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CHAPTER

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A Case Study in Neuroethology: The Escape System of the Cockroach

Having examined some key concepts of animal behavior in Chapter 2 and of cellular neurobiology in Chapter 3, we now turn to a neuroethological blending of these two subjects. In this chapter, we shall view a variety of problems faced by a single animal, the cockroach *Periplaneta americana*, in escaping from predators. As in many neuroethological studies, in those described here behavioral and neurophysiological experiments complement each other. Among the issues we will touch upon are the detection of biologically significant sensory signals, the discrimination of these signals from background noise, the localization of sensory cues, and the development and modifiability of behavior and of its neural controls. In subsequent chapters, most of these themes, as well as others, will be explored more deeply, each in a different animal species.

The Escape Behavior

Cockroaches, though all too common as cohabitators of human dwellings in the world's temperate zones, actually evolved in tropical Africa (Roth and Willis, 1960). They are still highly abundant in tropical rain forests, where they are nocturnally active (Schal, 1982). Colored dark brown, they are cryptic against the ground or against the bark of trees; nevertheless, they are visible, especially when they move, to a variety of predators.

Tests have been carried out on the behavioral responses of cockroaches to the strike of a natural predator, the toad *Bufo marinus* (Camhi *et al.*, 1978). This toad is generally sedentary and waits for prey to walk into its field of view. When a cockroach enters this field, it elicits a predatory strike. The insect responds to the strike by first turning its body away from the toad and then running (Figures 1 and 2). The cockroach's turn begins while the toad is still several centimeters away and before this predator's sticky tongue has begun to protrude from its mouth. Thus, the cockroach detects some cue or cues from the approaching toad and on this basis is notified of the presence and direction of this approach.

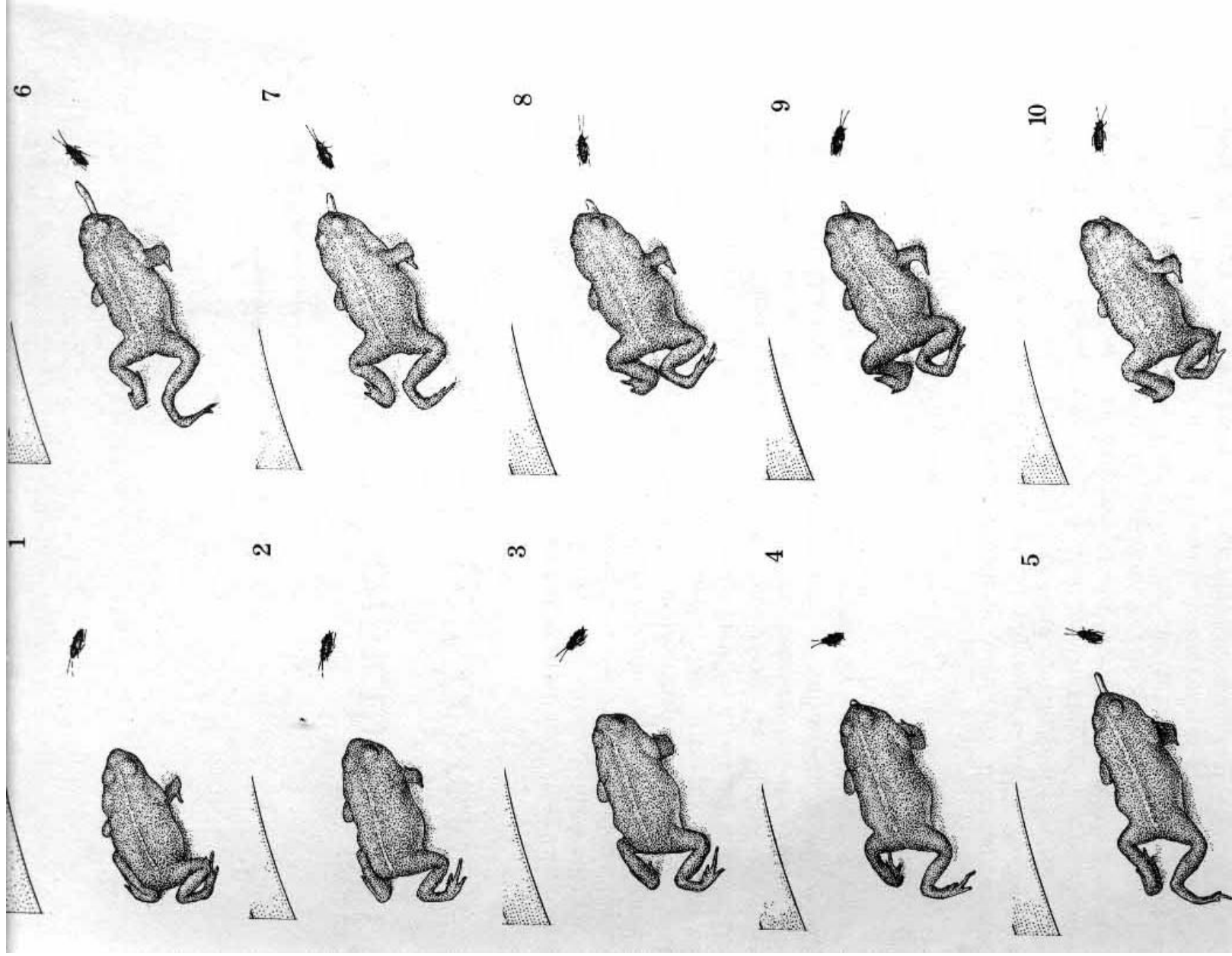


FIGURE 1. The escape of a cockroach from a toad (drawings from a motion picture sequence). The interval between frames is about 16 milliseconds. The toad has begun to lunge forward by frame 2. By frame 3, the cockroach has already begun to turn away. This turn causes the toad's tongue to miss its target. (From "The Escape System of the Cockroach" by J. Camhi. Copyright 1980 by Scientific American, Inc. All rights reserved.)

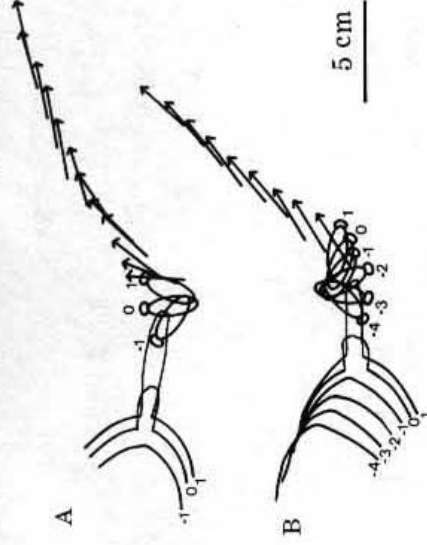


FIGURE 2. Close-up view of two strikes by toads at cockroaches. Shown are the outlines of the toad's head and tongue and of the cockroach's body. Profiles are derived from filmed frames preceding and including the frame showing maximal extension of the toad's tongue. Corresponding numbers on toad and cockroach indicate corresponding times; the frame on which the toad's tongue is first visible is labeled "0." Following this, the positions of the cockroach's body on successive frames taken during its run are shown by the series of arrows. (From Camhi *et al.*, 1978.)

BY WHAT SENSORY CUE DOES THE COCKROACH DETECT THE TOAD?

Attacks on cockroaches by toads in nature are likely to occur at night, when both predator and prey are active. Because little light is available and because the toad's strike is nearly silent, visual and auditory cues might be expected to play relatively small roles in the cockroach's detection of the approaching danger.¹ Moreover, cockroaches are not repelled by the odor of a toad, as they will literally climb upon a sedentary individual. One cue by which a cockroach might detect an approaching toad is the tiny wind gust created by the predator's movement. In fact, numerous hairlike wind-sensitive receptors are found on a pair of posterior antennalike appendages called cerci (singular: cercus) (Roeder, 1948, 1963). These are shown in Figure 3.

The possibility of wind as a cue was tested first by comparing the escape success of three groups of cockroaches: (1) normal individuals; (2) those that have had their cerci covered with glue and, thus, the cercal hairs inactivated; and (3) control animals with intact cerci but with glue placed on the ventral abdominal surface (Camhi *et al.*, 1978). The normal cockroaches escaped from 55% of the strikes and the control individuals from 47%—values that are not statistically different. By contrast, cockroaches with covered cerci escaped from only 8% of the strikes, a significantly lower percentage. Thus, something on the cerci greatly

¹In spite of the darkness, toads hunt their prey visually at night. However, unlike the cockroach, which must react to its predator very quickly after the strike has begun, the toad has considerable time to gather visual information as the prey walks into its field of view.



FIGURE 3. Adult male cockroach *Periplaneta americana*, showing the two cerci which bear the wind-receptive hairs on their ventral surfaces. (From "The Escape System of the Cockroach" by J. Camhi. Copyright 1980 by Scientific American, Inc. All rights reserved.)

aids a cockroach in escaping from a toad. This something might well be the wind-receptive hairs, though this remained to be proved conclusively.

Further evidence for wind as a cue to the approaching predator came when it was found that cockroaches made virtually identical movements in response to a toad as to a gust of air from a wind stimulator (Camhi and Tom, 1978; Camhi *et al.*, 1978). But the most conclusive evidence came when the wind created by the toad's strike was measured and was compared with the minimal puff size (produced by a wind stimulator) needed to evoke an evasive run (Camhi *et al.*, 1978; Camhi and Nolen, 1981; Plummer and Camhi, 1981). To measure the wind generated by a lunging toad, a cockroach was anesthetized with CO₂, tied to the end of a miniature fishing pole, and cast about on the floor of a chamber harboring the toad (toads strike only at objects that are moving or have just moved). As soon as the toad became alerted, the cockroach was positioned within a centimeter of a wind meter's measuring probe, which had previously been placed on the floor in the middle of the chamber. When the toad struck, the wind delivered to the cockroach was measured. The wind velocity was read out as the magnitude of a voltage displayed on an oscilloscope. Both the oscilloscope screen and the moving toad were viewed by a high-speed motion picture camera, so that on each frame of film, both the toad's position and the wind that it produced at the cockroach could be determined.

As the record of Figure 4 shows, the cockroach received wind throughout the entire strike of the toad, and the wind velocity increased at least until the toad's tongue emerged from its mouth (time 0). It had been learned from many previous filmed sequences of toads striking at unanesthetized, free-ranging cockroaches that the insect begins its escape movement at a mean time of 16 milliseconds before the emergence of the toad's tongue. Therefore, the wind intensity prior to this moment was a matter of crucial interest. But what precise moment was of interest, and what wind speed at this moment would indicate that the wind had evoked the cockroach's response? To determine this, let us turn for a moment to behavioral tests on cockroaches, tests in which a controlled wind stimulator was used in place of the toad.

Tests with controlled wind puffs showed that both a minimal wind velocity averaging 12 millimeters/second and a minimal wind acceleration averaging 600

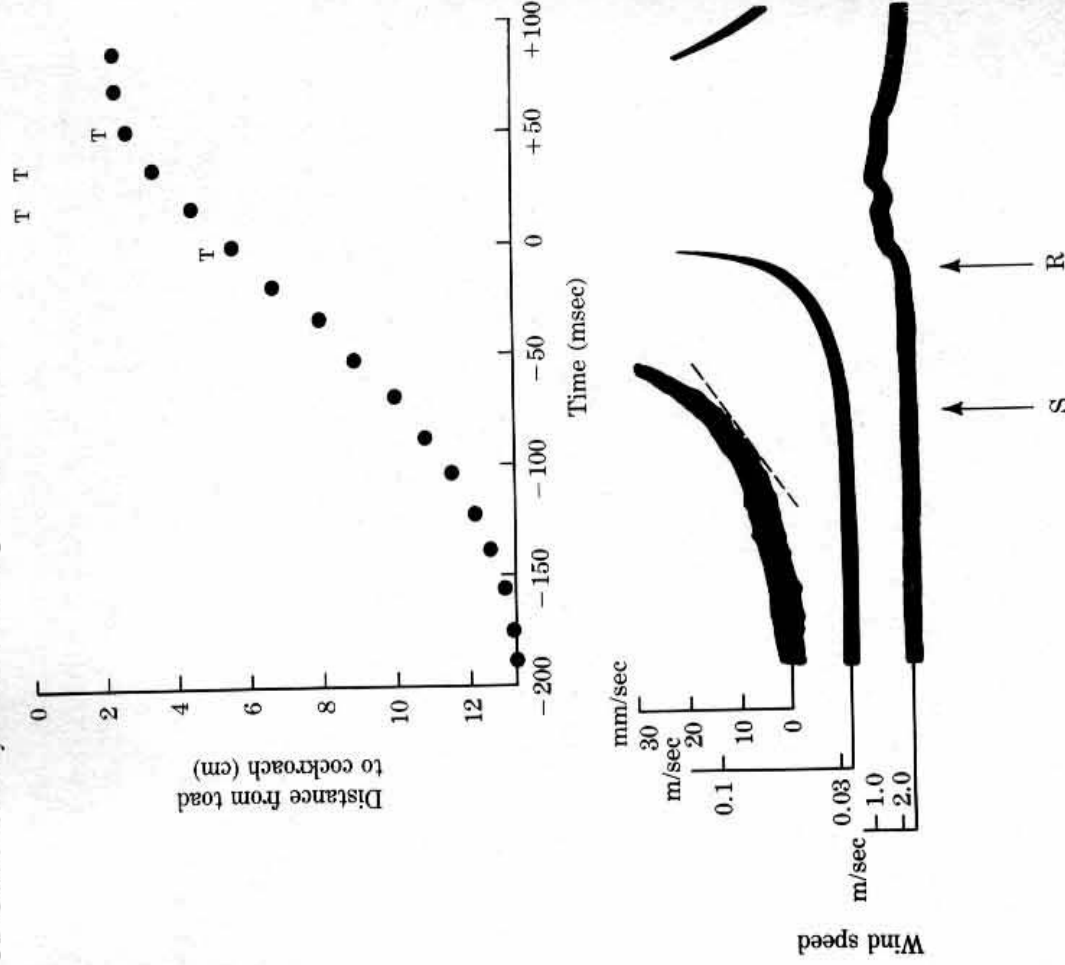


FIGURE 4. The wind delivered to a cockroach by a toad's predatory strike. The top graph shows the position of the front of the toad's head as it moves toward the cockroach. "T" represents the position of the tip of the toad's tongue, first visible at the time labeled "0" on the X-axis. The three traces below are three simultaneous recordings of the wind produced by the toad, made at three different sensitivities. "S" indicates the moment that the wind reached its critical magnitude for evoking running—at least 12 mm/sec velocity and at least 600 mm/sec² acceleration. (The slope of the dashed line represents an acceleration of 600 mm/sec².) "R" indicates the moment (derived by averaging data from many individual responses of cockroaches) that normal cockroaches respond to toad strikes (16 msec before the toad's tongue is first visible). Time scale is the same for wind traces as for graph. (From Camhi *et al.*, 1978.)

millimeters/second² were required to evoke an evasive run by the cockroach. (These wind values were obtained only if the stimulus was delivered either while the cockroach was walking slowly about or within 0.5 second after a pause in walking. If the insect was resting, greater stimuli were required; Camhi and

Nolen, 1981.) With these minimal puffs, the mean time from the onset of the wind stimulus at the cerci to the onset of the cockroach's movement response, called the BEHAVIORAL LATENCY, was 44 milliseconds (Plummer and Cambi, 1981).

Given this information, let us now reexamine the wind recording of Figure 4. If the wind from the toad's lunge were the *only* stimulus by which the cockroach detected the approaching toad, this wind should reach its critical value of 12 millimeters/second and 600 millimeters/second² about 44 milliseconds before the moment when cockroaches begin their movement response. The average moment of response (16 milliseconds before the tongue emerged) is labeled "R" below the wind traces of Figure 4. The critical value of wind was reached at the moment labeled "S." The interval from S to R in the particular experiment illustrated in Figure 4 is 56 milliseconds; but the *mean* interval from S to R, based on a large number of similar trials, was 41 milliseconds. This close agreement between the two values of latency (44 milliseconds for the wind stimulus *vs* 41 milliseconds for the toad) indicates that the wind generated by the toad's strike is a sufficient stimulus to account for the cockroach's response to the toad. This result was confirmed in independent tests in which toads struck at walking, unanesthetized cockroaches. Again the toad's wind was measured. But here, the latency from the arrival of the critical wind (12mm/sec; 600mm/sec²) to the onset of behavior could be measured directly. The mean latency again was 41 milliseconds (Plummer and Cambi, 1981).

Attempts to find cues other than wind that came from a striking toad and that could evoke escape by a cockroach have met with no success (Cambi *et al.*, 1978). The cues investigated included the sight of a toad striking from behind a Plexiglas barrier, the odor of a toad, and air-borne sounds or ground-borne vibrations of even much greater intensity than those made by the striking toad. Thus, the wind produced by the lunge appears to be the necessary stimulus for evoking the cockroach's escape from an approaching toad. Although wind is not usually thought of as containing much information, one can see that wind both contains and conveys to the cockroach information about the approach and the direction of a predator.

HOW DOES THE COCKROACH DISCRIMINATE SIGNALS FROM NOISE?

We have seen that wind stimuli whose peak velocity is just 12 millimeters/second evoke running behavior. This raises a substantial problem for the cockroach: how to discriminate between such small wind signals coming from a predator and other, nonthreatening sources of wind, which constitute the background noise² in this sensory channel. There are two major sources of noise. First is atmospheric wind, which, as measured at night in tropical rain forests, generally ranges up to about 150 millimeters/second (Schal, 1982). Second is wind created by the cockroach itself while it walks. A typical walking speed of 100 millimeters/second causes a wind of the same speed to flow posteriorly over the body—just as when

²The term *noise* as used here does not mean sounds, but rather energy of the same physical type as the signal, in the face of which the signal must be detected.

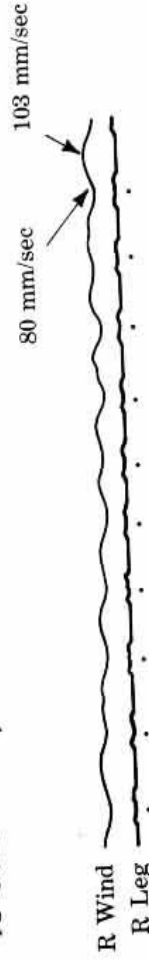


FIGURE 5. Wind gusts produced by the stepping movements of a cockroach's right hindleg. The wind was recorded at the right cercus. Stepping movements (bottom trace) were recorded by having the leg interrupt a beam of light shining on a tiny photocell each time the leg moved. The dots below the trace indicate the approximate moments when the leg reached its backwardmost position. These gusts were superimposed upon a roughly 80 mm/sec wind that represents the animal's forward progress at this speed through the air. (From Plummer and Camhi, 1981.)

you run, you create a headwind. These two sources of noise together, then, can range up to about 250 millimeters/second, or roughly 20 times greater than the critical windspeed for evoking a run.³ Moreover, the velocity of this self-generated wind fluctuates as the animal walks; each step of a hindleg produces a wind fluctuation which, as recorded at the nearer cercus, can be greater than the 12 millimeters/second critical wind speed (Figure 5).

Somehow the cockroach manages not to respond behaviorally to the large and complex background noise, and yet to respond with a run to the much smaller wind signal. A clue as to how the insect accomplishes this discrimination comes from the observation that the acceleration of the wind signal (the rate of change of its wind speed) is actually greater than the wind acceleration contained in the background noise. The maximal atmospheric wind acceleration, measured at night in tropical rain forests, is less than a few millimeters/second² (Camhi *et al.*, 1978). And the acceleration of the wind gusts produced by the stepping legs of a cockroach is below 300 millimeters/second² (Plummer and Camhi, 1981). By contrast, we have seen that a toad's strike delivers wind with accelerations of at least 600 millimeters/second² (Figure 4).

Is this difference in wind acceleration in fact the cue by which the cockroach discriminates signal from noise? To test this, wind puffs all having the same peak velocity (40 millimeters/second) but differing in acceleration (between 150 and 1700 millimeters/second²) were delivered to slowly walking cockroaches (Plummer and Camhi, 1981). The higher the acceleration, the greater the percentage of running responses (Figure 6). The lower the acceleration, the greater the percentage of trials with no response. Intermediate accelerations often evoked a pause in the cockroach's walking. These findings were independent of wind direction. Thus, the cockroach appears to attend specifically to the acceleration of the stimulus in order to weather windy conditions without jamming its prey-detecting system.

³Slowly walking cockroaches respond, though not by running, to wind stimuli even smaller than 12 millimeters/second. Specifically, puffs of just 3 millimeters/second consistently evoke a pause in walking. This pause presumably aids the cryptically colored cockroach in remaining undetected. This 3 millimeters/second signal, then, is about 80 times smaller than the background noise.

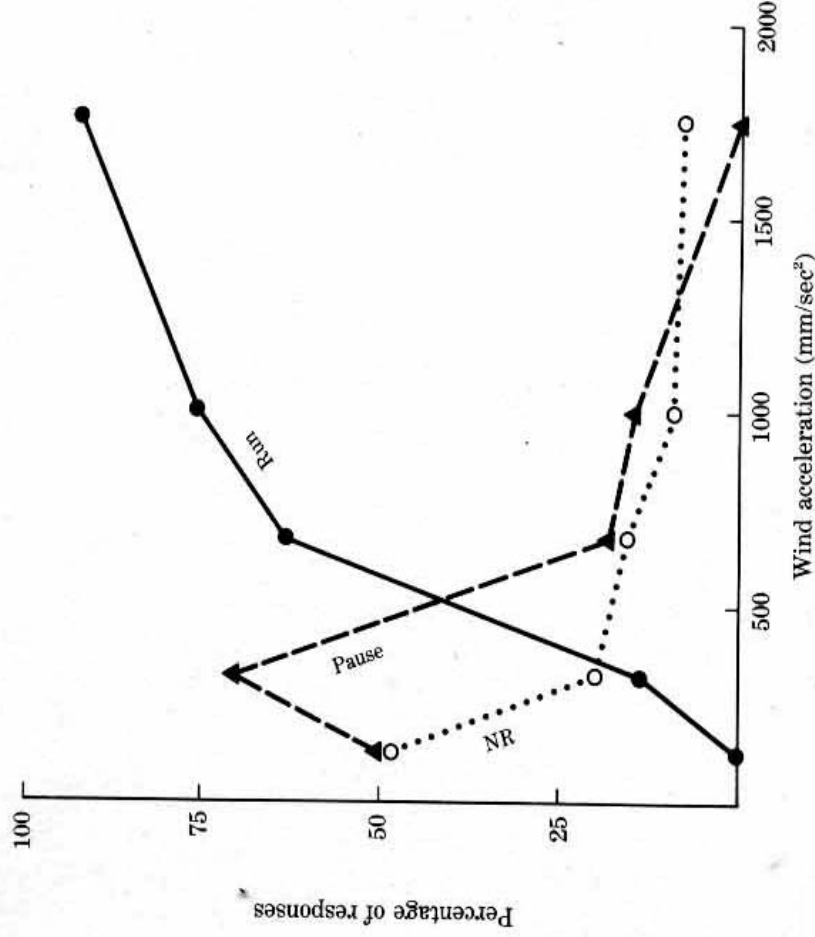


FIGURE 6. Effect of wind accelerations on the cockroach's response to wind stimuli. NR, no response. See text for explanation. (From Plummer and Camhi, 1981.)

How Does the Cockroach Nervous System Encode the Direction of an Approaching Toad?

Because cockroaches regularly turn away from an approaching toad or other source of rapidly accelerating wind, it is clear that this insect's nervous system can determine wind direction. Some of the neurons that appear to be involved in this determination are shown in Figure 7A. At the base of each of approximately 220 wind-receptive hairs on a cercus is the dendrite and cell body of a single sensory neuron. The axon of each sensory cell projects to the central nervous system. Like most higher invertebrates, the cockroach's central nervous system is subdivided into GANGLIA (singular: ganglion) and CONNECTIVES. The ganglia contain cell bodies, dendrites, and axons, whereas the connectives contain only axons. In the cockroach's terminal ganglion, the wind receptor cells excite, apparently monosynaptically, a group of GIANT INTERNEURONS (GIs), whose axons are of substantially greater diameter than any other interneurons in this nervous system (Roeder, 1948; Westin *et al.*, 1977). Figure 2 of Chapter 3 shows one of these GIs filled with cobalt sulfate.

The cockroach has seven bilateral pairs of GIs. Each GI can be identified

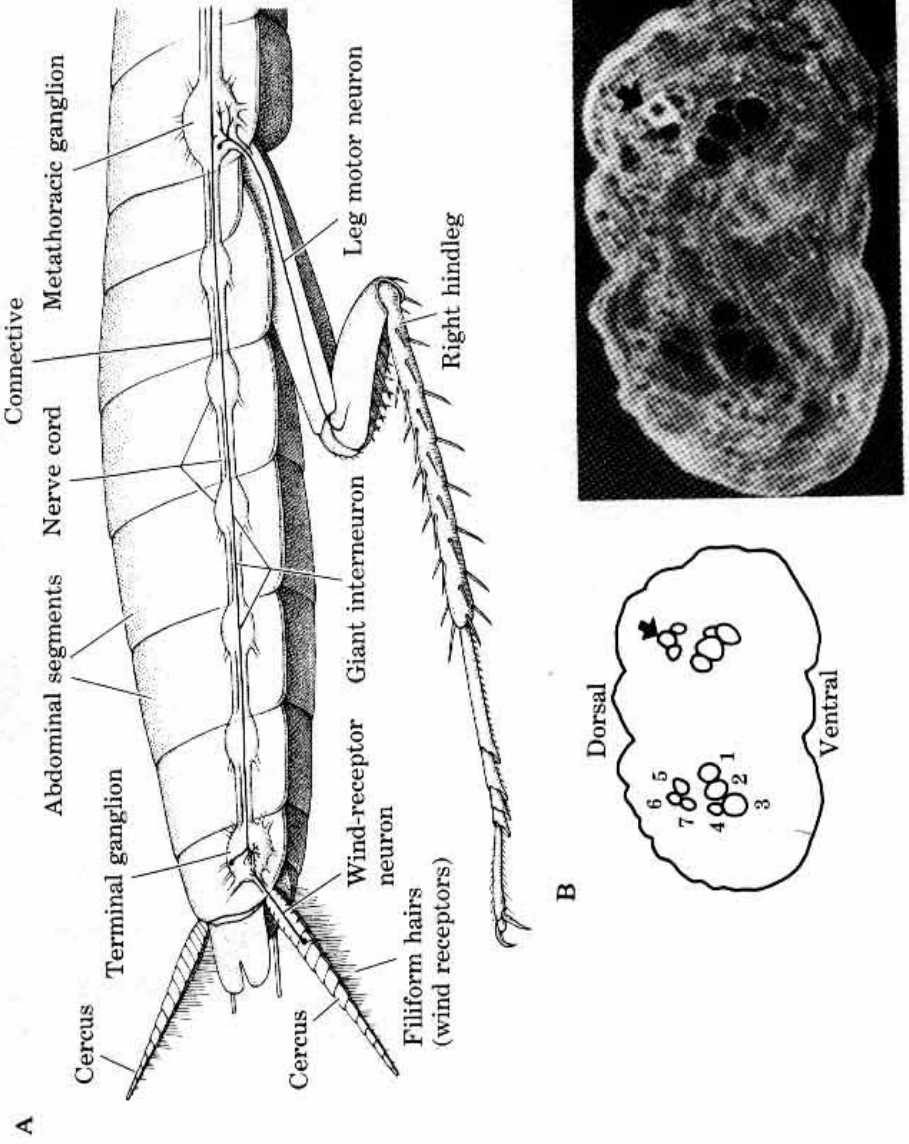


FIGURE 7. Some of the neurons of the cockroach escape system. A. Sketch showing one cercal sensory cell, one giant interneuron, and one leg motor neuron in their actual locations. B. On the right is a cross section through an abdominal ganglion. The seven large profiles on each side (drawn in isolation in the sketch on the left) are the cross sections of the seven bilateral pairs of giant interneurons (GIs). The right GI 6 (arrow) has been filled with the dye Procion yellow, following a recording from its axon. (A from "The Escape System of the Cockroach" by J. Camhi. Copyright 1980 by Scientific American, Inc. All rights reserved. B from Westin *et al.*, 1977.)

individually in all cockroaches of this species, on the basis of the shape of its dendritic tree (Daley *et al.*, 1981) or by the relative position of its axon as seen in a cross section of an abdominal ganglion (Figure 7B). The axons of the GIs ascend the nerve cord to the head (Spira *et al.*, 1969), passing through the thoracic ganglia. In the thorax, excitatory synaptic contacts (which have not been well characterized) are made onto motor neurons of those leg muscles that produce running behavior.

Where in this neural circuit does the cockroach's determination of wind direction occur? It begins with the individual cercal wind-receptive hairs. Close examination shows that the roughly 220 hairs on an adult cercus are organized

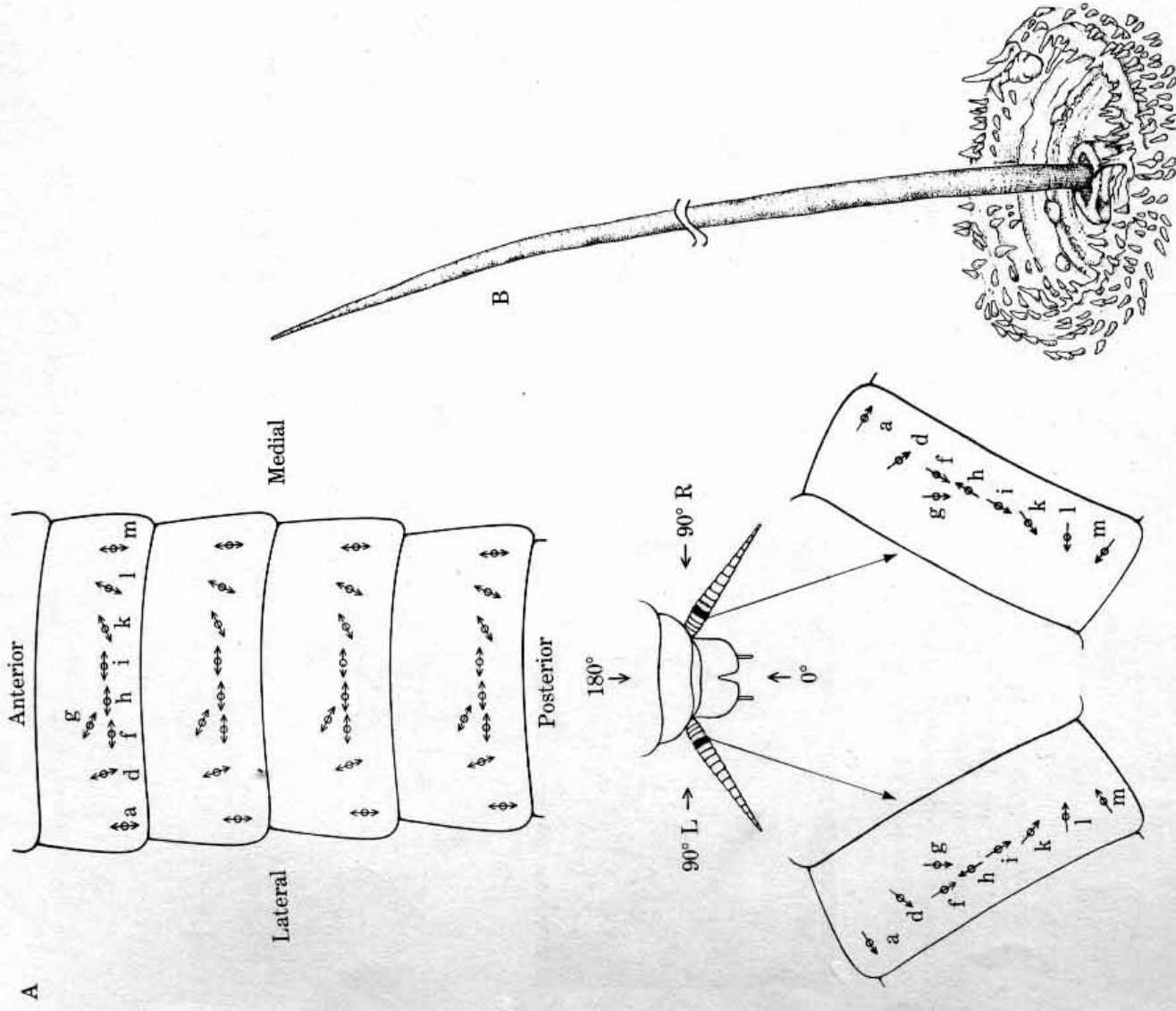


FIGURE 8. Organization of wind-receptive hairs on the cerci. A. Top: Underside of four of the 19 segments from an adult cercus. Each circle shows the position of a wind-receptive hair. Columns a, d, f, h, etc. run along most of the cercal length. Double-headed arrows show the two directions of maximal mechanical pliancy of each hair. Bottom: A single segment from each cercus. The single-headed arrows show the optimal wind direction for each hair. All hairs of a given column have the same optimal wind direction. B. A single wind-receptive hair, drawn to scale. At the hatch mark, three-fourths of the actual length of the hair has been omitted. (A from "The Escape System of the Cockroach" by J. Camhi. Copyright 1980 by Scientific American, Inc. All rights reserved.)

spatially into columns and rows (Figure 8). Each of the 19 cercal segments of the adult (except those near the tip and base) has a row of nine long hairs, which range from 0.5 to 1 millimeter in length. (Other, shorter hairs that are apparently not wind-responsive, as well as other types of sensory structures, are also found on the cerci.) The similarly placed hairs on each segment can be regarded as members of a column running from the cercal base to its tip. All the hairs in a given column are functionally alike in that they can be deflected easily in either of two (opposite) directions (double-headed arrows in Figure 8, top) and less easily at right angles to these directions. The directions of maximal pliancy are different from column to column (Nicklaus, 1965).

By recording with microelectrodes from individual sensory cells, it was found that pushing the hair in one of its two most pliant directions evokes a maximal number of action potentials. Pushing it in the other most pliant direction (180° away from the first) produces a maximal inhibition of spontaneously occurring action potentials (Nicklaus, 1965). The excitatory direction is thought to stretch the dendrite of the sensory cell and thus evoke a receptor potential and the resulting action potentials. The opposite (inhibitory) deflection is thought to slacken the sensory cell's dendrites (Figure 9).

The responses of a sensory cell to wind resemble these directional responses to the pushing of its hair from side to side. This was determined from extracellular recordings of the whole sensory nerve, made after all the cercal hairs except those in one column had been covered with glue (Dagan and Camhi, 1979). By giving wind puffs from many different directions within the horizontal plane, a single most excitatory wind direction for each column of hairs was identified (Figure 8, bottom, single-headed arrows). In other experiments, recordings were made intracellularly from the axons of individual sensory cells, again in response to wind puffs from different horizontal directions (Westin, 1979). Again, each cell showed a single wind direction that was most excitatory and an opposite direction that inhibited action potentials. However, the overall range of directions to which a given sensory neuron responded was found to be quite broad (Figure 10). Given

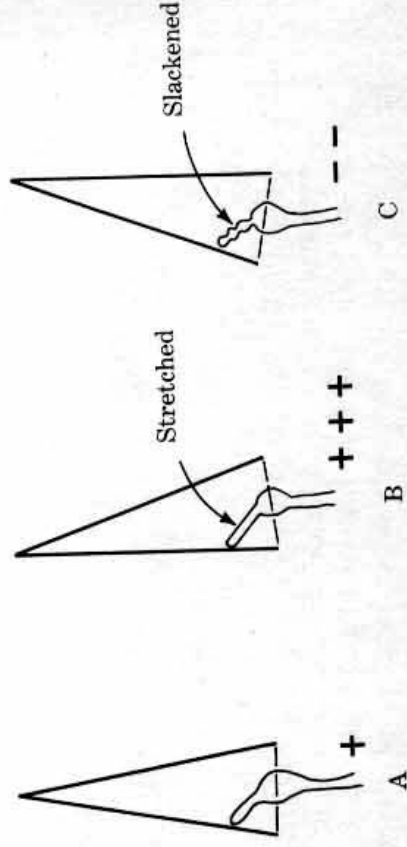


FIGURE 9. Excitation and inhibition of a wind-receptor cell by opposite deflections of its hair. A. Undeflected hair. B. A deflection that stretches the dendrite and excites the cell. C. A deflection that slackens the dendrite and inhibits the cell.

the many different best excitatory wind directions represented on each cercus (Figure 8, bottom) and the broad directional response of each sensory cell (Figure 10), a wind puff from any direction must excite sensory cells from several different columns on each cercus. A slight shift of wind direction, then, would result in different relative amounts of excitation of these various columns of sensory cells. Thus, each direction of wind inscribes on the sensory nerve its own signature in the form of the relative numbers of action potentials evoked in the different sensory columns.

Do the GIs, excited by the cercal neurons, preserve the directional information encoded by these sense cells, or is this directional information transformed or even lost in crossing the synapse to the GIs? These questions were answered by making intracellular recordings from each GI and by delivering identical wind stimuli from different horizontal directions (Westin *et al.*, 1977). Just after com-

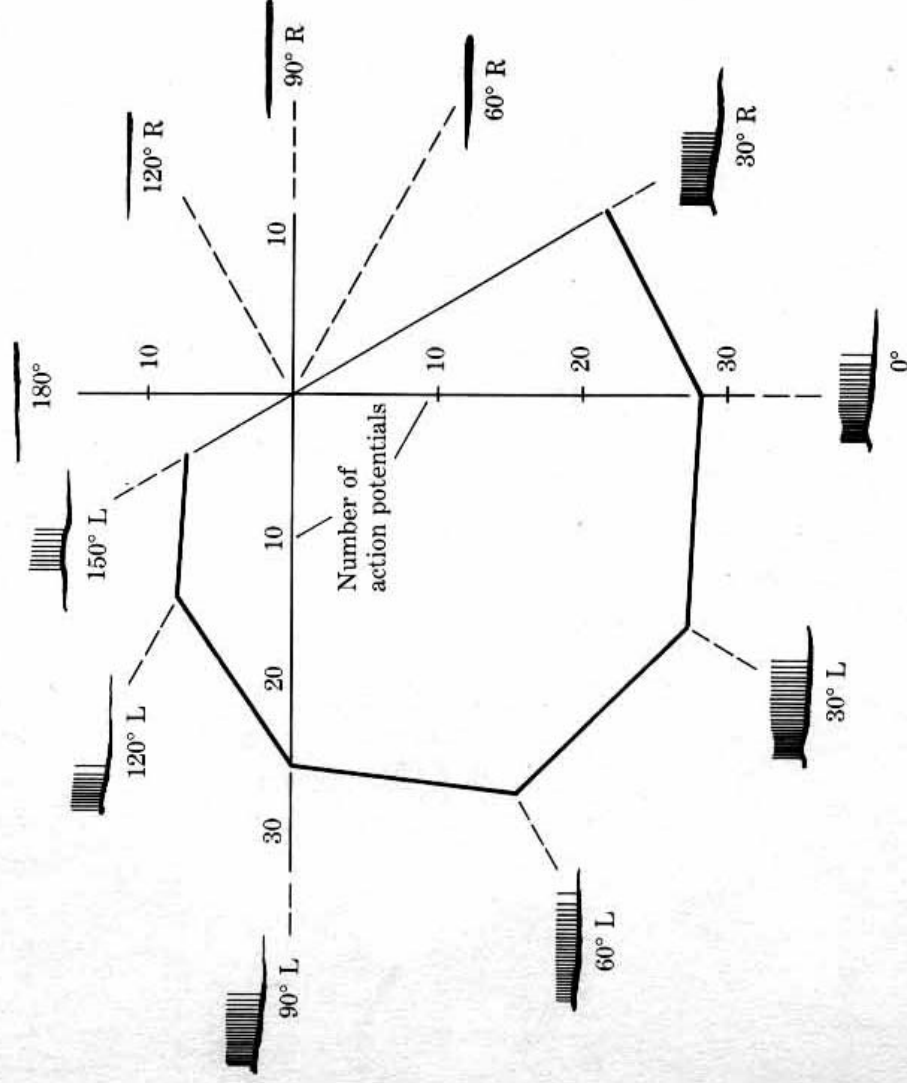


FIGURE 10. Directional response of a single wind-receptor cell. Constant wind puffs were delivered to the cockroach from different angles within the horizontal plane. The mean number of action potentials evoked from each angle is plotted. Representative recordings for each angle tested are also shown. This cell responded best to wind from the cockroach's left rear quadrant. Wind from the opposite quadrant (right front) evoked no action potentials. Though not shown here, the latter direction also inhibited any spontaneously occurring action potentials in the cell. (After Westin, 1979.)

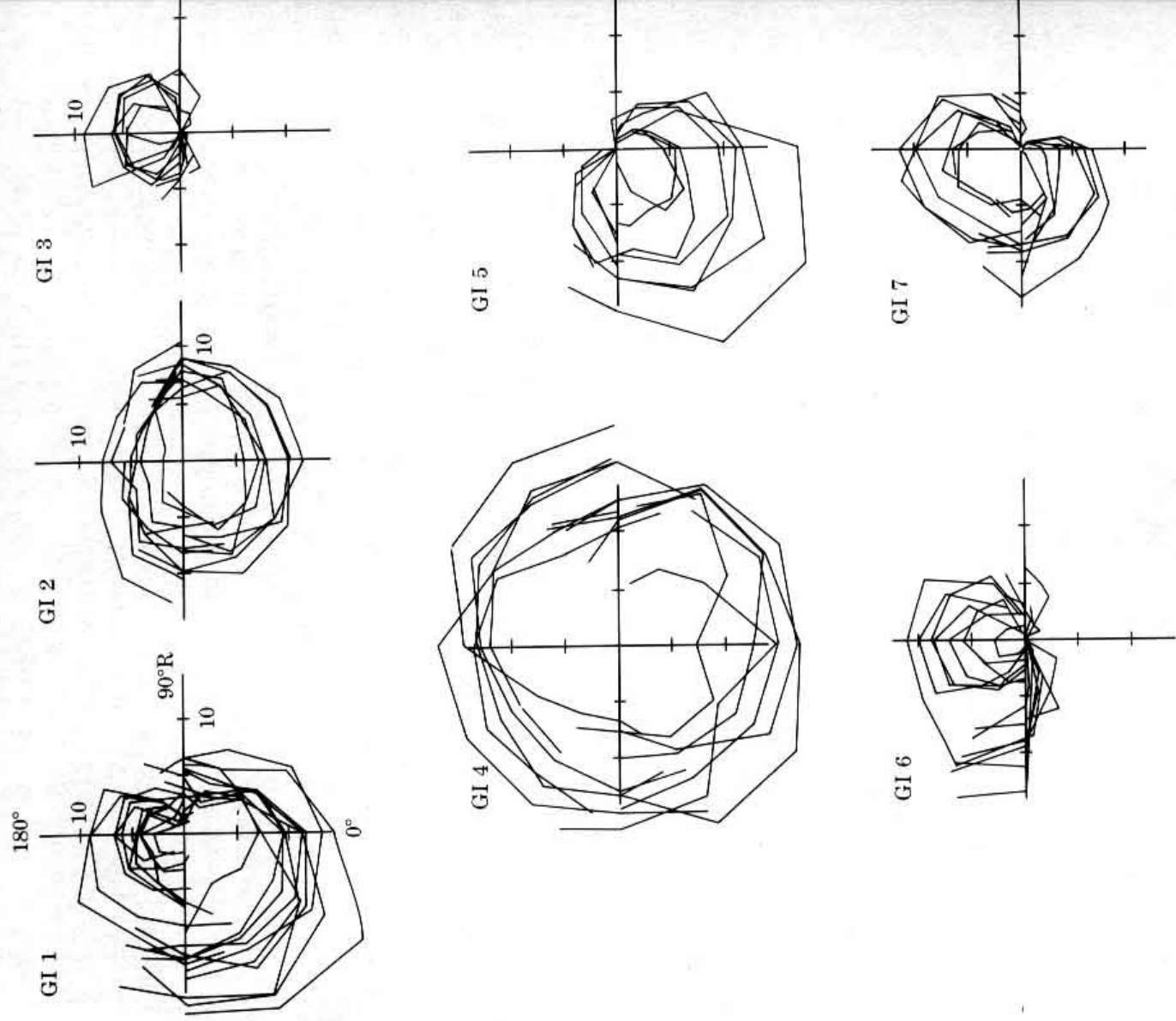


FIGURE 11. Directional responses of the seven left GIs to wind stimuli. (A left GI is one whose axon runs on the left side of the nerve cord, though its cell body is on the right. The seven right GIs give mirror image responses. Each line on any of the seven sets of axes represents the responses of a single cell. Thus, the same cell type from several animals is plotted on each set of axes; numbers on axes represent number of action potentials. The method of plotting is the same as that in Figure 10. For technical reasons, smaller wind puffs were used for stimuli from the front than from the rear, producing discontinuities in many of the graphs. (From Westin *et al.*, 1977.)

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peating a set of such recordings from a given cell, Procion yellow, Lucifer yellow, or cobalt was injected intracellularly from the micropipette electrode to enable subsequent identification of the particular GI recorded.

Of the seven GIs on each side of the nerve cord, two were found to respond with roughly the same number of action potentials to wind from any direction (GIs 2 and 4; Figure 11). Two others (GIs 1 and 7) respond most strongly to wind coming from the same side as the position of the GI's axon. The three remaining GIs on each side (numbers 3, 5, and 6) give responses that are directionally more restricted. Considering the GIs as a group, then, one can see that directional information is retained but in a form somewhat different from that of the sensory neurons.

The nature of this transformation has been studied by recording intracellularly from the cell bodies of giant interneurons after plucking out or covering up all the cercal hairs except a limited number from a single column (Daley and Camhi, 1980; Daley, 1982). In most of these experiments, six hairs of a column were left uncovered, and this number was then reduced one by one, by covering additional hairs. The experimenter in this way determined the number of hairs required to produce an action potential in a given GI, in response to a standard wind puff from a fixed direction. In different experiments, different combinations

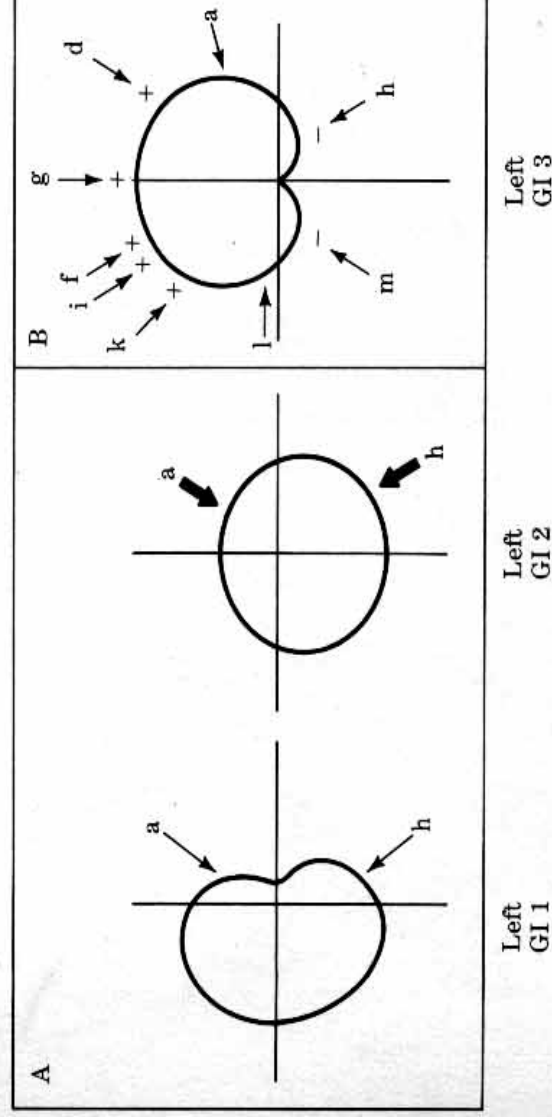


FIGURE 12. Mechanisms underlying the shapes of the directional response curves for three GIs. The directional curves for the left GIs 1, 2, and 3 are as shown in Figure 11. Lower case letters indicate particular columns of sensory hairs on the left cercus. The arrows indicate the optimal wind direction for each column, taken from Figure 8. A. The sensory input to left GI 1 differs from that to left GI 2 primarily in the functional strength of activation by two sensory columns, a and h. Their input is stronger to GI 2 (thicker arrows). B. Left GI 3 receives excitatory input (+) from sensory columns on the left cercus that encode wind from the front, and inhibitory input (-) from those columns that encode wind from the rear. Those that encode wind from the sides (a and l) evoke no detectable response. (Courtesy of D. Daley.)

of column and GI were tested. It was found, for instance, that GIs 1 and 2 receive excitatory input from all nine columns of hairs on the ipsilateral cercus (that is, the cercus on the same side as the GI's axon). The differently shaped directional responses of these two GIs (Figure 11) appear to result from the different synaptic strengths that the two GIs receive from certain columns of sensory hairs.⁴ In particular, columns a and h (Figure 8) from the left cercus excite the left GI 1 weakly but the left GI 2 strongly. This appears to account for the difference between the directional responses of these two GIs (Figure 12A). By contrast, GI 3 receives excitatory input only from those columns of sensory cells whose best wind direction is from somewhere near the front (columns d, f, g, i, and k). This GI receives inhibitory input from sensory cells of columns h and m, whose best excitatory directions are near the rear (Figure 12B). Columns a and l provide no detectable input to GI 3.

In summary, then, the directional coding of the sensory neurons results from the mechanical properties of their hairs and of the dendritic connections to these hairs. The transformation of these directional properties to the GIs involves the use of excitatory synaptic connections of different functional strengths, as well as inhibitory connections.

From Giant Interneurons to Behavior: How is the Directional Information Decoded?

Although directional information is available to the cockroach through its GIs, this does not prove that the insect actually uses these GIs to elicit the escape response. Indeed, there could be other, unidentified neurons that play this role. As we shall now see, however, there is good evidence that the GIs are important mediators of the escape behavior and that the directional information that they convey is crucial for a properly oriented turning response to wind. We will also see something of how this encoded directional information is decoded to execute a proper turn.

On theoretical grounds, one might suspect that the GIs are involved in the escape behavior because this behavior can occur very quickly and may thus require the rapid conduction of action potentials afforded by axons of especially large diameter (Chapter 3). Although the behavioral latency in response to the onset of a toad's wind was over 40 milliseconds (Figure 4), if one uses an even more rapidly accelerating wind puff as the stimulus, behavioral latencies as short as 11 milliseconds can be recorded (Camhi and Nolen, 1981). This interval, together with measured escape behaviors of a few other animals (Chapter 8), are among the shortest behavioral latencies known.

More direct evidence for a role of the GIs in escape behavior comes from experiments in which one or two GIs are stimulated electrically through intracellular electrodes. Each stimulus consists of a rapidly repeating train of current

⁴As we saw in Chapter 3, the functional strength of a synapse can be evaluated only by its effect on the trigger zone of the postsynaptic cell. In the present experiments, it was just such an effect that was determined, because the parameter measured was the production of an action potential.

pulses. The stimulus evokes a rapidly repeating train of action potentials, a pattern that resembles the barrage with which a GI responds to natural wind puffs. In order to prevent movements of the insect, which could dislodge the microelectrode from the stimulated GI, the cockroach's body was pinned to the substrate. Because the pinned insect could not move, any locomotory consequences that the GI stimulation might evoke were monitored by recording extracellularly from the axons of motor neurons to muscles of a hindleg. It was found that several of the GIs, when stimulated alone or together with one another, evoked bursts of action potentials in these axons (Ritzmann and Camhi, 1978; Ritzmann, 1981; Ritzmann and Pollack, 1981). The motor neurons excited are the very ones used to produce running behavior.

Perhaps the strongest evidence for a role of the GIs in escape comes from experiments in which selected GIs were killed and the cockroach's escape behavior tested the next day. The selective killing of a particular GI was accomplished by injecting this cell, through an intracellular microelectrode, with the proteolytic enzyme Pronase. Pronase digests the cell—that is, destroys it. Moreover, because this enzyme, like all enzymes, is itself a protein, its proteolytic actions soon cause its own destruction, so the neuron-killing ability of Pronase ceases before it has had an opportunity to destroy other cells. Figure 13 shows examples of three nerve cords in which Pronase was used to kill, respectively, the right GI #1, the left GI #2, and the left GIs 1 and 2. So far, this Pronase technique has been applied only to the three largest GIs, numbers 1, 2, and 3 (Figure 7B).

Before describing the behavioral results of the Pronase-lesioning of specific GIs, let us consider theoretically what results we might expect if the cockroach uses its GIs to determine the wind direction. First, we might expect that killing some or all of the GIs 1, 2, and 3, but leaving intact the smaller GIs 4–7, should interfere with proper turning. The reason concerns differences in the times of arrival at the thoracic ganglia of those action potentials carried by GIs 1, 2, and 3 *vs* those carried by the smaller GIs. Giant interneurons 1, 2, and 3, having nearly twice the diameter of the others, conduct action potentials from the terminal ganglion to the thorax in about 1 millisecond less than do the remaining GIs. Moreover, GIs 1, 2, and 3 are activated by wind about 5 milliseconds before the smaller GIs (Westin *et al.*, 1977). This total difference of about 6 milliseconds all but rules out GIs other than numbers 1, 2, and 3 as initiators of the escape response, at least on those occasions when the behavioral latency is at its minimum of 11 milliseconds (Camhi and Nolen, 1981). And since the initial part of the escape response is a turn, it would seem that GIs 1, 2, and 3 alone can initiate a proper direction of turning.

Suppose that this idea of left and right GIs 1, 2, and 3 as the turn initiators is true. Then these six cells must contain sufficient information to distinguish among at least four different wind directions—left front, left rear, right front, and right rear—each of which results in a different initial turning response. (For instance, wind from the left front produces a right turn of high angular velocity; and wind from the left rear produces a right turn of low angular velocity; Camhi and Tom, 1978). In fact, left and right GIs 1, 2, and 3 do encode sufficient information to discriminate among at least these four quadrants of horizontal space. As is shown in Figure 14A, when the wind comes from anywhere on the left side,

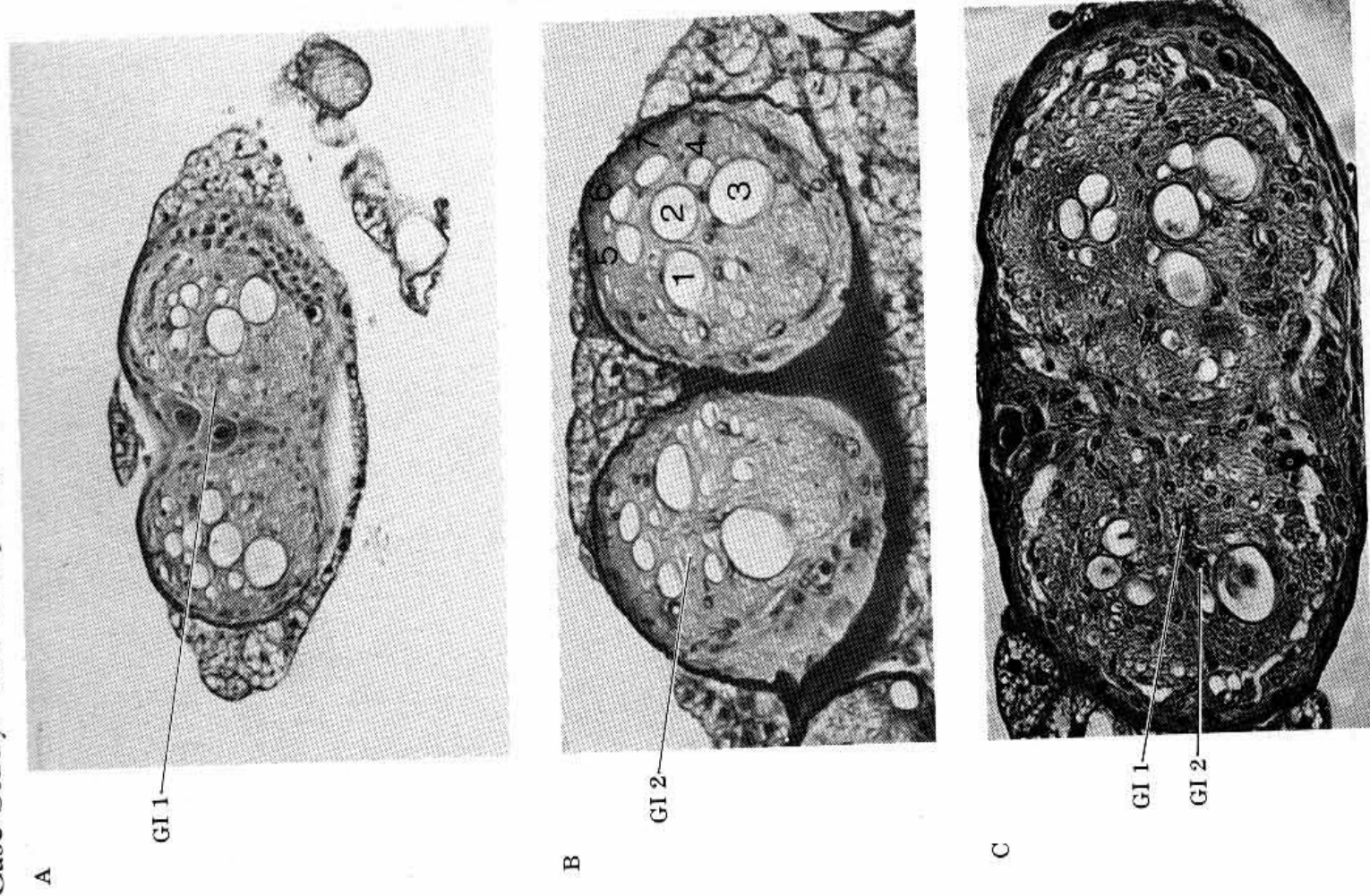


FIGURE 13. Cross sections of nerve cords in the abdominal regions of three different cockroaches. A. Right GI 1 has been injected with Pronase and is missing. B. Left GI 2 is missing after Pronase injection. C. Left GIs 1 and 2 are both missing after Pronase injection. Arrows point to the expected locations of the missing axons of these GIs.

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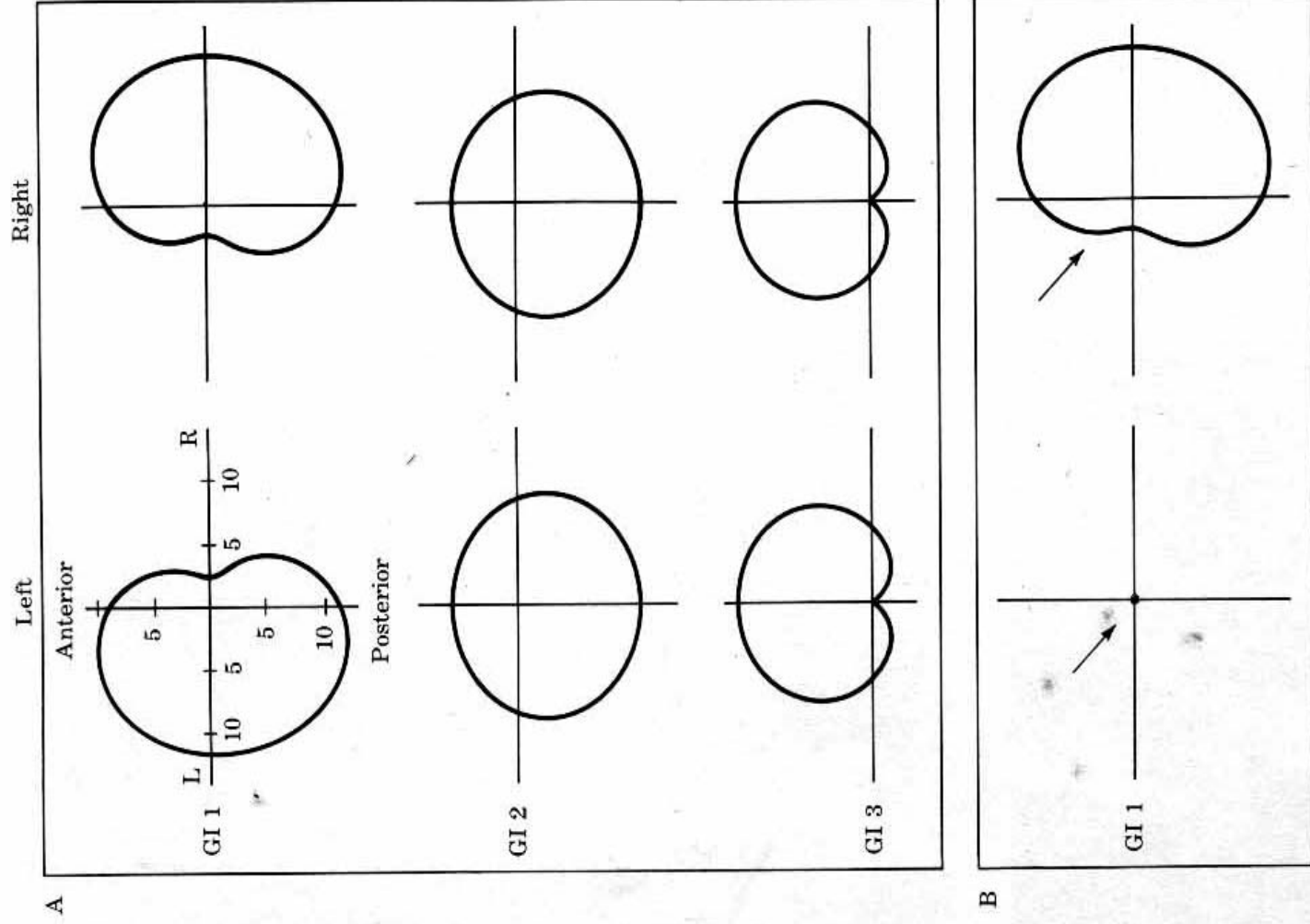


FIGURE 14. Hypothesis for directional specification by the left and right GIs 1, 2, and 3. The directional curves for these GIs are as shown in Figure 11. A. As explained in the text, these GIs contain sufficient information to specify at least the four quadrants of horizontal space around the cockroach. B. If the left GI 1 is destroyed, wind from the left (arrows) will excite right GI 1 but not left GI 1. Numbers on axes represent number of action potentials.

the left GI 1 gives more action potentials than the right GI 1.⁵ And when the wind comes specifically from the left *front*, both GIs 3 are activated; whereas if it is from the left *rear*, the GIs 3 are silent. Because the responses of the GIs 2 are not directionally selective, one might guess that these cells play no role in specifying wind direction.

Thus, a possible mechanism for decoding directional information from the GIs would involve some form of comparison by the nervous system between the responses of the left and right GIs 1, as well as a determination of whether or not the GIs 3 are active. If this were the actual mechanism, one would predict that after killing just the left GI 1 with Pronase, the animal would turn to the left not only when the wind comes from the right, but even when it comes from the left. The basis of this prediction is that a wind puff from the left would evoke a few action potentials in the right GI 1 but none, of course, in the killed left GI 1 (Figure 14B, arrows). Thus, a comparison mechanism would mistakenly calculate that a puff from the left had actually come from the right and would thus evoke a turn to the left.

In fact, cockroaches with their left GI 1 killed do turn left significantly more often than normal animals in response to wind from the left. But this occurred on only 25% of the trials, not on the great majority as had been predicted (Figure 15). (The remaining 75% of the trials produced right turns.) This surprisingly low incidence of left turns suggests that additional cells besides the two GIs 1 must be involved in determining whether a wind puff was from the left or the right. Because the directional curves of GIs 2 and 3 are bilaterally symmetrical (Figure 14A), they would not appear capable of a left-right discrimination. One would therefore predict that a cockroach with just one of these GIs killed would show unaltered behavioral discrimination of left *vs* right winds. As predicted, killing either of these cells did not significantly effect the turning direction (Figure 15). Surprisingly, however, when both left GI 1 and left GI 2 were killed, there was a much higher incidence of mistaken left turns than when just left GI 1 had been killed (Figure 15). In these experiments it was necessary to control for possible damage to neurons other than the one or two GIs one intended to kill. Such unintended damage could be caused by Pronase leaking from the electrode or from the injected GI, and could conceivably contribute to producing the altered turning directions. Injecting, not into a GI, but rather extracellularly in the vicinity of GIs 1, 2, and 3, did not significantly effect the turning direction (Figure 15, control).

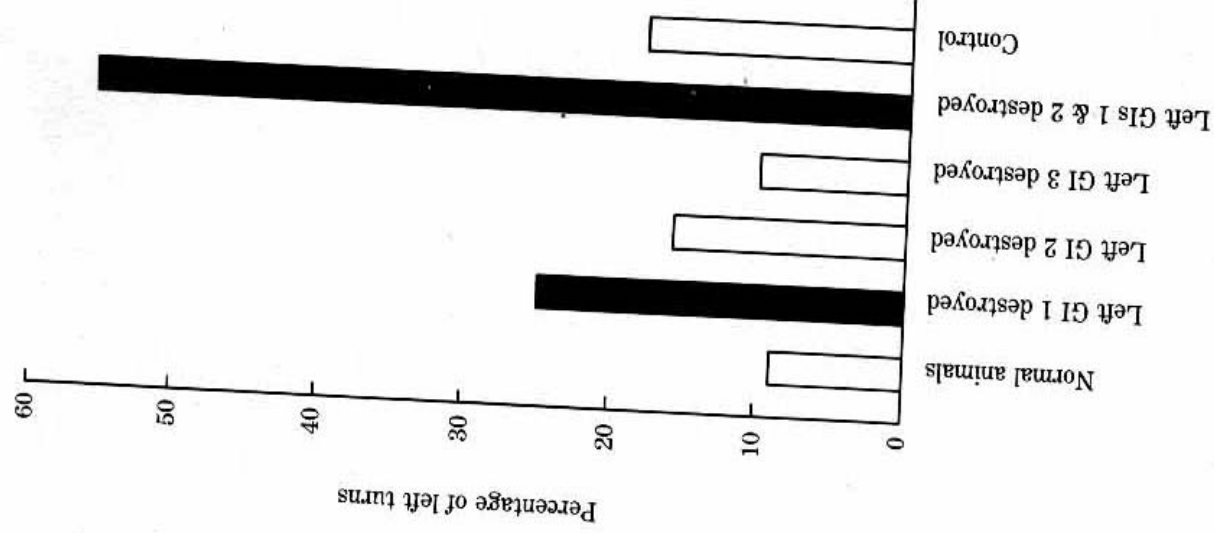
It is not yet clear how killing a cell that has a symmetrical directional response (GI 2) adds to the disruption of the behavior's directionality. Whether also killing the left GI 3 would further increase the percentage of left turns remains to be

⁵Although these graphs show number of action potentials as a function of wind direction, similarly shaped graphs result from plots of other parameters, such as the average frequency of action potentials within the evoked bursts, the duration of the bursts, and 1/latency to the first action potential of the burst (Westin *et al.*, 1979). The latency parameter is of particular interest because, by comparing the latencies among the different GIs, the cockroach could obtain directional information as soon as the GI bursts have begun, rather than waiting for these bursts to terminate. In fact, it is known that the cockroach can begin its escape movements in response to just the first one or two action potentials in each of the GIs 1, 2, and 3 (Camhi and Nolen, 1981).

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FIGURE 15.

Effects of destroying left GIs 1 and/or 2 on the direction of turning by cockroaches in response to wind from the left. All wind puffs were from within a range of 45° left of front. Only the solid bars represent percentages significantly different from those of normal animals. All responses that were not turns to the left were turns to the right. Wind puffs from the right front (not represented on this graph) usually evoked turns to the left, with no significant differences after destruction of any of the left GIs 1, 2, or 3. (Courtesy of C. Comer.)



seen. Nevertheless, one can already see that GIs 1 and 2 play an important role in reading the wind direction and in prescribing the initial turning direction. An understanding of the specific mechanisms by which the comparisons among the GIs are carried out must await a study of the synaptic interactions from these GIs onto their postsynaptic neurons.

IS THE COCKROACH BORN WITH A FUNCTIONAL ESCAPE SYSTEM?

When a cockroach hatches from an egg case, each of its cerci bears, not 220 wind-receptive hairs as in the adult, but just two (Figure 16). One can record the wind-evoked responses of the single sensory cell under each of the animal's four hairs. Its directional response (Figure 17) is similar to that of a sensory hair in the adult (Figure 10). Each of the four overlapping graphs for the hatching shows

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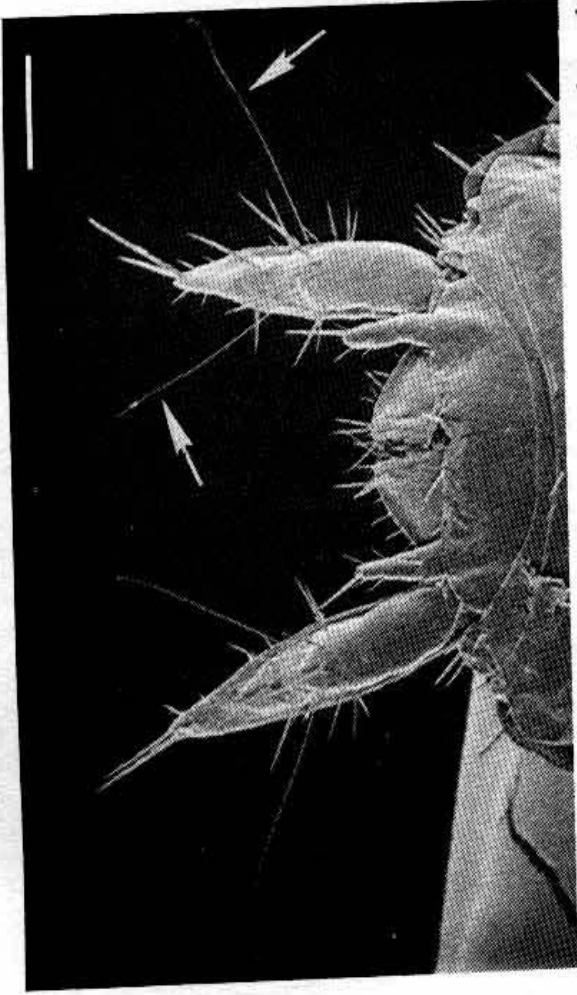


FIGURE 16. Scanning electron micrograph of the cerci of a newly hatched cockroach *Periplaneta americana*. Only two wind-receptive hairs like those found in the adult are present on each cercus (arrows). Calibration bar = 200 μ m. (From Dagan and Volman, 1982.)

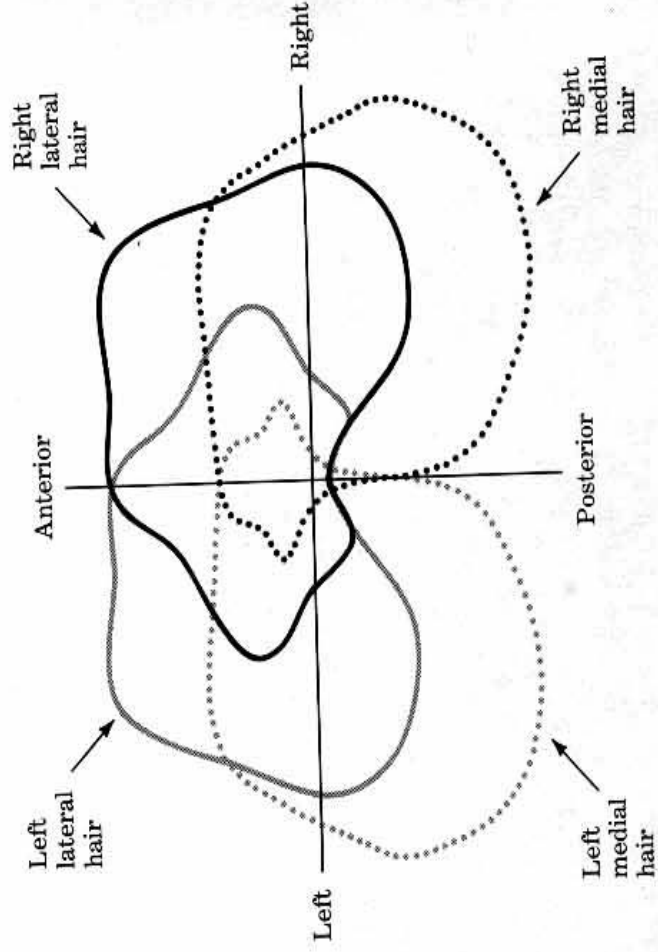


FIGURE 17. Directional responses of each of four wind-receptive hairs of a newly hatched cockroach. Each hair appears responsive to a different quadrant of horizontal space. (From Dagan and Volman, 1982.)