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Directional Sensitivity of Wind-Sensitive Giant Interneurons in the Cave Cricket *Troglophilus neglectus*

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ABSTRACT Unlike the situation in most cockroach and cricket species studied so far, the wind-sensitive cerci of the cave cricket *Troglophilus neglectus* Krauss (Rhaphidophoridae, Orthoptera) are not oriented parallel to the body axis but perpendicular to it. The effects of this difference on the morphology, and directional sensitivity of cercal giant interneurons (GIs), were investigated. In order to test the hypothesis that the 90° change in cercal orientation causes a corresponding shift in directional sensitivity of GIs, their responses in both the horizontal and vertical planes were tested.

One ventral and four dorsal GIs (corresponding to GIs 9-1a and 9-2a, 9-3a, 10-2a, 10-3a of gryllid crickets) were identified. The ventral GI 9-1a of *Troglophilus* differed somewhat from its cricket homologue in its dendritic arborisation and its directional sensitivity in the horizontal plane. The morphology and horizontal directionality of the dorsal GIs closely resembled that of their counterparts in gryllids. In the vertical plane, the directionality of all GIs tested was similar. They were all excited mainly by wind puffs from the axon-ipsilateral quadrant. The results suggest that directional sensitivity to air currents in the horizontal plane is maintained despite the altered orientation of the cerci. This is presumably due to compensatory modifications in the directional preferences of the filiform hairs. *J. Exp. Zool. 292:73–81, 2002.*

The wind-sensitive cercal sensory system of orthopteroid insects such as crickets and cockroaches is an intensively studied model system in invertebrate neuroethology for investigating sensory integration, and the guidance of escape responses (Ritzmann, ’93). In this system, air currents deflect filiform mechanosensory hairs on the cerci, triggering activity in the bipolar sensory neurons at their bases. These hairs are arranged in groups, each with a different directional sensitivity (Edwards and Palka, ’74; Tobias and Murphey, ’79; Landolfa and Jacobs, ’95). The primary afferents from these groups of hairs synapse with both local interneurons and ascending giant interneurons (GIs) within the terminal abdominal ganglion (TAG) (Boyan and Ball, ’90; Bodnar et al., ’91; Baba et al., ’95). Each GI then has a characteristic directional sensitivity that reflects the vector sum of the directionality of afferent inputs that converge on it (Bacon and Murphey, ’84; Jacobs and Miller, ’88), sharpened by additional inhibitory inputs from local interneurons (Levine and Murphey, ’80; Jacobs et al., ’86). The inputs from GIs are integrated with other sensory data within the thoracic ganglia in order to generate the turning and running behavior of the escape response (for reviews see Ritzmann, ’93; Comer and Dowd, ’93). This system has been studied most intensively in cockroaches (Westin et al., ’77; Daley et al., ’81; Kolton and Camhi, ’95; Levi and Camhi, 2000) and crickets (Mendenhall and Murphey, ’74; Kämper, ’84; Jacobs and Murphey, ’87; Heidelbach, ’90; Miller et al., ’91; Kanou, ’96), though some comparative studies have also been carried out on mantids (Boyan and Ball, ’86), tettigonids (Shen, ’83), and acridids (Boyan and Ball, ’89). However, in all the species studied, the cerci extend more or less parallel to the body axis and hence the substrate. This is not always the case. For example, the cerci of the European cave cricket *Troglophilus neglectus* are held perpendicular to the ground.

Orientation with respect to air currents might

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be especially important in a cave environment, e.g., in the absence of visual cues. Therefore, we have attempted to investigate the consequences of different posture of the cerci for the organization and physiological responses of the cercal GI system in this species.

Troglophilus neglectus Krauss (Rhaphidophoridae, Orthoptera) inhabits sub-alpine Karst forests of Slovenia and the Balkan Peninsula. It is a night-active, forest-dwelling species that hibernates in caves. However, many individuals can be found underground in caves, fissures, and cracks throughout the year (Remy, '31; Kastberger and Freitag, '93; Pehani et al., '97). Despite their nocturnal habits, they have normally developed functional eyes (Gogala, '64), but the long antennae and well developed cerci suggest a strong reliance on olfactory, tactile, and mechanosensory modalities. Furthermore, they have well developed subgenual organs that respond sensitively to substrate-borne vibrations and also to airborne sound over a narrow frequency range (Čokl et al., '95). However, tympanal organs in the forelegs are lacking (Jeram et al., '94), and there is no evidence for acoustic communication in this wingless species.

The cerci of *T. neglectus* are 4–5 mm long, densely covered with long filiform hairs, bristle hairs, and campaniform sensilla (Virant-Doberlet et al., '95). As in other orthopteroids, cercal stimulation with wind puffs elicits evasive behavior (Kastberger, '82; Schrader, 2000), presumably mediated by activation of GIs. In this study, we investigated the morphology and directional sensitivity of the cercal GIs in *Troglophilus* using intracellular recording and staining methods. A major aim was to test whether the directional sensitivity of identified GIs of cave crickets differs from those of other species, due to the altered orientation of the cerci. Other things being equal, one might hypothesize that the directional sensitivity of the system would be flipped by 90° from the horizontal to the vertical plane. In order to test this hypothesis, a stimulator was used that allowed wind puffs to be directed at the preparation from a wide range of angles in both the horizontal and vertical planes.

MATERIALS AND METHODS

Animals

Adult cave crickets, *Troglophilus neglectus* Krauss, were collected monthly in northwestern Slovenia. They were kept at 15°C on wet moss under a reversed diurnal rhythm. Both males and females, ranging in age from a few days to eight months after the adult molt, were used in experiments.

Dissection

The metathoracic legs were removed and the cricket was pinned to a wax-coated platform ventral-side-down. The abdominal nerve cord was exposed from the dorsal side by dissecting away the dorsal abdominal body wall and removing the gut and other internal organs. All abdominal segmental nerves were cut, except for the cercal nerves. A silver platform, inserted under the TAG to improve its stability, also served as a reference electrode.

Electrophysiology

Intracellular recordings were made from GIs in the posterior third of the TAG using thick-walled glass microelectrodes filled with 5% Lucifer Yellow in the tip and 0.5 M LiCl in the barrel (impedance 60–100 MΩ). Their responses to wind puffs were amplified conventionally and recorded on tape for later analysis. After collection of physiological data, the impaled neuron was stained with Lucifer Yellow, injected iontophoretically using a constant current of –5 to –7 nA for 5–7 min.

Wind stimulation

Wind puff stimuli were delivered via a plastic tube 3 cm in diameter and 3 cm distant from the cerci. Air flow rate was set at 0.2–0.5 l/min using the regulator valve on the compressed air supply, and wind puffs of 250 ms duration and frequency 0.4 Hz were generated using an electronically controlled valve. This directed the air either toward the insect through the nozzle or to an overflow pipe, thus avoiding pressure build-up between pulses. The nozzle was mounted on a turntable centered on the cerci so that stimuli could be applied from any required angle in the horizontal plane. Alternatively, the nozzle could be rotated transversely through 180° in the vertical plane, the axis being the midline of the insect's body. The experimental set-up, and the coordinate system used to describe stimulus directions, is shown in Fig. 1. Responses to wind puffs (n = 10) were recorded at angular intervals of 15° in both the horizontal and vertical planes. In practice, horizontal stimuli typically started at 0° and proceeded clockwise around the preparation at 30° intervals. Intermediate angles were tested on a subsequent counterclockwise sweep. Similarly, stimuli in the vertical plane were applied at 30° intervals (ten replicates), starting at the animal's left side (0°)

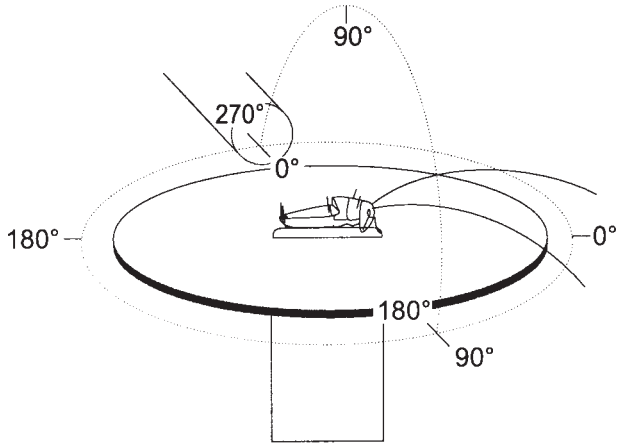

Fig. 1. Experimental setup and the coordinate system. The preparation was mounted dorsal-side-up on an elevated platform, and recordings were made from GIs via a vertically mounted microelectrode (not shown). Wind puffs were delivered via a plastic tube mounted on a turntable so that stimuli could be applied from a range of angles in both horizontal and vertical planes. The convention adopted to describe stimulus direction in the horizontal plane was that 0° indicates wind from frontal and 90° means from the animal's right side. For stimuli in the vertical plane, 0° indicates stimuli from the animal's left side, 90° from vertically above, and 180° from the animal's right side.

and ending at 180° with intermediate angles tested on a return sweep.

Analysis

Electrophysiological data were analyzed off-line using the NEM data-analysis software package (Amon, '93). Directionality plots were based on mean spike counts within a peri-stimulus time window of sufficient duration to include the longest observed response to a wind puff of any interneuron (816 ms, i.e., one-third of the stimulus duty cycle). Where interneurons were spontaneously active, the mean impulse frequency during the 816 ms prior to each wind puff was subtracted from that during the response. Directional characteristic curves for individual interneurons were constructed by expressing the response as a proportion of the peak response at the angle to which that neuron was most sensitive. Relative directional-sensitivity curves for each GI type were derived from the individual responses after smoothing the curves using a moving average procedure.

Responses were recorded from interneurons with their axons in both the left and right connectives but, for convenience, they are presented as if all had been made from the right-sided neurons. Thus, directional curves and anatomical drawings are shown in mirror-image where required so that horizontal directions between 0° and 180° always refer to the axon-ipsilateral side, while angles from 180° to 360° are axon-contralateral. Similarly, in the vertical plane, the axon-ipsilateral quadrant extends from 90° to 180°.

Neural morphology

The TAG was dissected out after dye injection, and fixed for one hour at room temperature in phosphate-buffered 4% formaldehyde (pH 7.4). Preparations were then dehydrated via an alcohol series, and cleared in methyl salicylate for wholemount photography. Wholemount preparations were then viewed and photographed using a Leica DMRB microscope and subsequently embedded in paraffin and sectioned transversely (10–20 m sections).

RESULTS

Interneuronal morphology

Five pairs of ascending interneurons that respond to wind puff stimuli were identified. Their morphology resembles that of GIs 9-1a, 9-2a, 9-3a, 10-2a, and 10-3a of other cricket species (Mendenhall and Murphey, '74; Jacobs and Murphey, '87). Therefore, the same nomenclature is adopted here. In the morphological descriptions that follow, the terms "ipsilateral" and "contralateral" refer to the side of the axon.

All of the GIs identified in *Troglophilus neglectus* share a broadly similar morphology (Fig. 2). Each has a short primary neurite leading to a commissural fiber that crosses the midline in the same neuromere as the soma. Their large diameter axons ascend through the entire CNS (Boyan and Ball, '86), and their dendritic fields are largely confined to the posterior third of the TAG.

The most obvious differences between GIs are in soma position and the precise layout and extent of their dendritic arborisations. As indicated by the naming system, three GIs have their somata in the ninth neuromere and two in the tenth neuromere. Soma position is dorsal in 9-1a, 9-3a, and 10-3a, but ventral in 9-2a and 10-2a (Fig. 2B, D, F, H). The commissural fibers of GIs 9-1a, 9-2a, and 10-2a cross the midline in the dorsal anterior commissure of the corresponding neuromere, whereas those of GIs 9-3a and 10-3a run in the dorsal posterior commissure. The axons of GIs 9-2a, 9-3a, 10-2a, and 10-3a ascend in the dorsolateral tract of the connective, while that of GI 9-1a runs in the ventromedial tract.

GI 9-1a has one large and several small dendritic branches. The smaller dendritic branches

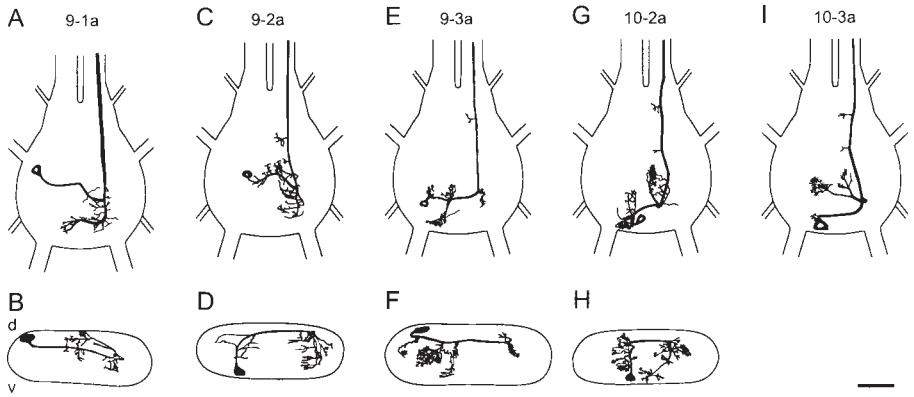

Fig. 2. Comparison of the morphology of five identified GIs in the TAG of *Troglophilus neglectus*. Dorsal views are based on Lucifer Yellow fills viewed as wholemounts (**A**, **C**, **E**, **G**, **I**). Transverse views (**B**, **D**, **F**, **H**) are reconstructed from serial TS sections of the corresponding preparation (Scale bar, 200 μm). The naming scheme corresponds to that adopted for other cricket species.

ramify centrally in the TAG near the posterior commissure. The larger and more prominent dendritic arborisation originates ipsilaterally and posteriorly relative to the axon; it crosses the midline and terminates contralaterally under the dorsal surface of the ganglion (Fig. 2A, B).

GI 9-2a also has one major dendritic branch and several smaller ones. The smaller branches terminate in the ventromedial region of the TAG, near the dorsal commissure. The main dendritic branch extends posteriorly and then subdivides into numerous parallel finer branches that extend first ventrally, then laterally toward the midline (Fig. 2C, D).

GI 9-3a has four discrete arborisations within the TAG. Proceeding from the soma, the first originates from a dendritic branch close to the soma that extends anteriorly and ventrally. Further along the commissural fiber, a prominent dendritic branch extends posteriorly and ventrally to a dense arborisation near the root of the contralateral cercal nerve. A third arborisation, extending ventrally and anteriorly, also originates from the commissural fiber near the midline. A number of fine dendritic branches, extending dorsally and ventrally near the junction of the axon and commissural fiber, form the fourth dendritic field. (Fig. 2E, F).

GI 10-2a has two main regions of dendritic branching: one ipsilateral, and the other contralateral. The ipsilateral field is formed from the branches of two large dendrites originating near the junction of the axon and the commissural fiber. One of these branches arborises ipsilaterally and medially; the other has its branches ventrally near the midline. The contralateral field consists of branches extending anteriorly from the neurite, near the soma (Fig. 2G, H).

The main dendritic fields of GI 10-3a originate from one major branch that extends medially and then subdivides (Fig. 2I). One branch extends laterally and terminates in a dense contralateral arborisation. The other branch extends anteriorly to a more diffuse ipsilateral dendritic field. Typically, GI 10-3a also has a group of short, fine branches originating from the neurite very close to the soma.

Responses to wind puff stimuli

Sufficient physiological data was obtained to characterize the responses to wind puffs of GIs 9-1a, 9-2a, 9-3a, and 10-2a. Each GI type showed a characteristic pattern of directional sensitivity in the horizontal plane (Figs. 3A, 4A, 5A, 6A), whereas directional sensitivity in the vertical plane was rather similar in all the GI types tested (Figs. 3B, 4B, 5B, 6B).

GI 9-1a responded preferentially to wind stimuli from ipsilateral directions (Fig. 3A). Wind puffs evoked a phasic depolarization at stimulus onset ('ON'), and a smaller one at the end of the stimulus ('OFF'). The 'ON' response reached threshold and evoked a brief train of impulses in response to ipsilateral stimuli (Fig. 3C). Stimuli from contralateral directions resulted in subthreshold 'ON' depolarization and single action potentials at the end of the stimulus. In the vertical plane stimula, suprathreshold responses were mainly confined to the ipsilateral quadrant (Fig. 3B).

GI 9-2a responded best to horizontal wind puffs from behind, i.e., 90°–270° (Fig. 4A). These responses consisted of a phasic-tonic impulse dis-

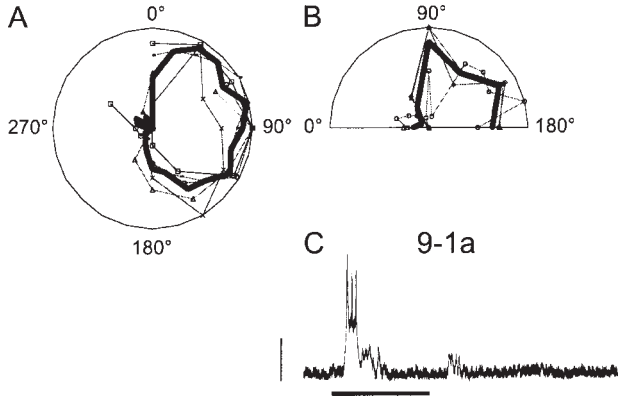

Fig. 3. **A**, **B**: Directional sensitivity of GI 9-1a to wind puffs in the horizontal and vertical planes, respectively. The fine lines indicate the directionality of individual interneurons, while the bold curve shows the mean directionality derived from all neurons tested (A, n = 5; B, n = 4). **C**: Typical response to a horizontal wind puff from 30° (i.e., just to the right of frontal). The horizontal bar shows stimulus timing (duration, 250 ms); vertical scale, 5 mV.

charge, followed in some cases by a brief 'OFF' response. Responses to horizontal air puffs from the anterior sector were, in most cases, small by comparison. On average, GI 9-2a was most sensitive to stimuli from directly behind, and there was no obvious preference for ipsi- or contralateral stimuli. In the vertical plane, there was a strong preference for stimuli from the ipsilateral side with peak sensitivity at elevations between 120° and 150°.

GI 9-3a responds best to horizontal air puffs in a sector from 300° to 120°. Peak responses occurred on average at 30°–45°, i.e., slightly to the right of frontal (Fig. 5A). Responses to stimuli from preferred directions consisted of a phasic-tonic impulse discharge rarely lasting for the duration of the stimulus (Fig. 5C). Responses to wind puffs from the anti-preferred direction had both excitatory and inhibitory components. Typically, there was a brief early phase of depolarization

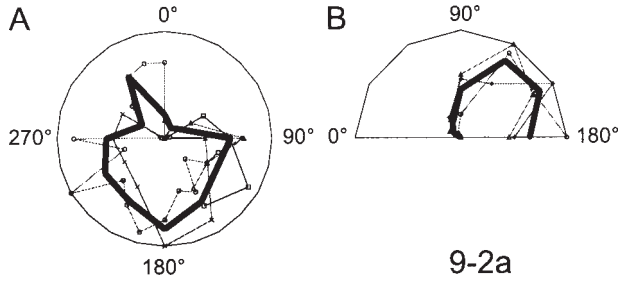

Fig. 4. Directional sensitivity of GI 9-2a in the horizontal (**A**) and vertical (**B**) planes. In each case, bold curves indicate the mean directionality (A, n = 4; B, n = 3) while the fine lines represent responses of individual interneurons.

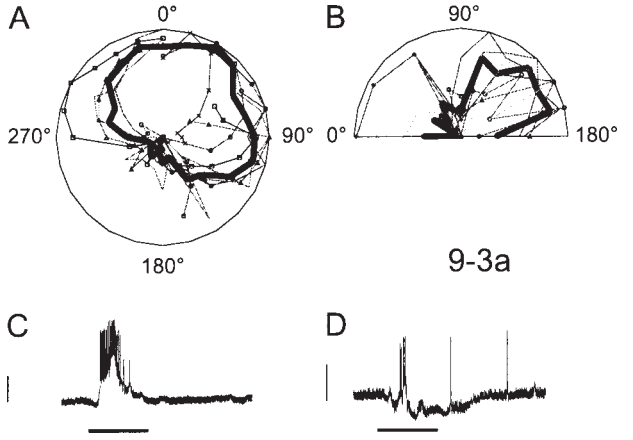

Fig. 5. **A**, **B**: Directional sensitivity of GI 9-3a in the horizontal and vertical planes, respectively. Bold curves show the mean directionality derived from all recorded cells (A, n = 7; B, n = 6). Responses of individual interneurons are indicated by fine lines. **C**,**D**: Typical excitatory response of GI 9-3a to a horizontal wind puff stimulus from 0° (anterior), and inhibition in response to stimulation from 180° (posterior), respectively. Both responses were recorded from the same cell. Horizontal bar indicates stimulus timing (duration, 250 ms); vertical scale, 5 mV.

resulting in discharge of a few impulses. However, this early phase was counteracted by post-synaptic inhibition leading to a net hyperpolarization of the interneuron for the duration of the wind

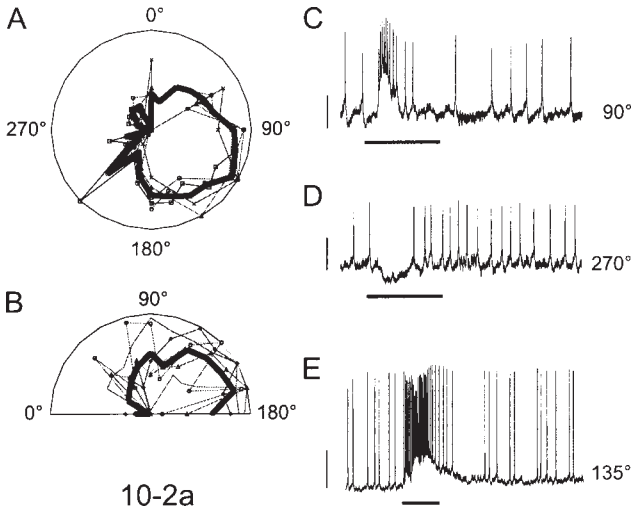

Fig. 6. **A**, **B**: Directional sensitivity of GI 10-2a in the horizontal and vertical planes, respectively. Bold curves show the mean directionality derived from all recorded cells (A, n = 5; B, n = 5). Responses of individual interneurons are indicated by fine lines. **C**–**E**: Characteristic responses of GI 10-2a to horizontal wind puffs from various angles: 90°, i.e., axon ipsilateral (C); 270°, i.e., axon-contralateral (D); and 135°, i.e., rear ipsilateral quadrant (E). Responses in C and D are from the same cell. Horizontal bars show stimulus timing (duration, 250 ms); vertical scales, 5 mV (C, D); 10 mV (E).

puff (Fig. 5D). In the vertical plane, GI 9-3a, like the GIs described previously, was only weakly responsive to stimuli from the contralateral side (0°–90°). Peak sensitivity occurred for ipsilateral stimuli in the elevation range 105°–165° (Fig. 5B).

In the horizontal plane, GI 10-2a was best stimulated by ipsilateral wind puffs. On average, the cell was most sensitive to stimuli from about 120° (Fig. 6A). In the vertical plane, GI 10-2a responded primarily to ipsilateral wind puffs, and on average was not very sensitive to elevation within that range (Fig. 6B). The nature of the responses is shown in Figure 6C–E. GI 10-2a was always found to be spontaneously active in the absence of wind (5–50 imp/s, n = 5). Horizontal wind stimuli from preferred directions superimposed a high frequency burst of impulses elicited by a large compound EPSP (Fig. 6C, E). Wind puffs from the anti-preferred direction elicited post-synaptic inhibition, resulting in membrane hyperpolarization that transiently reduced or eliminated the spontaneous discharge (Fig. 6D).

DISCUSSION

Organization of the cercal GI system

We identified five pairs of wind-sensitive giant interneurons in *Troglophilus* but this may not be the full complement. Cross-sections of the connectives in lucifer yellow-stained preparations showed that the neurons described here are those with the largest fiber diameter. However, there are three other ventral pairs of large diameter axons (5–10 μm) in the last abdominal connectives, some of which might also belong to wind-sensitive giant interneurons. The basic structure of the wind-sensitive GIs found in *Troglophilus* resembles that found in representatives of other orthopteroid groups that have been studied. Thus, key features such as soma position, the commissures in which neurites cross the midline, and the tracts in which axons ascend, can be used to assign probable homologies with corresponding interneurons in other species without a detailed study of the embryonic origins of each neuron (Jacobs and Murphey, ’87).

The precise layout of dendritic arborisations between different orthopteroid groups is more variable. Given the taxonomic position of *Troglophilus* in the Rhaphidophoridae, it was unclear prior to this study whether patterns of dendritic branching in its GIs would most closely resemble those found in blattids, tettigonids, or crickets. The results clearly show a similarity with the GIs of crickets, so we adopted the naming system developed for cricket GIs and compare their directional sensitivity with their putative cricket homologues. There can be little doubt about the homology of the dorsal GIs 9-2a, 9-3a, 10-2a, and 10-3a between crickets and cave crickets. Neuroanatomically, they appear to be virtually identical, not only in the three main diagnostic features, but also in the shape and position of their dendritic arborisations (compare Mendenhall and Murphey, ’74; Kämper, ’84; Jacobs and Murphey, ’87; Heidelbach, ’90; Kanou, ’96). This cannot be said of the ventral GI 9-1a in *Troglophilus*. Though it resembles its namesake in other cricket species in terms of the key features, there are substantial differences in the extent and location of the dendritic arbour compared to gryllids (Mendenhall and Murphey, ’74; Kämper, ’84; Jacobs and Murphey, ’87; Heidelbach, ’90; Kanou, ’96). In crickets, the dendritic field of 9-1a is narrowly confined and strictly ipsilateral to the axon, whereas in cave crickets the arborisation is more extensive and includes a prominent axon-contralateral dendritic field (Fig. 2A, B).

Physiological responses and directional sensitivity

A full investigation of GI directionality would require testing the responses to wind puffs at a full range of azimuths and elevations in order to build up a three-dimensional map of each neuron’s response. Measured against this standard, our study of responses in only the vertical and horizontal planes is very limited. However, it does reveal that, in the vertical plane, all the GIs studied have rather similar directional characteristics. All responded vigorously to ipsilateral wind puffs, almost irrespective of elevation, and responded much more weakly to contralateral stimuli. Thus, although there is little evidence for discrimination of different stimulus elevations, there is, at least, a strong and consistent lateralization of the response. This would be sufficient to direct an escape jump away from, rather than toward, a lunging predator.

In contrast, each of the identified cave cricket GIs recorded showed a marked and characteristic directional sensitivity to wind puffs in the horizontal plane. In the case of the dorsal GIs 9-2a, 9-3a, and 10-2a, the directionality resembled those of their neuroanatomically similar counterparts in gryllids (Bacon and Murphey, ’84; Miller et al., ’91; Kanou, ’96). The situation is different in the case of the ventral GI 9-1a. Measurements in *G. campestris* and *G. bimaculatus* suggested peak

sensitivity to wind from anterior and antero-ipsilateral directions (Bacon and Murphey, '84; Kanou, '96). The directionality of GI 9-1a in *Troglophilus* is different, since its best direction is ipsilateral (Fig. 3A). The distribution of preferred directions of GIs, i.e., centered on about 30° (9-3a), 90° (9-1a), 110° (10-2a), and 180° (9-2a), suggests some form of spatial range fractionation that underlies the animal's directional, wind-evoked escape responses (Schrader, 2000). However, the further processing of these inputs must be complex given the very different response patterns and sensitivity of the individual units. For example, the GI 9-1a response was phasic, GI 9-2a and 9-3a responses were phasic-tonic, and the response of 10-2a was tonic and superimposed on a resting discharge.

The directional sensitivity of GIs was clearly not determined solely by the strength of direct excitatory inputs from cercal afferents. At least in 9-3a and 10-2a, the directionality was partly shaped by post-synaptic inhibition elicited by wind puffs from anti-preferred directions (Fig. 5D, 6D). This inhibition was of longer latency than the concurrent monosynaptic excitation from cercal afferents, indicating its likely poly-synaptic origin. A consequence of this was that there was often a brief excitatory response to wind puffs from nonfavored directions before the inhibitory inputs took effect (Fig. 5D). The role of such poly-synaptic inputs in shaping GI directionality has long been recognized in particular GIs of crickets, e.g., GI 8-1a (Matsumoto and Murphey, '77), GI 10-2a (Levine and Murphey, '80), and 10-3a (Levine and Murphey, '80; Jacobs et al., '86). Concurrent inhibitory inputs may also serve to extend the dynamic range of excitatory responses (Jacobs et al., '86; Baba et al., 2001). Baba et al. ('95) described many spiking and nonspiking local interneurons in the cricket TAG and proposed a general model of their connectivity and role in processing wind inputs. However, to our knowledge, firm evidence for specific connections between particular inhibitory local interneurons and GIs is still lacking. In cave crickets, one local spiking and one nonspiking interneuron have been identified so far (Schrader, 2000), but their function remains to be investigated in detail.

Clearly, the 'null' hypothesis that a 90° shift in cercal orientation relative to that in most gryllids would lead to a comparable shift in the plane of optimum directional discrimination is not correct. At some level, compensatory adaptations have been built in so that strong directional sensitivity and range fractionation in the horizontal plane is retained despite the altered orientation of the cerci. These compensatory adaptations are not at the level of GI neuroanatomy. With the possible exception of GI 9-1a, the dendritic arbors of the GIs in *Troglophilus* and gryllids are very similar. Below, we argue that this compensation involves reorientation of the directional sensitivity at the level of the cercal sensory array.

In crickets, the sensory hairs on the horizontally aligned cerci can be divided into four groups based on their directional preference. Two of these groups, consisting of hairs that deflect longitudinally to the cercus (L hairs), respond best to anterior and posterior stimulation, respectively. The other two groups of hairs deflect transversally to the cercus (T hairs) and respond best to stimuli from the left and right sides (Edwards and Palka, '74; Tobias and Murphey, '79). The sensory neurons innervating the hairs with the same directionality then project to the same areas of the TAG (Bacon and Murphey, '84). Consequently, anterior, posterior, lateral, and medial stimulus directions are represented in four specific areas located bilaterally within the TAG. The dendritic arborisation of each GI receives input from a particular subpopulation of cercal afferents, and GI directionality is then largely determined by the vector sum of directional sensitivities of that sub-population (Bacon and Murphey, '84; Jacobs and Miller, '88).

Where the cerci are oriented vertically, as in *Troglophilus*, the situation is rather different, since all wind directions in the horizontal plane are perpendicular to the cercus and will thus deflect only T hairs. Thus, the observed GI directionality in this plane must reflect some degree of topographic projection of T hair afferents with particular directional tuning. The projection pattern of cercal afferents with different directionalities has not been investigated in cave crickets. However, the remarkable similarity in morphology and directionality of dorsal GIs in *Troglophilus* and gryllids suggests that they have similar topographic projections of directional information into the TAG via the cercal afferents. What has changed is the polarity of the hairs on the cerci required to provide the necessary directional information. In the one case where GI directionality in *Troglophilus* differed significantly from that found in crickets, there is a corresponding difference in GI morphology. Specifically, the presence of a contralateral arborisation of GI 9-1a that is absent in crickets is correlated with a shift in best direction from antero-ipsilateral to ipsilateral. One explanation of this shift is that the contralateral

arbor receives additional inputs from sensilla on the axon-contralateral cercus that are sensitive to axon-ipsilateral directions.

One remaining question concerns which sensillae are activated in response to stimuli in the vertical plane. Here, L type hairs would be expected to play a role. However, they are relatively few in number in *Troglophilus* (Virant-Doberlet et al., '95). Therefore, we suspect that a major component of responses to stimuli in the vertical plane is due to deflection of transverse sensory hairs by the horizontal component of oblique air currents. If so, then one would expect that the best direction in the vertical plane would be 180° (i.e., ipsilateral). In practice, peak responses occurred at intermediate elevations. However, the reduced responses at 180° may well be caused by a reduced stimulus intensity due to drag effects near the ground plane.

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