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Responses of Giant Interneurons of the Cockroach *Periplaneta americana* to Wind Puffs of Different Directions and Velocities *

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Summary. 1. Controlled wind puffs of different directions and velocities were delivered to the cerci of cockroaches (*Periplaneta americana*), while the responses of individually identifiable giant interneurons (GI's) were recorded intracellularly.

2. All fourteen histologically identified GI's (seven bilateral pairs) respond with a burst of action potentials to wind from some or all directions. The directional sensitivity of a given GI is consistent from animal to animal (Fig. 7).

3. Varying the angle of delivery of wind puffs revealed that, in each side of the nerve cord, two GI's (2, 4) show little or no directional selectivity, two GI's (1, 7) have a greater response to wind from the ipsilateral side, two GI's (3, 6) respond primarily to wind from in front of the animal, and one GI (5) responds primarily to wind from the ipsilateral rear quadrant (Fig. 7). These directional properties are independent of wind velocity up to at least 2.6 m/s (Fig. 8).

4. Varying the peak velocity of the wind stimuli (delivered from each GI's maximal response angle) showed that the number of action potentials evoked increases with wind velocity up to at least 2.6 m/s for some GI's (1, 5, 6, 7), while the number does not increase with velocity beyond 0.5 m/s for others (2, 3, 4) (Fig. 9).

5. Covering or removing the cercus contralateral to a given GI reduced the response of each GI without appreciably altering its directional selectivity (Fig. 11A). Eliminating the ipsilateral cercus also moderately reduced the responses of some GI's (4, 5, 7), but nearly or completely abolished responses in others (GI's 1, 2, 3, 6) (Fig. 11B).

* A preliminary account of this work has been published (Langberg, Westin and Camhi, 1976)

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6. The spike frequencies of the GI's in response to "standard wind puffs" (peak velocity 0.6 m/s or 2.6 m/s) are high, with maintained frequencies often over 300 spikes per s (Table 1), and instantaneous frequencies some times over 900 per s (Fig. 10).

7. The directional selectivity, high spike frequency, and rapid conduction velocity of the GI's may be adaptations for mediating the short latency, directional evasive behavior of the cockroach. The results are discussed in terms of the presumed role of the GI's in this behavior and implications for sensory integration.

Introduction

A puff of air directed at a cockroach, *Periplaneta americana,* evokes evasive running behavior (Roeder, 1948). This response is oriented away from the source of wind (Camhi and Tom, in preparation). Giant interneurons (GI's) of the cockroach were originally assumed to mediate this evasive behavior (Roeder, 1948). Subsequently, the role of the GI's was questioned (Dagan and Parnas, 1970; Iles, 1972). However, recent evidence supports the original view, since selective stimulation of individual GI's can result in the excitation of leg motor neurons involved in escape behavior (Ritzmann and Camhi, 1976 and in preparation). Since the GI's appear to be involved in an oriented behavior, one might predict that they encode information about wind direction. This seemed especially likely, since the sensory neuron known to excite the GI's are directionally selective (Nicklaus, 1965). Thus, the major goal of our work was to determine whether the GI's respond selectively to wind direction.

The sensory neurons which excite the GI's are connected peripherally with filiform hairs on the cerci, two posterior abdominal appendages. Each sensory cell is excited when air displacement deflects its filiform hair (Pumphrey and Rawdon-Smith, 1937; Roeder, 1948; Callec et al., 1971). (Very similar hairs of caterpillars have been shown to respond to air displacements and not to fluctuations in air pressure; Markl and Tautz, 1975.) Each hair has a preferred plane of deflection which confers upon its single sensory neuron a limited angular range of responsiveness (Nicklaus, 1965; Gnatzy, 1976). Specific connectivity patterns between these afferents and the GI's could therefore give rise to directional selectivity in the GI's.

Each side of the ventral nerve cord of *Periplaneta* contains the axons of at least 7 GI's (20–50 μm in diameter) (Parnas and Dagan, 1971). Their cell bodies are located in the terminal abdominal ganglion, and some of their axons extend through the nerve cord at least to the prothoracic ganglion (Spira et al., 1969; Farley and Milburn, 1969). The axons of 14 GI's (seven bilateral pairs) can be individually identified histologically, since each assumes a characteristic position in the abdominal ganglia (Harris and Smyth, 1971; Camhi, 1976; see also below).

We have characterized the responses of the 14 identifiable GI's to wind from different directions and of different velocities. Each histologically identified GI shows a consistent response pattern from animal to animal. Some GI's

respond to wind from all directions, while others are excited by wind from a restricted range of angles. Lowering the intensity (peak velocity and acceleration) of the wind stimulus decreases the number of action potentials evoked but does not appreciably affect the directional selectivity. The GI's differ in the range over which they detect changes in wind velocity. These and other properties of the GI's are discussed in relation to their sensory inputs and the evasive behavior which they apparently control.

Materials and Methods

Adult male *Periplaneta americana* were used in all experiments. These were raised locally on Agway Laboratory Chow and kept at 22–24 °C. At the start of an experiment, an animal was anesthetized with CO_2. We then cut off the legs and wings and pinned the insect dorsal side up on a wax platform. The animal was positioned so that the cerci protruded over the edge of the platform. The nerve cord was exposed by removing the abdominal terga and the gut. A pair of hook electrodes was placed under the connectives between the 1st and 2nd, or 2nd and 3rd abdominal ganglia (A1–2 or A2–3) and insulated with a mixture of Vaseline and paraffin oil. We recorded intracellularly from axons in the A4–5 connectives, which were carefully raised onto a wax-covered platform and superfused with saline (Callec and Satelle, 1973). Action potentials were recorded intracellularly from the GI's using glass microelectrodes filled with 4% Procion Yellow plus 0.2 M KCl (resistance 50–200 Megohms). These were amplified with a WPI M701 D.C. preamplifier. Extracellular action potentials from the whole cord were amplified with a Grass P511 AC amplifier. The neural responses and a monitor of the wind stimulus were displayed on a Tektronix 547 oscilloscpe and photographed with a Grass kymograph camera.

At the end of each experiment, Procion Yellow was iontophoresed into the putative giant axon by passing 1.5×10^{-7} amps (DC or 200 ms pulses at 2 Hz) for approximately $^1/_2$ h. The abdominal nerve cord was then fixed in aqueous Bouin's fixative for 10 min, or in 10% formalin in saline overnight. The fixed tissue was dehydrated with a standard alcohol series, embedded in paraffin and serially sectioned at 10 μm. We subsequently identified procion-filled cells by observing cross sections of the abdominal ganglia with a fluorescence microscope.

The experimental set-up is shown in Figure 1. A wind puff was generated when a solenoid depressed a rubber membrane stretched across the wide end of an 8″ funnel, and this puff was delivered to the animal through a curved copper tube of 19 mm internal diameter. The copper tube could be pivoted about a coaxial joint located directly above the cerci. When so rotated, the open end described a circle in the horizontal plane, whose center was the midpoint between the bases of the two cerci (Fig. 1). Because of the coaxial joint, the internal geometry of the delivery tube was independent of the angle of the tube.

To reduce turbulence, the wind puffs were filtered by several fine metal screens placed at intervals within the tube (Fig. 1A). The cockroach was positioned such that the bases of the cerci were about 1 cm from the open end of the tube. Considering the peak velocity of the wind, the delivery tube diameter, the filtering screens and the position of the animal, it was theoretically probable that wind arriving at the cockroach's cerci would be laminar.[1] We tested the laminarity of the wind using the miniature probe of an anemometer (Flow 55A1, Gould Corp., Wilmington, Mass.) located just between the cerci. The resonant frequency of the hairs (250 Hz; Counter, 1976) falls within the instrument's frequency range (approx. 0–1 kHz). Since little turbulence is

[1] We calculated the maximum Reynolds number $\left(R = \frac{\text{tube diam.} \times \text{air vel.} \times \text{air density}}{\text{air viscosity}}\right)$ (Venard and Street, 1975) for a "standard" outward puff (see below) in our system as 3600. Though a Reynolds number above 2100 may cause turbulence, laminarity is still probable because of the filtering screens. For wind leaving an open tube, laminar flow is maintained within a conical volume extending from the perimeter of the open tube to a point centered approximately one diameter (19 mm) in front of the tube. The cerci were within this cone

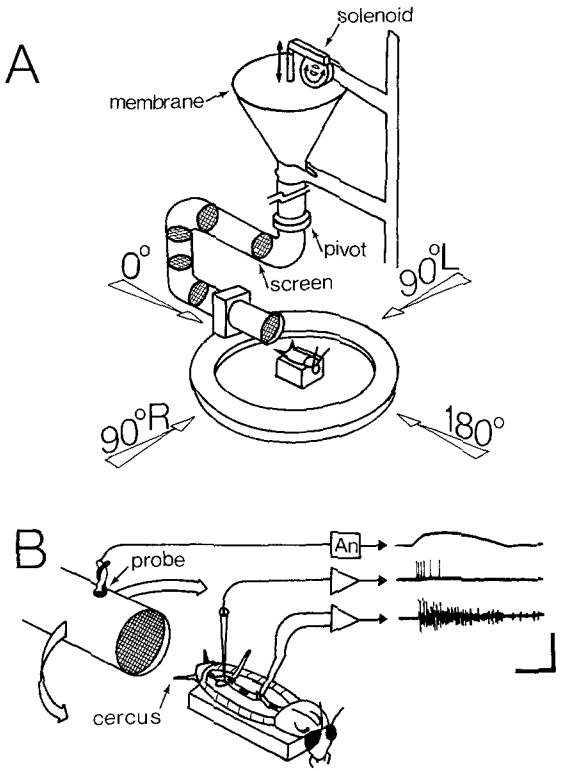

Fig. 1A and B. Experimental set-up. **A** Apparatus used to produce wind puffs (see text for details). Wind angle labels show conventions used throughout this paper. **B** Arrangement of recording electrodes and wind monitor probe. An: anemometer. Top trace: Instantaneous wind velocity (peak velocity 2.6 m/s). Middle trace: Intracellular recording from GI 2. Bottom trace: Extracellular recording from the whole nerve cord. Horizontal calibration bar: 20 ms, vertical calibration bar: 100 mV (intracellular trace)

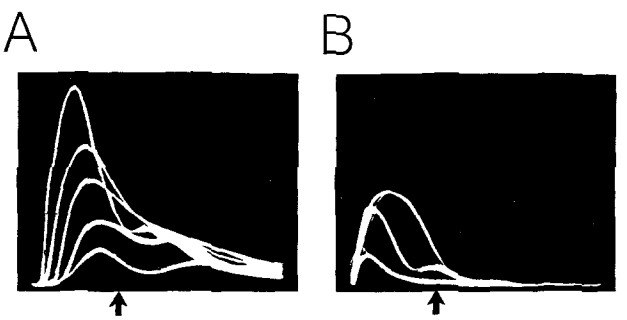

Fig. 2A and B. Wind stimulus. **A** Wind expelled from the wind delivery tube at peak velocities of 2.6 m/s (standard puff), 1.4 m/s, 0.6 m/s, 0.3 m/s and 0.1 m/s (5 traces superimposed at each velocity). **B** Wind drawn into the tube at peak velocities of 0.6 m/s (standard puff), 0.4 m/s, 0.1 m/s (5 traces each). Calibration bar: 50 ms. The responses of all GI's are generally terminated by the time indicated with an arrow

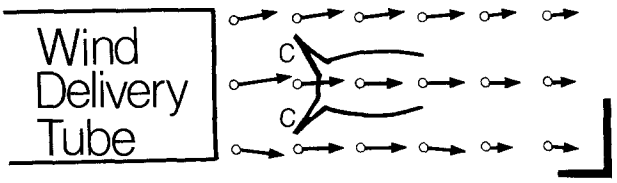

Fig. 3. Map of "wind field". The wind delivery tube and an outline of the experimental animal are shown (vertical calibration bar: 1 cm). The peak velocity of a standard outward puff at points represented by hollow circles is indicated by the length of the attached arrows (horizontal calibration bar: 2.6 m/s wind velocity). The direction of air movement at each point corresponds to the direction of the arrow. The direction of air displacement was measured by observing the deflection of a small (1 mm) wax sphere suspended by an extremely fine wire. The local velocity was calculated by measuring with an anemometer the wind velocity in a 2 mm ID tube positioned at different points, and normalizing this value with respect to the known standard wind puff velocity at the base of the cerci

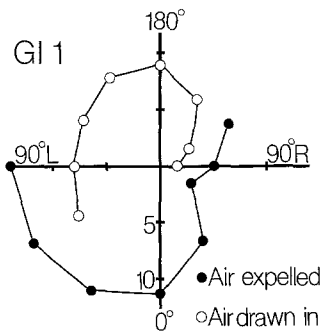

Fig. 4. Method of plotting data. Polar plot of number of action potentials per wind puff vs. stimulus angle for a left GI 1. The center corresponds to the midpoint between the bases of the cerci, and wind angle is represented by angle about this point (Fig. 1A). Distance from the center represents number of action potentials, and bars on radii indicate increments of 5 AP's. Closed circles represent responses to wind expelled from the tube, open circles to wind drawn into the tube. (Each point is the mean of five trials. $\sigma < 1$ for all points.) The two halves of the curve are not continuous, presumably because of the different peak velocities (or accelerations) of the outward and inward wind puffs (Fig. 2)

seen superimposed on the recorded wind puff (Fig. 2), our wind puffs are probably causing unidirectional deflections with little or no vibration of the hairs. In fact, displacement, but not vibration, is visible under the dissecting microscope at 25X.

In some experiments, the intensity of the wind puff was varied by mechanically limiting the excursion of the solenoid. The experimental apparatus did not allow for 360° rotation of the delivery tube. However, release of the solenoid caused air to be drawn into the tube. This inwardly drawn puff was used to simulate wind originating from 180° with respect to the delivery tube.

During experiments, the wind stimulus was monitored using the miniature probe of the anemometer positioned in the center of the delivery tube, 1.5 cm from the open end. This signal had been calibrated by comparison with the signal from a second probe placed directly between the tips of the cerci. The wind stimulus recorded at the cerci is highly reproducible within an experiment (Fig. 2). We generally used wind puffs of 2.6 ± 0.3 m/s peak velocity for wind expelled from the tube, and 0.6 ± 0.1 m/s peak velocity for wind drawn into the tube. We shall refer to these as "standard puffs" of outward and inward wind. Such "standard puffs" and wind puffs of lower peak velocities are shown in Figure 2. Note that outward wind puffs with greater peak velocities also had greater accelerations (Fig. 2).

A map of the "wind field" (the magnitude and direction of air movements at several points) for wind expelled from the tube, shows that wind angle varied by no more than 10° and velocity by less than $\pm 5\%$ in the region of the cerci (Fig. 3).

Throughout this paper, we will use the conventions for wind angle shown in Figure 1A: 0° corresponds to wind moving from posterior to anterior along the long axis of the body, and 180° to wind moving from anterior to posterior. 90° R represents wind moving from right to left perpendicular to the long axis of the body, and 90° L represents wind moving from left to

right (Fig. 1A). In each experiment, the angle of the delivery tube was varied between 120° R and 90° L in increments of 30°. The sequence was 0° to 90° L, then 0 to 120° R, ending with a retest at 0°. At each angle, the responses to five equal puffs of outwardly flowing air were recorded alternately with the responses to five inward puffs. The interval between successive stimuli at a given angle was 10 s, and between successive angles greater than 10 s. In only 11% of the experiments was there a difference of greater than 30% between initial and final responses recorded with the delivery tube positioned at 0°. Data from these experiments were not used in our analysis. In some experiments, the responses to several different velocities of wind were also recorded at some or all angles. The method of plotting data is shown in Figure 4.

Results

A. Position of the Fourteen Giant Interneurons

GI's that were impaled were identified histologically (Fig. 5). The axons of the GI's form a dorsal and a ventral bundle in each of the two connectives of the nerve cord. The GI's of the ventral bundle have been numbered 1–4 (Harris and Smyth, 1971). We have designated the dorsal GI's as 5, 6 and 7 (Fig. 5A). Although the relative positions of the GI's in the connectives may vary, the ventral GI's consistently occupy characteristic positions in the abdominal ganglia (Camhi, 1976). The positions of the dorsal GI's in the ganglia are almost as invariant. In only two out of 46 experiments on dorsal GI's was there a discrepancy between the position of the axon and the response pattern found for that position in other animals. A procion filled right GI 6 is shown in Figure 5B.

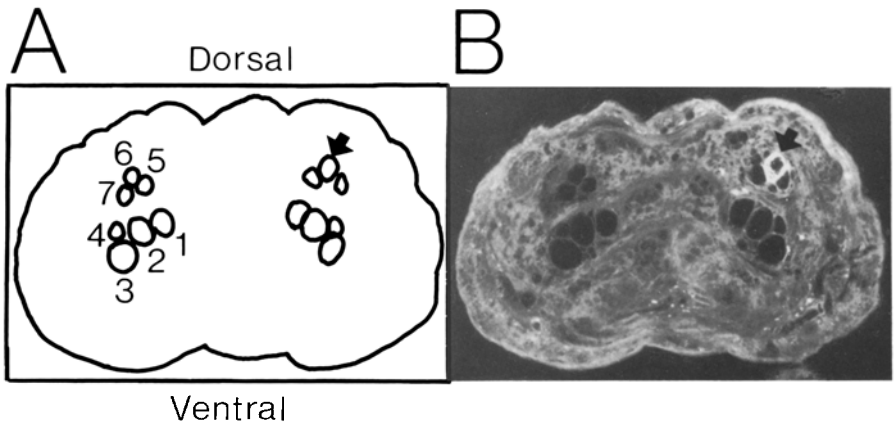

Fig. 5A and B. Identification of GI's. **A** Diagram of a cross-section of an abdominal ganglion showing the characteristic positions of the seven identified GI's in each half of the nerve cord. **B** Cross-section of an abdominal ganglion photographed through a fluorescence microscope. The right GI 6 (arrow) is filled with Procion Yellow

B. Directional Selectivity of the Giant Interneurons

Each of the fourteen GI's (seven bilateral pairs) responds with a burst of spikes to a "standard" puff of wind (see Methods section) from at least some directions. Only GI 4 (left and right) shows ongoing activity in the absence of a stimulus. The responses to puffs from different angles were analyzed in terms of four parameters—number of spikes evoked, mean spike frequency, burst duration and 1/latency. For a given GI, most of these parameters showed similar variation with wind direction (GI's 2 and 5, Fig. 6). Because of the ease of analysis, we shall present all subsequent directional data in terms of numbers of spikes evoked per wind puff.

We have measured the directional responses of one hundred and five GI's identified by Procion injection: 21 GI 1's, 17 GI 2's, 15 GI 3's, 6 GI 4's, 15 GI 5's, 20 GI 6's,14 GI 7's. We have also recorded from 67 wind responsive units for which the Procion fill was inadequate for identification. The directional curves of all these units were consistent with one of the seven GI's from that connective. Also, two wind responsive units were recorded for which the Procion fill indicated that the axon was not one of the 14 identified GI's. (Both were ventro-medial to the ventral bundle of GI's, and their responses were directional.) Contralaterally homologous GI's showed directional responses that were mirror images of each other. Consequently, to simplify presentation of the data, direc-

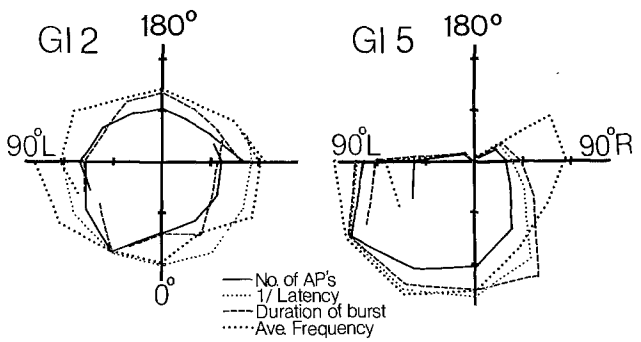

Fig. 6. Variation of response parameters with wind angle for a GI 2 and a GI 5. Polar plots constructed as in Figure 4. *No. of AP's:* number of action potentials per wind puff. Bars mark intervals of 5 AP's. Graphs of other parameters are drawn to a scale such that all graphs intersect at 30° L (GI 2) or 60° L (GI 5), the angles giving the greatest number of AP's in these two experiments. *Latency* is measured from the moment voltage is applied to the solenoid to the occurrence of the first AP. *Ave. frequency:* average frequency of action potentials within a burst. The values of all parameters (mean of five trials) for this GI 2 at 30° L and for this GI 5 at 60° L are as follows:

	GI 2	GI 5
No. of AP's	10.2	14.4
1/Latency	$1/14\ ms^{-1}$	$1/20\ ms^{-1}$
Duration of burst	30 ms	50 ms
Ave. frequency	$315\ s^{-1}$	$252\ s^{-1}$

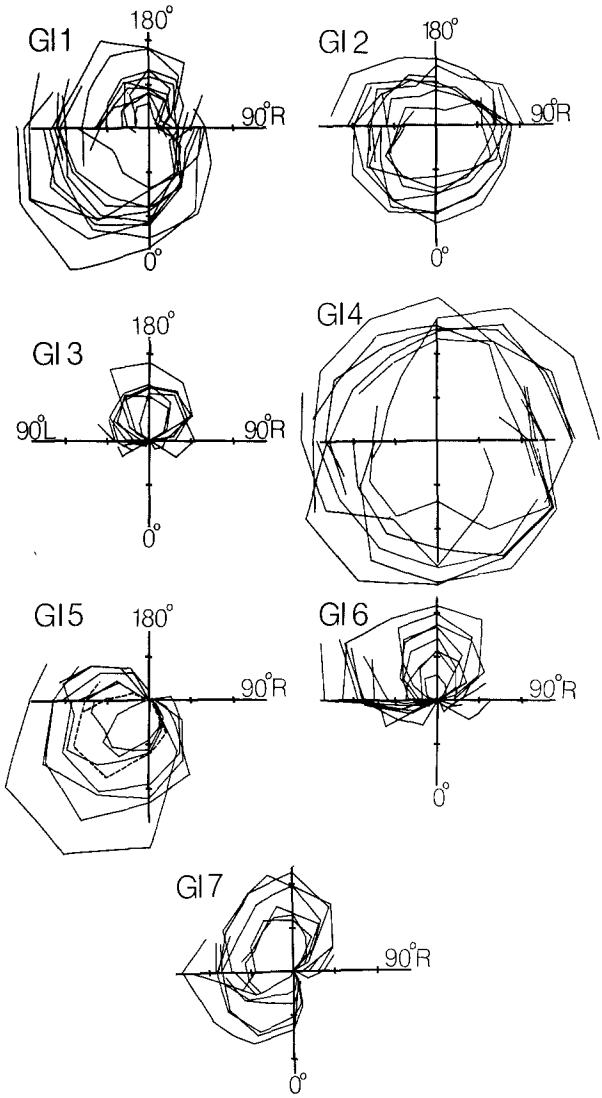

Fig. 7. Directional selectivity curves for all seven histologically identified GI's. Polar plots of number of action potentials vs. wind angle constructed as in Figure 4. For each GI, curves from several different animals are plotted as if recorded from the left connective (see text for details). Each point represents the mean of five trials, all σ's < 1.5. Dotted line of GI 5 explained in text

tionality curves are plotted as if all recordings were from the left connective. Curves of data from the right connective are plotted as mirror images.

Figure 7 shows the responses of the GI's to standard puffs of wind from different directions. For each GI, curves of data from several animals are plotted. For each of the seven GI's on each side, the shape of the directional response curve is consistent from animal to animal. GI's 1, 2 and 4 respond to wind from all directions, though GI 1 has a smaller response to wind from its contralateral side. GI 7 is similar to GI 1, except that it shows a region of no response

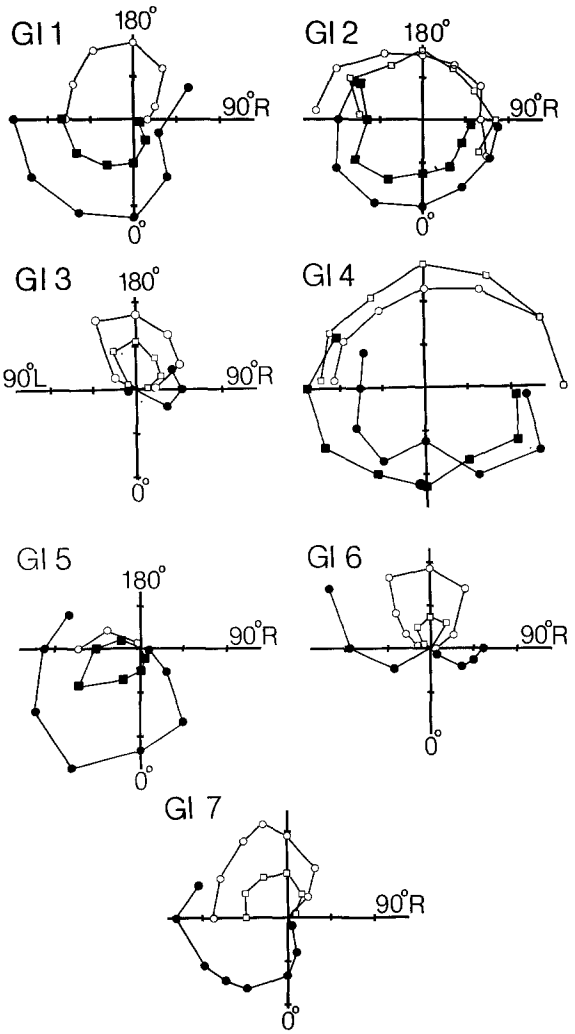

Fig. 8. Effect of peak wind velocity on directional selectivity. Polar plots contructed as in Figure 4. Circles represent number of action potentials in response to standard wind puffs of about 2.6 m/s peak velocity for outward puffs (closed circles), and 0.6 m/s for inward puffs (open circles). Squares represent responses from the same animal to a lower peak velocity of outward (closed squares) or inward (open squares) wind. Lowered velocities of wind used are as follows: GI 1 – 0.1 m/s, GI's 2, 3 and 4 – 0.01 m/s, GI 5 – 0.1 m/s, GI 6 – 0.04 m/s, GI 7 – 0.3 m/s. When responses to reduced velocity are shown for both outward and inward puffs (GI's 2 and 4), the outward and inward peak velocities were the same. Curves shown are representative of a total of 37 successful experiments of this type

in its contralateral rear quadrant. The other cells are more directionally selective: GI's 3 and 6 respond primarily to wind from the front of the animal[2], and

[2] GI's 3 and 6 have similar directional curves for wind drawn into the tube. However, GI 6 seems to have a greater ipsilateral response for wind expelled from the tube. Wind drawn into the tube may have a greater variation in its directional components than wind expelled from the tube (Fig. 3)

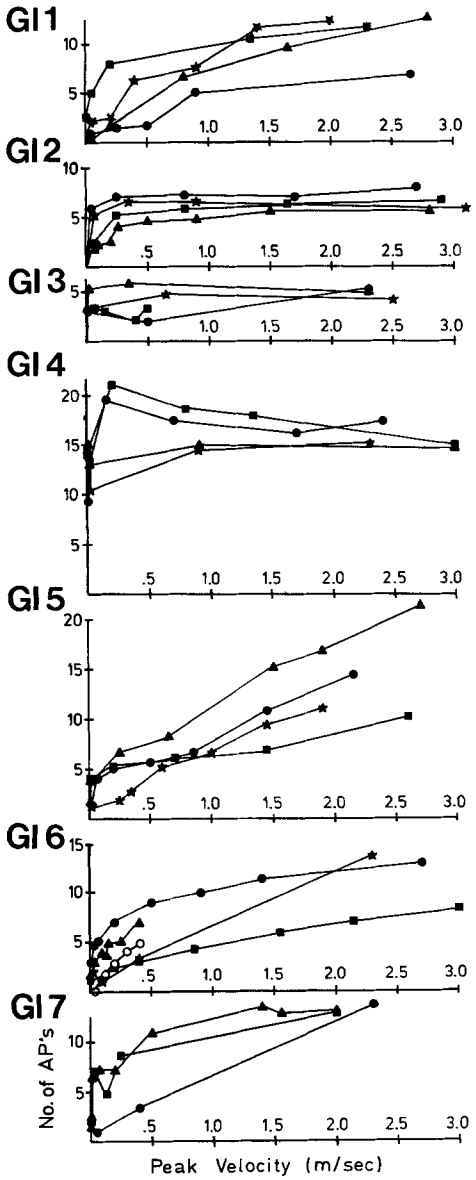

Fig. 9. Effect of peak wind velocity on response magnitude. Number of action potentials (ordinate) in response to different peak velocities of wind (abscissa). For each GI, curves from several different animals are plotted. Where possible, outward wind puffs were delivered from the maximal response angle for a given GI. In GI's 3 and 6, whose maximal responses occur at angles where inward puffs must be used, we sometimes used the angle giving the best response to outward puffs (longer curves), and sometimes the angle giving the greatest possible response (shorter curves)

GI 5 responds primarily to wind from the rear ipsilateral quadrant. Although we systematically investigated responses to wind only within the horizontal plane, we recorded from one identified GI 5 in an animal whose last few abdominal segments, and thus the attached cerci, had been fixed downward at an angle of about 30°. The directional curve of this cell was indistinguishable from that of other GI 5's (dotted curve in Fig. 7).

We investigated the effect of wind intensity on the directional selectivity of the seven GI's. (Though we measured changes in peak wind velocity, the

acceleration of the puff also varied.) Wind puffs of lower intensity never altered the general shape of the directional curve (Fig. 8).

C. Encoding of Wind Intensity by the GI's

We measured the number of spikes evoked by wind puffs of different intensities delivered from the angle of maximal response of each GI. All the GI's respond to puffs of less than 0.1 m/s peak velocity (Figs. 8, 9). For many of the GI's, the number of action potentials per stimulus increases with increasing intensity up to at least 2.6 m/s. However, the responses of GI's 2, 3 and 4 plateau below 0.5 m/s. Other parameters (1/latency, mean spike frequency, and burst duration) show similar, but more erratic, variation with velocity for the different GI's. GI's 2 and 4 (which are the least directional GI's; Fig. 7) differ from each other in that the curve for GI 4 shows a more rapid rise and higher plateau (Fig. 9), and GI 4 shows ongoing activity.

D. Temporal Properties of the Responses in the GI's

The GI's also differ in terms of the time course of their response. Figure 10 shows the instantaneous frequency vs. time for the response of each GI to a standard puff of wind delivered from its optimal angle. The instantaneous spike frequency generally decreases over time. The burst of GI 2 has the highest initial frequency, the most rapid decline in frequency, and the earliest termination. The mean spike frequency of a GI response to a standard puff is unusually high – over 350 spikes per s in GI 2 (Table 1). The instantaneous spike frequency for the first interspike interval of GI 2 was often over 900 per s (Fig. 10).

GI	Mean spike frequency $\pm\sigma$ (per s)	n
1	323 ± 65	8
2	354 ± 79	11
3	290 ± 62	5
4	307 ± 35	7
5	269 ± 34	8
6	207 ± 61	8
7	214 ± 57	7

Table 1. Mean frequencies of action potentials in different GI's. For each burst, mean frequency was calculated as: [# of AP's − 1] duration of burst (s). For each animal, we averaged the mean frequencies of five bursts recorded at the angle of maximal response. (Thus, for GI's 3 and 6, inward puffs were used.) For each GI, we then averaged the mean frequencies of several (n) animals

E. Sensory Inputs to the Giant Interneurons

It is known that sensory neurons from the cercal filiform hairs excite at least some of the GI's (Roeder, 1948; Callec et al., 1971). However, to insure that this sensory input is responsible for the responses reported here, we carried

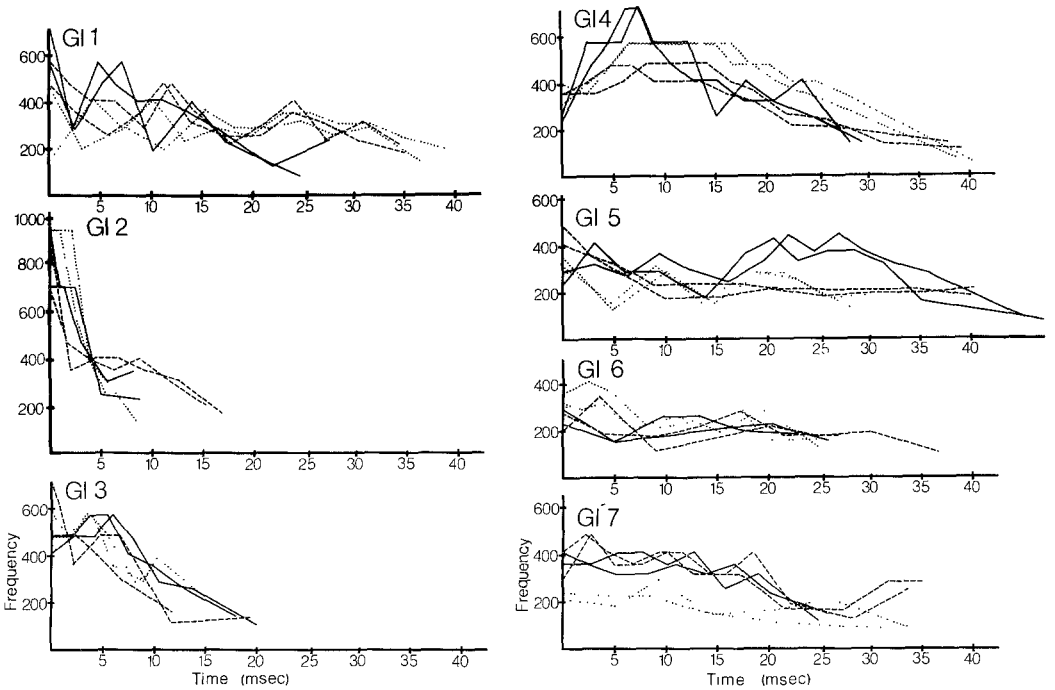

Fig. 10. Time course of response bursts in different GI's. Instantaneous frequency of action potentials (per s) (ordinate) plotted vs. time (abscissa). Zero time corresponds to the middle of the first interspike interval, and other points are plotted in the middle of successive intervals. The wind was always delivered from the maximum response angle. (Thus, for GI's 3 and 6, inward puffs were used.) For each GI, two curves each from three different animals are shown. (Curves from the same animal are drawn with the same type of line – solid, dashed or dotted.)

out the following experiments. In one group of animals, we covered the entire cuticular surface, except the cerci, with vaseline. Normal responses were recorded from all GI's impaled (GI 1, 2, 5, 6; in two animals). In a different group of animals, we covered only the cerci with vaseline. Responses were completely abolished in all GI's (each tested in at least two animals). Furthermore, when we eliminated the input from one cercus by either ablating or covering it with vaseline, the response of each GI to a standard puff of wind was decreased. For some GI's (1, 2, 3 and 6), removal of the contralateral cercus resulted in a moderate decrease in the number of spikes per burst without affecting the general shape of the directional sensitivity curve (Fig. 11A); whereas the removal of the ipsilateral cercus drastically reduced or abolished the response (Fig. 11B). For others, (GI's 4, 5 and 7), removal of either cercus caused a moderate reduction in the response without altering the directionality in a consistent manner (Fig. 11). (Though the shapes of the directionality curves for GI's 4 and 7 changed slightly following the removal of a cercus, these changes were not consistent from one animal to another.)

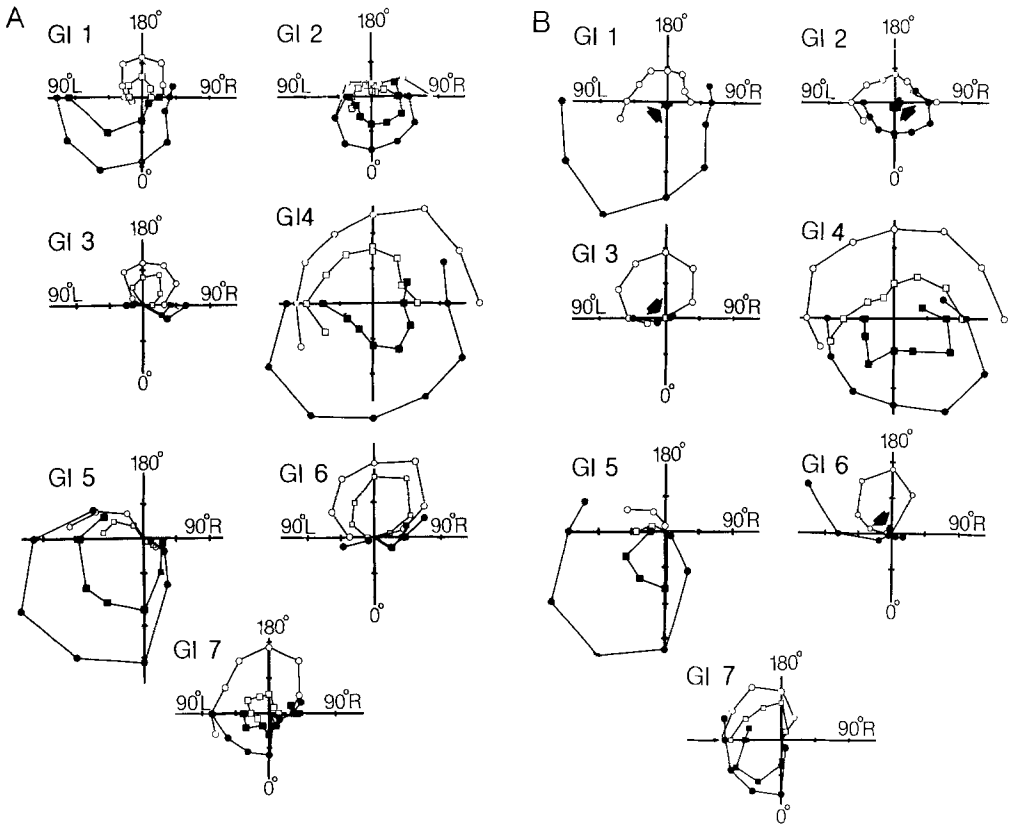

Fig. 11A and B. Effect of eliminating one of the two cerci. **A** Removal of the *contralateral* cercus. Circles represent responses with both cerci intact (as in Fig. 4). Squares represent responses of the same GI after removal or covering of the contralateral cercus. Filled circles and squares represent responses to wind expelled from the tube, and open circles and squares represent responses to wind drawn into the tube. **B** Removal of the *ipsilateral* cercus. Symbols as in **A**, except that squares represent responses after covering or removing the ipsilateral cercus. Arrows indicate the greatly diminished or abolished responses found in GI's 1, 2, 3 and 6 after removal of the ipsilateral cercus. (The response was completely eliminated in GI 2, in 2 out of 4 animals; in GI 3, in 3 out of 3 animals; and in GI 6, in 3 out of 5 animals.) Curves shown in **A** and **B** are representative of 41 successful experiments of this type

Discussion

A. Encoding of Directional Information by the Giant Interneurons

This study has demonstrated that all 14 individually identifiable giant interneurons of *Periplaneta americana* respond to stimulation of the cerci by wind, and the response pattern of each GI is consistent from animal to animal. Several of the GI's are directionally selective in their response to wind. This selectivity

might be used to orient the escape response of the cockroach away from a source of wind (Camhi and Tom, in preparation).

Although the GI's contain directional information, the response of any single GI does not unambiguously indicate wind angle. Ambiguity arises because the same response may be evoked from two or more angles (Fig. 7), and because both wind intensity and direction affect the magnitude of the response (Fig. 8). Moreover, no unique temporal pattern of spikes appears to be associated with particular wind angles for any of the GI's. Therefore, angular discriminations must be achieved by other means, presumably by comparison of the activity in two or more GI's.

GI's 2 and 4, the least directional units we have found (Fig. 6), are also among the least sensitive to changes in wind velocity above 0.5 m/s. Thus, they may be reporting to the animal the general information "wind on". Alternatively they may be specialized for discriminating differences in intensity for wind puffs of low peak velocity (or acceleration).

B. High Spike Frequencies

A striking feature of the response of the GI's is the high frequency of action potentials. Mean frequencies of over 300 spikes per s are common (Table 1), and instantaneous frequencies are sometimes over 900 per s (first interval of GI 2, Fig. 10). Such high frequencies may be important in the rapid transmission of directional information. If trains of action potentials are necessary for the animal to determine wind angle, then both fast conduction and high spike frequencies are necessary to permit the rapid initiation of an oriented evasive movement (Camhi and Tom, in preparation).

The high frequency of action potentials is also of interest in relation to blocking of action potentials in the ventral GI's within the metathoracic ganglion (Spira et al., 1976). Frequency-dependent conduction blockage has been observed for trains as brief as 5–10 spikes at a frequency of 200 per s (I. Parnas, personal communication). Our data show that such trains would occur in many of the GI's in response to gentle wind puffs. This indicates that high spike frequencies required for blocking in the thoracic ganglia are within the natural range of activity of these neurons.

C. Implications for Mechanisms of Sensory Integration

We can envision numerous mechanisms which might give rise to the directional selectivity of the GI's. One is a comparison by the left and right cerci of some feature of the stimulus, such as time of arrival. Such a mechanism is involved in numerous sensory processes such as auditory localization in crickets (Murphey and Zaretsky, 1972), frogs (Feng et al., 1976) and mammals (Whitfield, 1967). At least some of the GI's do have sensory input from both cerci (Roeder, 1948; Callec et al., 1971; and our Fig. 11). However, the directional

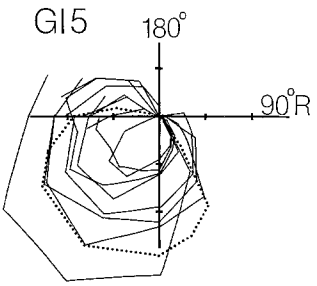

Fig. 12. Directional selectivity of a receptor potential in a sensory neuron compared with the directional selectivity of GI 5. Values for the receptor potential are from Nicklaus (1965). The curves for GI 5 are taken from our Figure 7. The maximal receptor potential, which occurs when a hair is deflected in its preferred plane, has been plotted so as to coincide with the maximal response angle of a representative GI 5 (at 30° left). The dotted line then represents the variation in receptor potential in response to deflections of the hair in directions other than its preferred plane

selectivity of the GI's is often maintained when the input from a single cercus is eliminated (Fig. 11). Thus, bilateral comparisons are not necessary to account for directionality of the GI's. Moreover, this suggests that animals with one cercus missing may be capable of determining wind direction. This could be adaptively important, since we frequently find animals with damaged or missing cerci.

A second possibility is that the cerci might "scan" the environment. Inputs received at different positions might then be compared. Although the cerci are movable, we have not observed them to make scanning movements in intact animals. In addition, cercal scanning seems unlikely because of the time which would be required to compare inputs from two different cercal positions.

A more likely mechanism to account for directionality of the GI's is selective projection of directional primary afferents. Each cercus has on its ventral surface roughly 220 filiform hairs arranged in 14 longitudinal columns. All the hairs in a given column appear to have the same preferred plane of deflection in response to wind (Nicklaus, 1965). The single sensory cell innervating a given hair is maximally depolarized and excited by wind flowing in one direction along this preferred plane, and hyperpolarized by wind in the opposite direction (Nicklaus, 1965). At least some of the GI's appear to be excited monosynaptically by these sensory neurons (Callec et al., 1971). Excitation by sensory neurons from a single column of hairs could account for the response of the most directionally selective GI's. This is suggested by Figure 12 where the receptor potential of a given sensory hair (Nicklaus, 1965) is shown to vary with angle in a manner similar to the response of GI 5.

Selective projection of receptors associated with directional hairs has been shown to account for directionality of interneurons in other systems. For example, in the cricket, projection of sensory neurons from specific cercal hairs onto giant interneurons results in the directional selectivity of these interneurons to low frequency sound (Palka and Olberg, 1977; Matsumoto and Murphey, 1977). In the crayfish, some sensory hairs are innervated by two mechanoreceptive sensory cells. One of these cells is excited by anterior deflection, the other by posterior deflection (Wiese, 1976). Selective projection of these two types of sensory neurons from hairs on the telson accounts for the directional selectivity of certain mechanoreceptive interneurons (Wiese et al., 1976).

Among the 14 rows of hairs on a single cercus of a cockroach, there are represented at least six different preferred planes of deflection (Nicklaus, 1965).

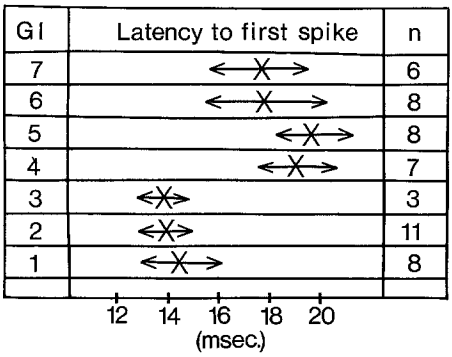

Fig. 13. Latencies of responses in different GI's. Latency is measured as the time between application of voltage to the solenoid and occurrence of the first action potential in a given GI. All latencies were measured at the angle where an *outward* puff evoked the greatest number of action potentials in that GI. (Thus, for GI's 3 and 6, this was not the maximal response angle.) For each GI, the mean of latencies obtained in several (n) different animals is plotted with an X. Arrows represent two standard errors of the mean on either side. The mean latencies of the larger GI's (1, 2 and 3) are significantly different from those of the smaller GI's (4, 5, 6 and 7) (Student's T-test, $P < 0.005$)

In contrast, there are primarily two preferred planes on a cricket cercus, and only one on the crayfish telson (Edwards and Palka, 1974; Wiese, 1976). The greater diversity of directional receptors of the cockroach cerci appears to allow the GI's to achieve a greater level of angular resolution than the system described in either cricket or crayfish (Edwards and Palka, 1974; Wiese et al., 1976).

Single unit recordings apparently from GI 2 have demonstrated that epsp's follow action potentials in single afferents from filiform hairs one-for-one at frequencies up to 400 per s. The synaptic delay is 0.68 ms (Callec et al., 1971; Callec, 1974). Thus, sensory to GI connections appear to be monosynaptic, at least for GI 2. In our recordings, action potentials from GI's 1, 2 and 3 all occurred with essentially the same latency (Fig. 13). Conduction velocities of the three largest GI's are very similar (all within 6–7 m/s, Roeder, 1948). These findings suggest that synapses between sensory neurons and GI's 1 and 3 could also be monosynaptic. The latencies of the responses in the smaller diameter GI's (4, 5, 6 and 7) were generally 4–5 ms longer than those in the larger GI's (1, 2 and 3) (Fig. 13). Only a small fraction of this difference in latency can be accounted for by the slower conduction velocity of the smaller GI's.[3] The remainder could be due to polysynaptic inputs to the smaller GI's, longer sumation times to reach threshold, or later arrival of action potentials in their sensory neurons.

The difference in latency between the smaller and larger GI's may be functionally significant. Each group of GI's includes a relatively nondirectional cell type (GI 2, GI 4), a cell type which could differentiate left from right (GI 1, GI 7), and a cell type that could differentiate anterior from posterior (GI 3,

[3] The larger GI's conduct action potentials at approximately 6–7 m/s and the smaller ones at 4–5 m/s (Spira et al., 1969). The conduction distance from the terminal abdominal ganglion to our recording electrode was approximately 3 mm. Thus, the difference in conduction time to our recording electrode would be only 0.25–0.5 ms

GI 6). Either group thus contains considerable directional information. It is possible that the two groups of GI's have different roles in controlling the directional escape.

D. Behavioral Significance

The high conduction velocity, high spike frequency, and directional selectivity of the GI's make them well-suited for mediating a rapid, oriented behavior. Low velocity wind puffs (lower than our standard puffs) cause the animal to turn and run away (Camhi and Tom, in preparation). Also, electrical stimulation of individual GI's evokes spiking activity in appropriate leg motor neurons (Ritzmann and Camhi, 1976, and in preparation). Thus, the GI's may have evolved as a means of rapid localization of a source of air currents, such as an approaching predator or other environmental disturbance which would require a rapid, directed escape.

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