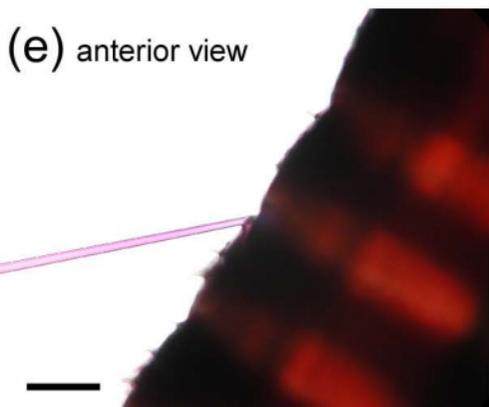
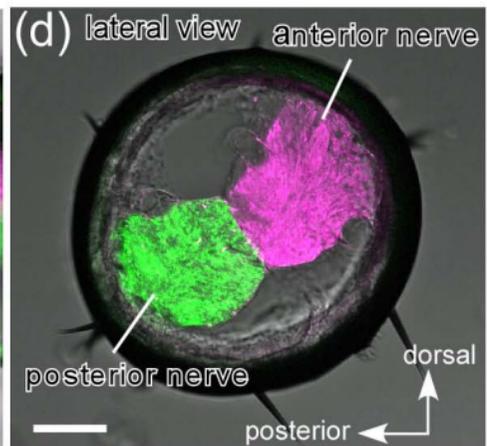
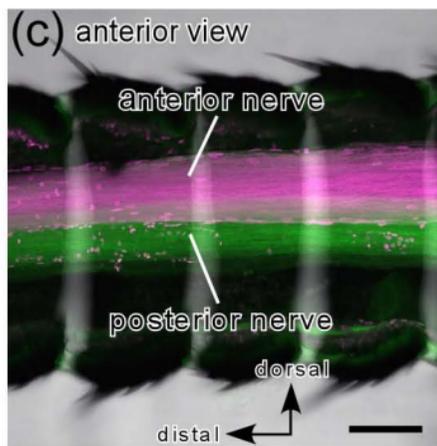
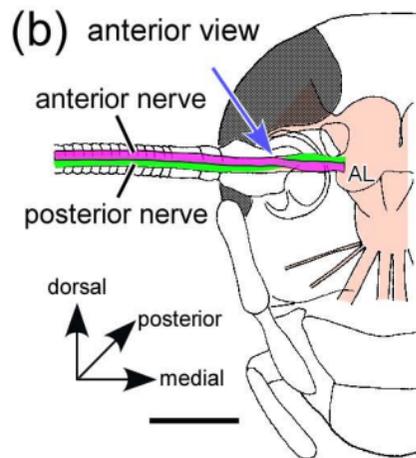
anterior view

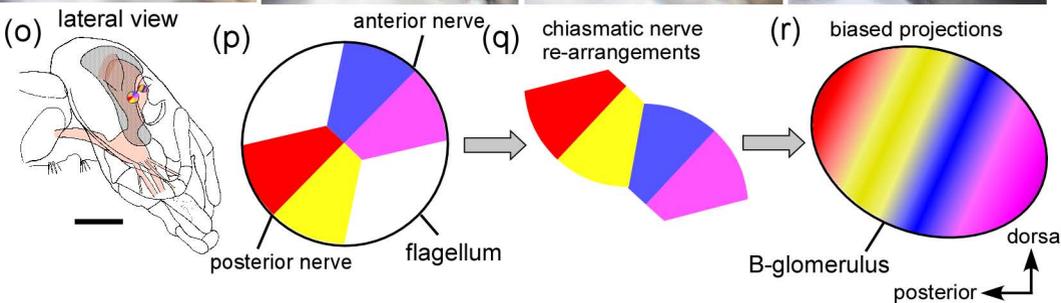
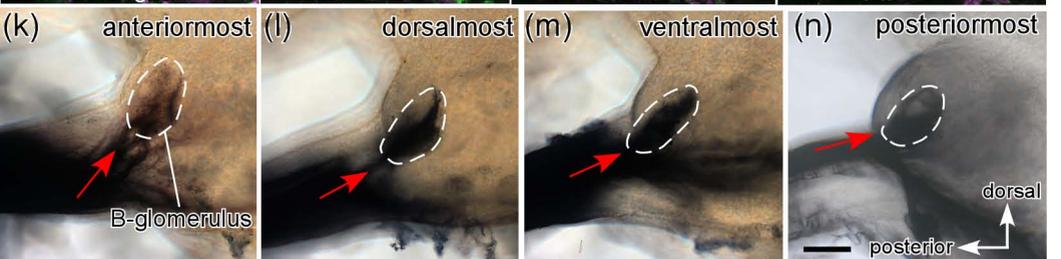
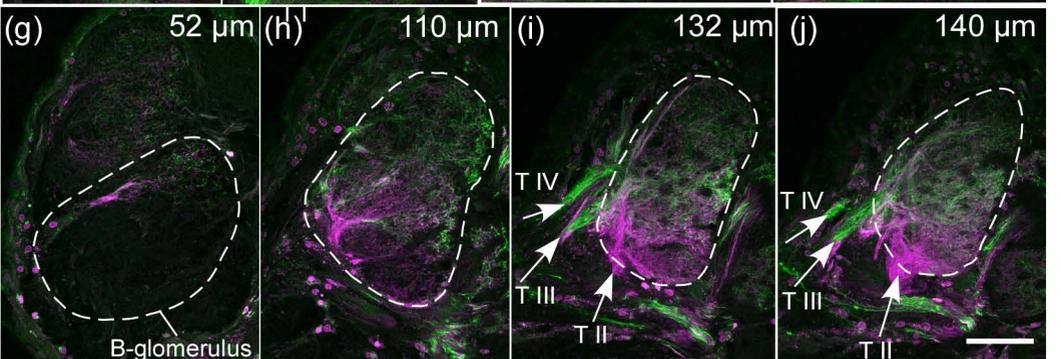
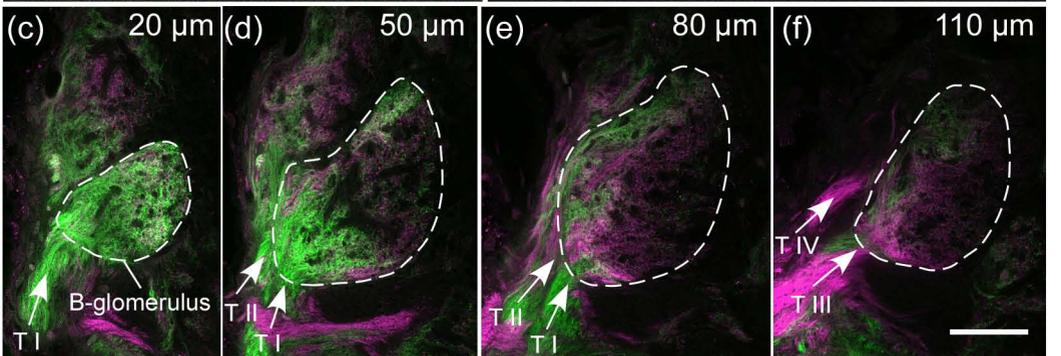
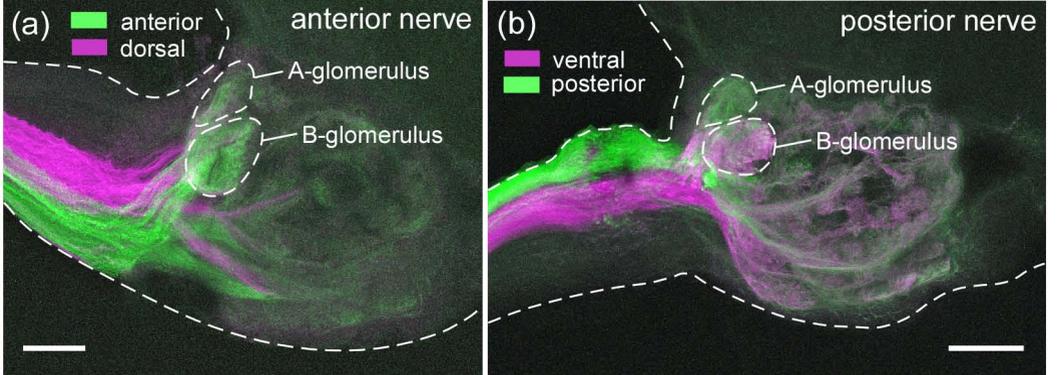
lateral view

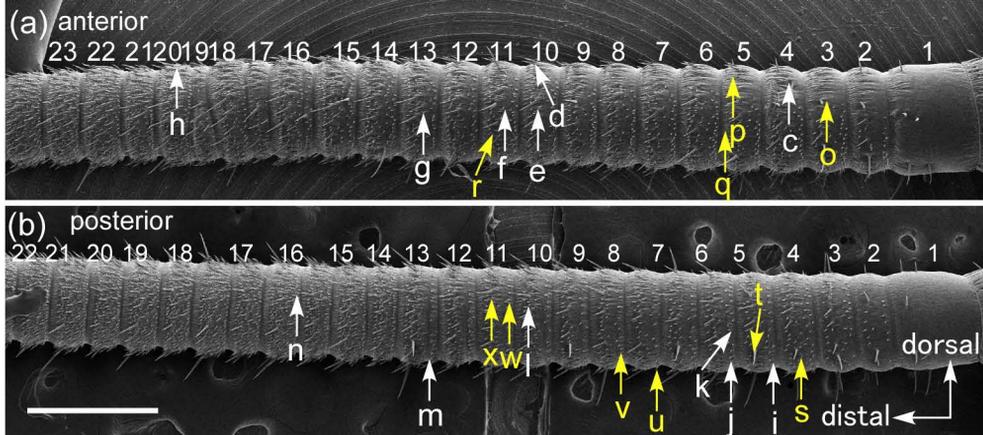


Highlights

- Pheromone-sensitive axons from different antennal surfaces show biased projections.
- Pheromone-sensitive axons undergo chiasmatic rearrangements.
- Axonal entry patterns are reflected in biased afferent projections.
- Afferents from anterior/posterior antennal surfaces are spatially segregated.







antero-dorsal surface (upper: anterior view; lower: dorsal view)

