34 Wine, J. J., and Krasne, F. B., The cellular organization of crayfish escape behavior, in: The Biology of Crustacea, vol. 4, pp. 241–292. Ed. D. E. Bliss. Academic Press, New York 1982.

35 Wine, J. J., and Mistick, D. C., Temporal organization of crayfish escape behavior: Delayed recruitment of peripheral inhibition. J. Neurophysiol. *40* (1977) 904–925.

36 Zucker, R. S., Crayfish escape behavior and central synapses. I. Neural circuit exciting lateral giant fiber. J. Neurophysiol. *35* (1972) 599–620.

37 Zucker, R. S., Kennedy, D., and Selverston, A. I., Neuronal circuit mediating escape responses in crayfish. Science *173* (1971) 645–650.

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Escape behavior in the cockroach: Distributed neural processing

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Summary. Escape reactions are often considered to be among the simplest behaviors. The nerve circuits guiding these reactions are also generally thought to be simple. For instance, in several species a single interneuron is sufficient to trigger normal escape. The evasive response of the cockroach, however, appears to be more complex both behaviorally and physiologically. In this review, several complications of the behavior are pointed out, based on a recent computer-graphic analysis of the leg movements. Next described is the cooperative role of several interneurons – not just one – in evoking an escape turn away from the stimulus. A model of this multicellular code for stimulus direction is then presented that correctly predicts the turning behavior under many different experimental conditions. Finally, an overall scheme of the information processing for escape behavior is presented.

Key words. Escape behavior; giant interneurons; cockroach; *Periplaneta americana;* feedback.

Introduction

One of the major reasons for selecting an invertebrate animal for neuroethological study is the possibility of working at the level of individually identified neurons. Among the behaviors whose controlling neurons are easiest to identify are escape reactions. Here the rapid conduction of impulses that is essential for quick evasion from a predator is produced by axons of especially large diameter. The 'giant neurons' sporting such axons have well repaid investigation in crayfish [21], earthworms [17], crickets [20, 23], cockroaches [3] and other invertebrates. One of the few vertebrate systems in which individual interneurons have been identified and studied is also an escape system, that of teleost fish [18].

It is generally accepted that escape behaviors are simple and highly stereotyped, at least with regard to the initial movements [18, 39]. It is also held that neuronal circuits for escape are quite simple. For example, rather than the numerous small interneurons that characterize many other types of circuit, there is often a limited number of giant interneurons. Some of these are even able, individually, to trigger a normal escape movement, as in crayfish [21], teleost fish [18] and flying crickets [26]. Moreover, a given 'lateral giant interneuron' of the crayfish not only triggers escape, but also carries out by itself three other behavioral functions: 1) making the decision whether or not to escape from a given stimulus [27], 2) silencing competing behaviors by sending inhibitory signals to their control circuits [40], and 3) serving as the focus for certain modulatory influences on the escape behavior [19, 40].

Through recent studies of the cockroach escape system a different, more complex, picture is beginning to emerge. The behavior involves aspects of information processing not previously known for this system, some of which are described below. Also, though there are giant interneurons, there are many of them, and responsibility is widely shared among them. In this review I address primarily these selected aspects of the escape system, focussing substantially on our own work, much of which is still in progress. An excellent comprehensive review [30], and two more general reviews [2, 3] have appeared in recent years.

The behavior

The escape response of the cockroach to an approaching predator is usually a turn in the opposite direction followed by a run [7, 8]. The major or only sensory cue used by the cockroach to detect the predator's approach and determine its direction is the wind gust that precedes the predator's moving body [8].

Recent computer-graphical analysis of high speed films [5] (J. M. Camhi and A. Levy, unpublished observations), together with earlier analyses [7, 13] reveal the details of movement during the turn. For instance, a wind puff from the left front elicits a sharp right turn that consists, at least initially, of a pivot about the most posterior point on the body. Later, forward translatory movement is added to the pivot, followed by purely foward movement (fig. 1). The pivot to the right begins with the left hind leg in a swing phase (leg lifted off the ground and brought forward), in roughly half the trials, and in a stance phase (leg remaining on the ground) in the other half of the trials. The remaining legs virtually always begin the turn with a stance phase. The stance phase of the right hind leg is particularly prolonged, often outlasting

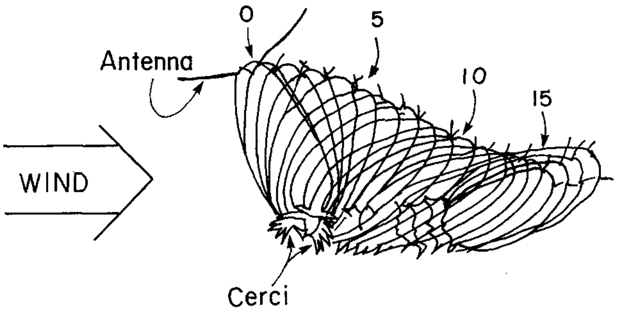

Figure 1. Turning response of a cockroach away from a wind puff. The body's silhouette is shown at successive 4-ms intervals, as drawn from cine frames. The body's position prior to the response (0), and on frames 5, 10 and 15 is indicated by the numbers. The initial pivot about the cerci is typical.

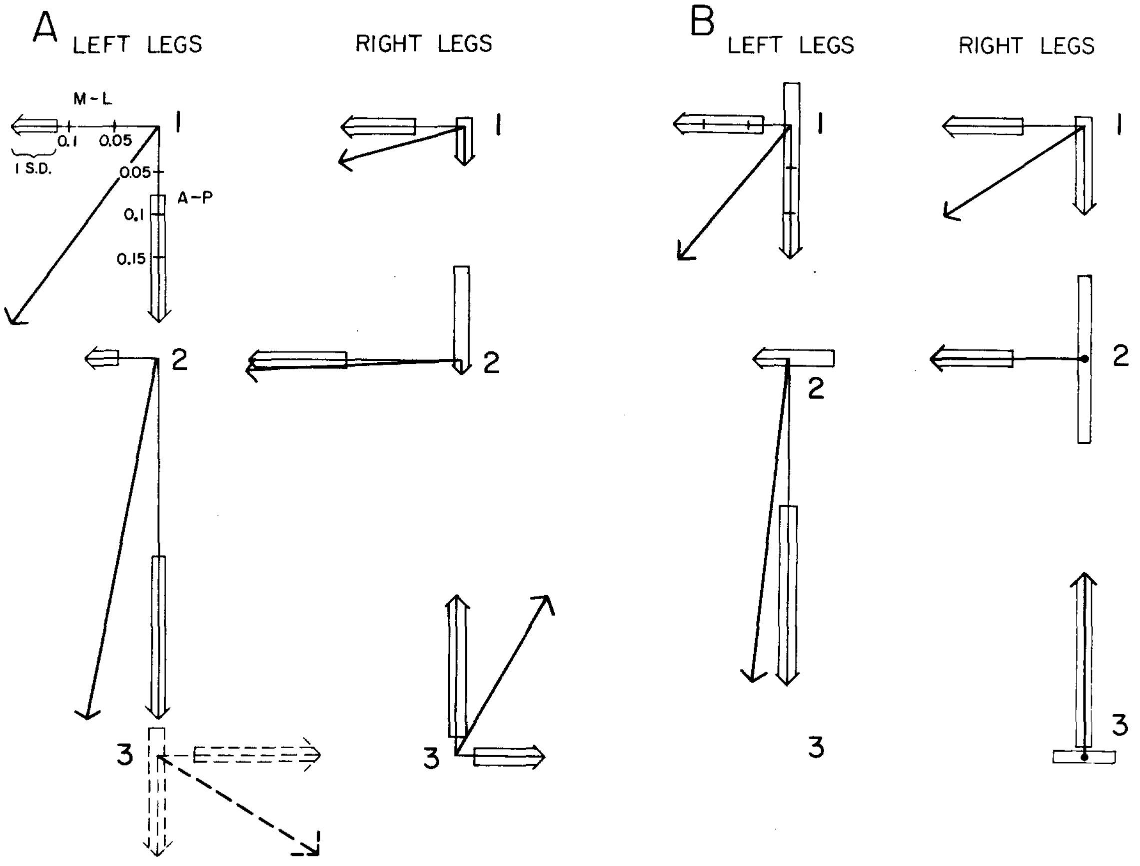

Figure 2. Leg movements *relative to the body* during pivots to the right in response to wind puffs from the left front. (Left pivots showed mirror-image movements.) Movements shown are only from each leg's first stance phase. Since a leg's tarsus is fixed on the ground during these movements, it causes the body to turn in the direction opposite the arrows. Thus, for instance, a leftward movement of a front leg causes the front part of the body to move to the right. *A* Free-ranging animals. For each leg, the A-P and M-L components and their vectorial sum are shown by separate arrows. The scale shown for the left front leg (1) indicates distances moved in each direction, measured in body lengths. The same scale applies to all legs. The wide portion of each A-P and M-L arrow indicates one standard deviation. Data are from 23 turns of 7 different cockroaches. The dashed lines for the left hind leg (3) indicate that only those trials in which this leg was in a stance phase, and not a swing, are included. This was 48 % of the trials. *B* Animals pinned on a slick surface (see text). Same format as in *A*. The left hind leg (3) is not represented since on the slick surface it was not possible to discriminate between this leg's stance and swing phases. All movements of other legs are the same as in *A*, except for the lateral movements of the right hind leg (3).

two complete cycles of the other legs. This overall pattern differs from running, in which three legs are in stance and three in swing at any moment[16]. This latter, running-specific pattern is established by roughly the third step of the turn. Figure 2 A shows the movements relative to the body of each leg's initial stance movement in a right pivot. Both the mean anterior-posterior (A-P) and medial-lateral (M-L) component are shown, together with their vectorial sum. Considering first just the M-L components, the right front and middle legs pull in sharply toward the body, while the right hind leg pushes outward. The left front and middle legs push outward from the body, while the left hind leg (on those trials when it is not in swing phase) pulls inward. These M-L movements alone would be expected to cause a pivot to the right. The axis of this pivot (which is at the posterior end of the body) would be determined by complex leg interactions that have not been analyzed. In addition to the M-L movements, there are strong posterior movements of all three left legs, and anterior movements of the right hind leg.

Of the various movement components shown in figure 2A, some may represent mere passive reflections of a leg's remaining on the ground while the body is pivoting over it. That is, a given component of a leg's movement may not represent an active force produced in that direction by that leg, but rather the result of compound forces exerted on the body by other legs. To test which components of each leg's movement are active, one can pin the cockroach by its posterior abdominal region to an oiled glass plate on which the legs slip freely during their stance phase[6]. There is sufficient friction for the body to be caused to turn slightly, permitting verification of an intended pivot in the proper direction away from the wind. Yet there is sufficient slickness that the legs are largely decoupled mechanically from one another. Analysis of leg movements carried out under these conditions show that all components represented in figure 2 A are present except for the lateral movements of the right hind leg (fig. 2 B). Thus, all components but this one are active.

Is the initial movement that a leg makes influenced by its standing position prior to the escape turn? The question is of interest because an affirmative answer would mean that some source of feedback information regarding leg position is included in the escape circuitry. Leg proprioceptors are, in fact, known to influence some of the interneurons thought to participate in escape[24]. However, the overall organization of this proprioceptive influence on the escape system is not yet understood.

One influence of leg position can be seen in the left hind leg's movements during right pivots (and vice versa). In the 52 %

of the trials in which this leg began with a swing, the initial tarsal location relative to the body was significantly more posterior than in the remaining trials, in which this leg began with a stance (unpublished observations). Thus some source of feedback information appears to by used in the escape circuit.

Feedback information on a leg's A-P position also appears to be involved in another way. Since the initial body movement is a pivot about a rear point, with five or six legs standing on the ground, it seems likely that a leg whose ground contact happens to be located close to the pivot point would move less, relative to the body, than one located far anterior or posterior to this point. Figure 3 shows, in fact, that this is the case. For right turns, the amount and direction of M-L movement depends on a leg's initial A-P location. Thus, for instance, if the left middle leg's ground contact is far anterior it moves strongly outward from the body; but if more posterior, it moves less or even reverses direction. This appears not to result from a structurally-based inability of the leg to move laterally when in a posterior position; the hind legs are of similar structure, and yet the right hind leg moves laterally more strongly when it is posterior than when anterior. This same dependence on initial A-P position is found also in pinned animals, and thus is a function of a leg's own forces. This implies that to perform a turn, some central command instructs a leg's motor circuitry to make not a fixed pattern of muscle contractions, but rather one of a range of patterns, the specific one being determined by feedback. The source of feedback could be sensory[42] and/or corollary discharge from tonic signals that determine a leg's stance position prior to the turn.

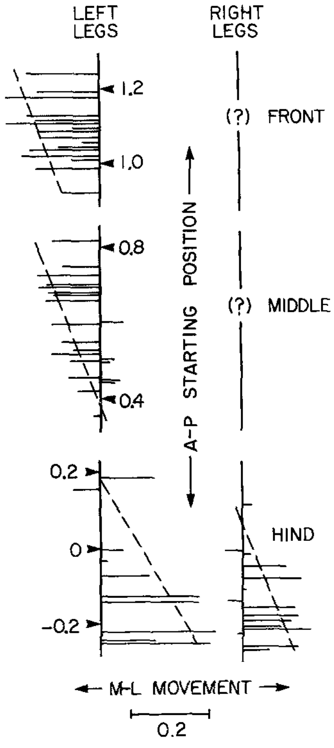

Figure 3. The size and direction of a leg's M-L movement during a turn is correlated with the leg's A-P position prior to the turn. Data shown are for turns to the right, only for those legs whose entire first stance phase is normally visible. (The right front and middle legs normally pull under the body on a right turn, so the extent of their M-L movements could not be measured.) The starting A-P positions for different trials are shown on the y axis, the scale extending from roughly -0.2 to $+1.2$, where 0 represents the A-P level of the cerci, and 1.0 that of the head. The direction and length of each horizontal line represents the direction and extent of the M-L movement on the different trials (scale below, in body lengths). The dashed lines are the first order regression lines, each of which shows a statistically significant relationship ($p < 0.05$). There was no significant relationship between a leg's starting A-P position and its starting M-L position.

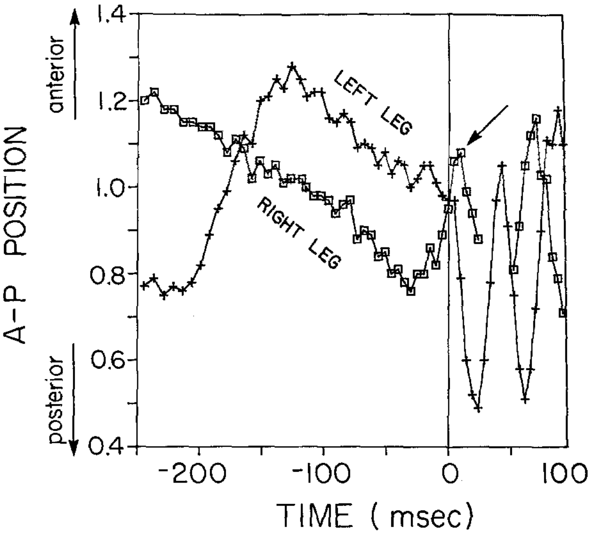

Figure 4. Transition from slow walking to turning in response to wind, in an animal pinned to a slick surface. The A-P positions of the left and right front legs are shown as functions of time. Time 0 represents the last frame before the body's turn began. The animal received a wind puff from the left front that evoked a turn to the right. In such right turns, the right front leg makes a small posterior movement (fig. 2). However, the stimulus came during an anterior (swing) movement of this leg. The leg immediately reversed its direction (arrow) and carried out the expected posterior movement. (On the 4th frame after the arrow, this leg disappeared under the body owing to its medial movement, so its graph shows a blank space.) In all 8 trials showing a similar situation the result was the same.

Cockroaches respond to wind stimuli by turning, not only when they are standing still, but also when they are walking slowly[6]. Does the insect employ its ongoing walking movements, simply speeded up and with a superimposed turning component, to carry out such turns? Or does it revert to the special pattern of leg movements used to turn from a standing start? Analysis shows that it uses movements just like those shown in figure 2. Moreover, in trials where a given leg is moving, just prior to the start of a wind-evoked turn, opposite to the direction in which it would move during the turn, it immediately reverses its direction (fig. 4). This implies that the escape circuit may inhibit the circuit controlling walking movements. A similar cancelling of competing behaviors has been seen in the crayfish escape system, where the lateral giant interneuron inhibits several other circuits[40].

A sketch of the neural circuit for escape

Figure 5 shows a highly simplified sketch of the neural circuit for escape, as understood to date. The responsible wind receptors are located, exclusively or almost so, on the cerci, two posterior abdominal appendages[7,13]. These are filiform cuticular hairs, about 220 on each adult cercus, that are deflected in their sockets by wind. Such deflection activates the single sensory neuron at the base of the hair[25,36]. Each sensory cell sends its axon to the last abdominal ganglion where it activates, apparently monosynaptically, giant and other interneurons[1].

There are seven bilateral pairs of individually identified giant interneurons (GIs). Each has its cell body in the last abdom-

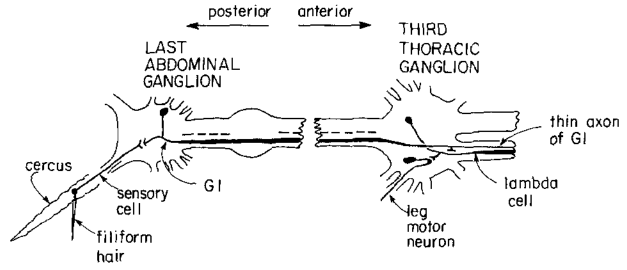

Figure 5. Sketch of the neural circuit for escape in the cockroach. One neuron of each major known category is shown; sensory cell, GI, thoracic interneuron (represented by the lambda cell) and leg motor neuron. Anterior to the third thoracic ganglion, the GI axons taper. In this region, the lambda cell and others have axons of considerably greater diameter. Not shown are the neurons' dendritic trees or axonal branches, such as a posterior branch of the lambda cells that runs posteriorly from the third thoracic ganglion[31].

inal ganglion and sends its axon anteriorly in the contralateral connective[15, 32]. The GIs are subdivided, anatomically and apparently physiologically, into a ventral group (GIs number 1 through 4) and a dorsal group (GIs 5 through 7) on each side[14, 15, 31]. The axons of the ventral GIs extend to the head, but the dorsals are not yet known to extend beyond the second thoracic ganglion. Anterior to the third thoracic ganglion, the GI axons taper. Thus, whereas the diameters of the ventral GIs within the abdominal connectives are 50–60 μm, between the first and second thoracic ganglia they are only 10–15 μm[32].

In the third thoracic ganglion, the giant interneurons synapse upon another group of interneurons, some of which in turn synapse on motor neurons that control the hind legs[31]. Each of the eight identified interneurons in the third thoracic ganglion also sends an axon anteriorly and/or posteriorly in the nerve cord. These interneurons appear to be subdivided into two groups, one of which is contacted by the ventral GIs, and the other by the dorsals. Of those contacted by the ventrals, one interneuron of particular interest, the lambda cell, sends anteriorly an axon of 25 μm diameter. Given that this axon would conduct impulses faster in this region than would the thinner GI axons, the lambda cell is among the potential candidates for distributing the motor command among the three thoracic ganglia. Such a distribution seems important, since all the legs participate in the turn in a temporally well coordinated fashion. It is not yet known whether leg motor neurons of the first and second thoracic ganglia are activated by the ascending GIs themselves, by ascending branches of the third thoracic interneurons such as the lambda cell, and/or by interneurons intrinsic to these more anterior ganglia.

A multicellular code for wind direction

As mentioned in the introduction, in the crayfish, teleost fish and flying crickets, an individual interneuron is able to initiate normal escape behavior. In fact, in the crayfish a single lateral giant interneuron (LGI) is both necessary and sufficient for producing escape[27, 38].

How does the activity of the cockroach GIs compare with the crayfish's command for escape? Greatest attention has been focussed on the three pairs of GIs having the greatest axonal diameter, left and right GIs 1, 2 and 3, all ventrals. Wind puffs delivered to the cerci from either front right or front left evoke spike trains in all six of these GIs[37] and in most or all of the other GIs and non-giant interneurons that have been recorded from. Yet the animal discriminates behaviorally between left front and right front winds, turning appropriately away from each direction. Thus, among the GIs, there is no exclusively left-activated cell that evokes a right turn or vice versa. Rather, some aspect of the relationship among the spike trains in the different GIs specifies wind direction, and thus the required turn direction.

Related to this, the range of wind angles that activate a given GI (i.e., its receptive field) is as broad or broader than that of the sensory cells. For instance, the sensory cells all respond to a range of roughly 180° within the horizontal plane[36]. By contrast, GIs 1 and 2 respond to the full 360°[37]. This receptive field broadening is the reverse of what would be expected of a labeled line system in which a given GI sharply specifies a given direction. Rather, it is consistent with a direction code based upon multicellular processing. Considerable effort has been devoted to defining the multicellular code for wind direction among the GIs.

Some insight into the problem comes from experiments involving gross manipulation of the cerci or the giant interneurons. If the GIs (and other wind-responsive interneurons) of one side are silenced by either covering or ablating the ipsilateral cercus, or cutting an abdominal connective on that side, the animal responds to wind from either side by turning toward the silenced side[7, 11, 34]. Thus, discrimination of left versus right winds appears to involve some form of left-right comparison.

To determine which GIs might be especially important in this comparison, selective lesions were produced in one or two of the GIs by means of intracellular pronase injection, and their influence on the direction of turning was tested a few days later[9] (C. Comer, pers. comm.). Figure 6 shows the number of turns to the *left* in response to wind stimuli from the left front (that is, wrong turns) in normal animals, and in those in which one or two left GIs are missing. Killing GI 3 had no effect on turn direction, so this cell may play little or no role in discriminating left from right winds. However, killing GI 1, or GIs 1 plus 2 produced a significant increase in the percent of wrong turns. (Killing GI 3 together with a second GI has not yet been tested.) Turning responses to wind from the right were unaffected by killing these left GIs[9]. Thus, GIs 1 and 2 appear to be important in the code for wind direction. Nevertheless, these cells do not carry the *entire* code, since killing them produced only 52% wrong turns. By contrast, cutting the left connective, which silences impulse traffic in all the left GIs and other left interneurons[11], or covering the left cercus, which largely silences the left GIs and perhaps other interneurons[7], produced 100% wrong turns in response to left front winds.

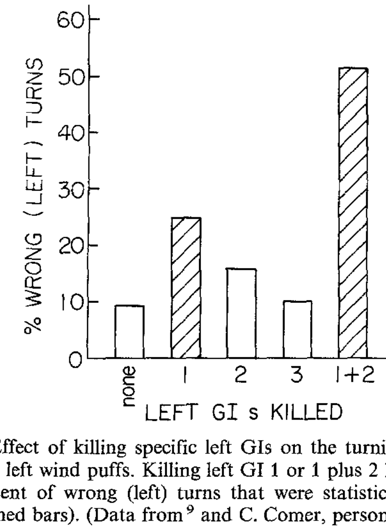

Figure 6. Effect of killing specific left GIs on the turning direction in response to left wind puffs. Killing left GI 1 or 1 plus 2 led to increases in the percent of wrong (left) turns that were statistically significant (cross-hatched bars). (Data from[9] and C. Comer, personal communication).

This apparent role of GIs 1 and 2 but not 3 fits in with their directional specificity. Wind puffs from 15° left versus 15° right of center (near the limits of the animal's behavioral discrimination) are discriminated about equally well by GIs 1 and 2, but less so by GI 3, as determined by numbers of action potentials or other spike train parameters (J. M. Camhi, unpublished observations). This also fits with the observation that electrical stimulation of a single GI 1 evokes leg motor responses, and that these are enhanced by stimulating also GI 2, but not GI 3[29].

When one or two GIs are killed, there is little or no effect on the responses to wind of the remaining GIs on the same or the opposite side[4]. Thus, one can consider the lesion of a GI in these experiments as a highly specific removal of the information conveyed to the thoracic ganglia only in the killed cell. This permits one to search for a quantitative correspondence between the physiological and the behavioral deficits, as a tool in analyzing the code for wind direction among the GIs.

This search has recently been carried out by developing models (J. M. Camhi, unpublished) in which the observed responses of the GIs could account quantitatively for the percentages of wrong turns in normal animals and in those with specific GIs missing (i.e., data of fig. 6). Models are useful here, since the system is too complex to understand on the basis of simple cell-to-cell interactions.

Insights from studies of auditory systems are helpful in guiding the design of models in the cockroach escape system. The coding of wind direction by the left and right GIs resembles the coding of sound direction by two ears in various animals[22,41]. To localize the source of a pure tone, three major parameters can be used; binaural differences in time of arrival, in intensity, and in the phase of the sound. In the case of trains of action potentials in the left and right GIs in response to a left wind puff, the cockroach likewise could use bilateral differences in either time of arrival (that is, on which side does the first action potential reach the thoracic ganglia?), or intensity (on which side is there a greater number of action potentials within a given sample time?). There is no counterpart to bilateral phase differences of the sound waves, since a wind puff corresponds to only one half cycle of near field sound stimulation, and thus phase differences reduce to time of arrival differences.

Accordingly, two general categories of model have been tested. One, called the 'first impulse model', focusses on differences in the time of arrival of the first left, vs the first right, GI action potential at the third thoracic ganglion. Though space does not permit an explanation, it is possible to show that this model is incompatible with the timing properties of the GIs (J. M. Camhi, unpublished observations). The other category of model, called here the 'relative intensity model', relies upon differences in the number of lefts vs right GI action potentials. This model is seen in three variations in figure 7. In figure 7A, it consists of a summation of the number of action potentials during a given sample time in the left GIs 1, 2 and 3 by a left summator, S_L, a separate summation of the homologous right GIs by a right summator S_R, and a comparison of these two sums. Signal parameters other than number of action potentials, such as spike frequency, could also be used.

For each cell in figure 7A, the mean number of action potentials recorded in response to a standard left front wind puff is shown (J. M. Camhi, unpublished observations). Since the sum for these three left GIs is consistently greater than for their right homologs, this comparison of the two sums could specify whether the wind was from the left or the right. However, by removing from the model, say the left GI 3, the right sum now becomes greater than the left. Thus, the model predicts that an animal in which the left GI 3 is missing would, on most trials, misjudge the direction of a left front wind. But such errors do not occur upon killing GI 3 (fig. 6). As mentioned above, there are also other reasons for assuming that GI 3 does not participate in left-right directional specification. This GI was therefore removed from the relative intensity model.

Including in the model just GIs 1 and 2 (fig. 7B) is still problematic. Removing from this reduced model the left GI 2 again leaves the right side with a greater sum than the left, and thus predicts that after killing the left GI 2, the animal should turn wrong on most trials in response to a left front wind. This same prediction follows from removing the left GI 1 rather than GI 2. Neither prediction is upheld by the behavioral experiments (fig. 6).

In the version of the model shown in figure 7C, the roles of GIs 1 and 2 are shared with other cells. The model does not specify the identity of these cells, but rather calls them 'X'. They could of course be other GIs. The left and right groups X are assumed to have the same degree of directionality in their responses to wind as GIs 1 and 2 have. A computer program was used to vary the total number of action potentials in the group X and check the resulting behavior of the model. It was found that if the X group on either side gives about 2.5 times as many action potentials as the ipsilateral GIs 1 and 2 together, then the model responds to removal of individual or pairs of left GIs 1 or 2 by predicting turn directions that match rather closely the animal's actual behavior (fig. 7D). These numbers – 32 for the left X and 23 for the right X, are entered in the model of figure 7C. Interestingly, these are roughly equal to the numbers of action potentials that would be given by *all* the GIs together except GIs 1, 2 and 3, in response to a wind puff from the left front[37].

Several further predictions of the model were then tested. None was a critical test, but all provided supportive evidence

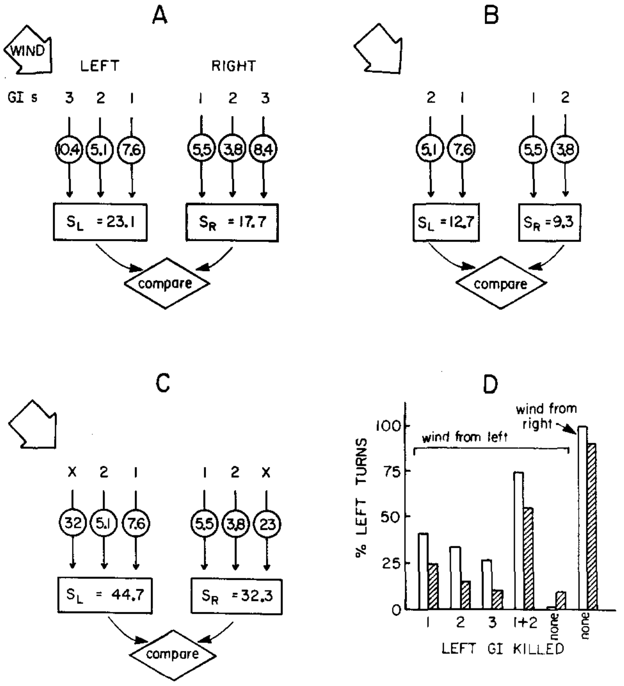

Figure 7. Relative intensity model for the multicellular GI code of wind direction. *A, B* Two versions of the model that can account for the directional responses of an intact animal, but not of one in which particular left GIs are missing, as explained in the text. The numbers in the circles indicate the mean number of action potentials recorded from that GI for wind from the left front. *C* The preferred version of the model. *D* Test of the version shown in part *C*. Open bars show the predictions of the model, and cross-hatched bars show the actual results as in figure 6.

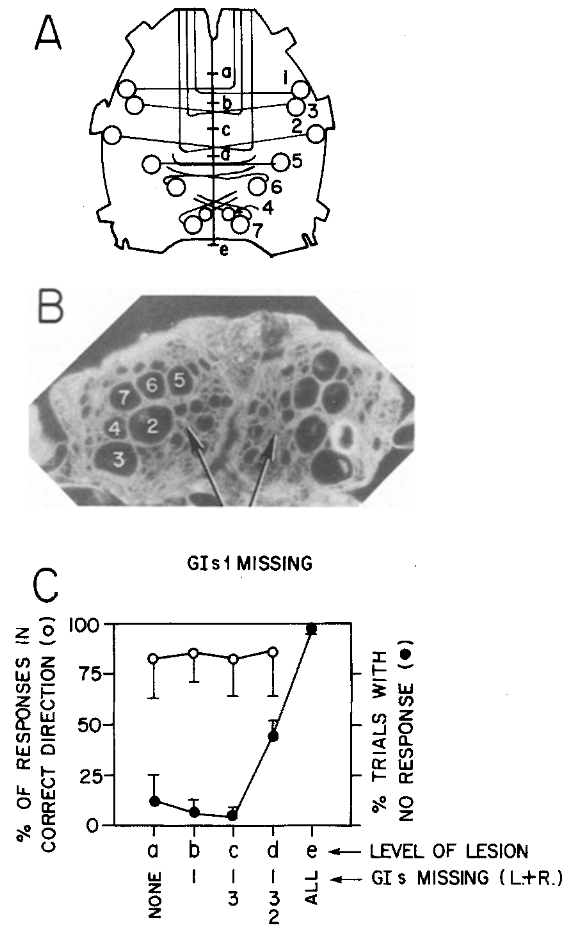

Figure 8. Further tests of the relative intensity model of figure 7C. *A* Locations of cell bodies, initial segments, and ascending axons of each of the seven left and right GIs in the last abdominal ganglion (based on Daley et al.[15]). Micro-knife lesions were made along the midline from anterior to points a, b, c, d or e. These severed the initial segments of specific subsets of bilaterally homologous GIs. Lesions as far as level c or d do not cut through any processes of GIs other than numbers 1, 2 or 3, nor sensory axon branches, though many unidentified neurons would be cut. *B* Cross section of a nerve cord made 8 days after a lesion to level b of part *A*. Both GIs 1 are missing, though all others are present, as expected. Right GI 4 is filled with Lucifer Yellow dye, injected after recording from this cell following behavioral tests. Both this cell, and the unfilled putative right GI 2 that was recorded gave normal responses to wind puffs. *C* Behavioral results from animals in which bilaterally homologous sets of GIs are missing. The nerve cords of all animals were examined for the absence of GIs as in part *B* of this figure, and in most preparations one or more intact GIs were recorded from after the behavioral tests, and shown to give normal responses to wind. All combinations of killing symmetrical sets of ventral GIs produced no change in the percent of correct turns. Killing all 3 bilateral pairs of GIs 1, 2 and 3 increased substantially the percent of trials on which there was no response, though it did not affect the directionality of the responses. With all the GIs killed there was never a response to wind. Data from 13 animals.

for the model of figure 7C. For instance, the model suggests that killing both the left and the right GIs 1 should leave the animal with a substantial number of other directional cells (X plus GI 2 on each side), perhaps sufficient to specify a correct turn. Moreover, killing left and right GIs 1 and 3 should also permit correct turning, since GI 3 is not even part of the model. In fact, killing all six left and right GIs 1, 2 and 3 would still leave the group X on each side, and the directionality of this group could be sufficient for correct turning. These three tests were carried out. The method of killing left and right sets of homologous GIs was a micro-knife cut in the midline of the last abdominal segment, from the anterior end posteriorly. As figure 8A shows, whereas a small cut (a) should sever no GIs, a slightly longer cut (b) should sever the initial segments of left and right GIs 1, a still larger cut (c) should add both GIs 3, a still larger cut (d) should add both GIs 2, and cutting fully through the ganglion (e) should sever all the GIs. The severing of GIs 1, or 1 and 3, or 1, 3 and 2 (in cuts b, c and d respectively) should cause degeneration of the axons of these specific combinations of cells without causing degeneration of other GIs or wind-sensory axons, all of which are located more posteriorly[15]. Figure 8B, from a preparation that had been cut to level b, shows that such lesions do give rise to specific degeneration as expected, which usually occurs within 5–8 days. Figure 8C shows that the removal of all three combinations of GI pairs mentioned above leaves the direction of escape turns largely unaffected, though the percent of trials with no response increases if all three of these GI pairs are killed, and increases further if all the GIs are killed.

Thus, cells other than the three pairs of GIs 1, 2 and 3 must be providing the directional information in these lesioned animals. During the 5–8 days between the lesion and the behavioral test, it is possible that functional reorganization occurred. However, this seems unlikely since other forms of plasticity known in the escape behavior require nearly a month to appear[10, 34, 35]. Moreover, recordings made from various non-lesioned cells show that these continue to respond to wind puffs in an unaltered manner. Thus, it is likely that the normal turns seen in these lesioned animals come about by means of the normal contribution to directional specification by cells other than GIs 1, 2 and 3, rather than by some abnormal contribution recruited as a result of the lesion.

From the present perspective, what all this indicates is that the directional information is even more widely distributed than among just the largest set of GIs. In fact, a useful feature of the relative intensity model is that it suggests roughly how many additional cells may be involved – namely, a number equal to all the remaining GIs.

Discussion

Figure 9 summarizes much of our current knowledge and ideas about information processing in the cockroach escape system. A predator approaching from the left front activates the left cercal hairs, left sensory cells and left GIs more than their right homologs[12, 25, 37] (and J. M. Camhi unpublished observations). According to the relative intensity model, a left-right comparison of the summed number or frequency of action potentials in certain GIs of the two sides results in a command to turn to the right. This command (carried by as yet undetermined neurons) may activate the leg motor neurons directly[31], rather than by way of the central oscillator for walking, since the initial movement of each leg is so different from that seen in walking. Each leg's motor response is determined in part by feedback information on that leg's initial position. Since ongoing stepping movements are cancelled by an escape turn (fig. 4), the central neuronal oscillator (CNO) for walking is shown as receiving an inhibitory input from the turn command. However, since running movements follow, the central oscillator is shown as being turned on by the turn command after a delay (D). A similar delayed excitation of a second stage of escape in crayfish is reported by another contributor to this review[28].

Many of the functions shown in figure 9 are carried out by a multi-cellular array. This begins at the sensory level. Roughly 450 sense cells serve as the input to this system, even though in the first instar nymph, only 2 such cells are found on each cercus, and these are sufficient to evoke a turn as accurate as in the adult[13]. At the interneuronal level, several

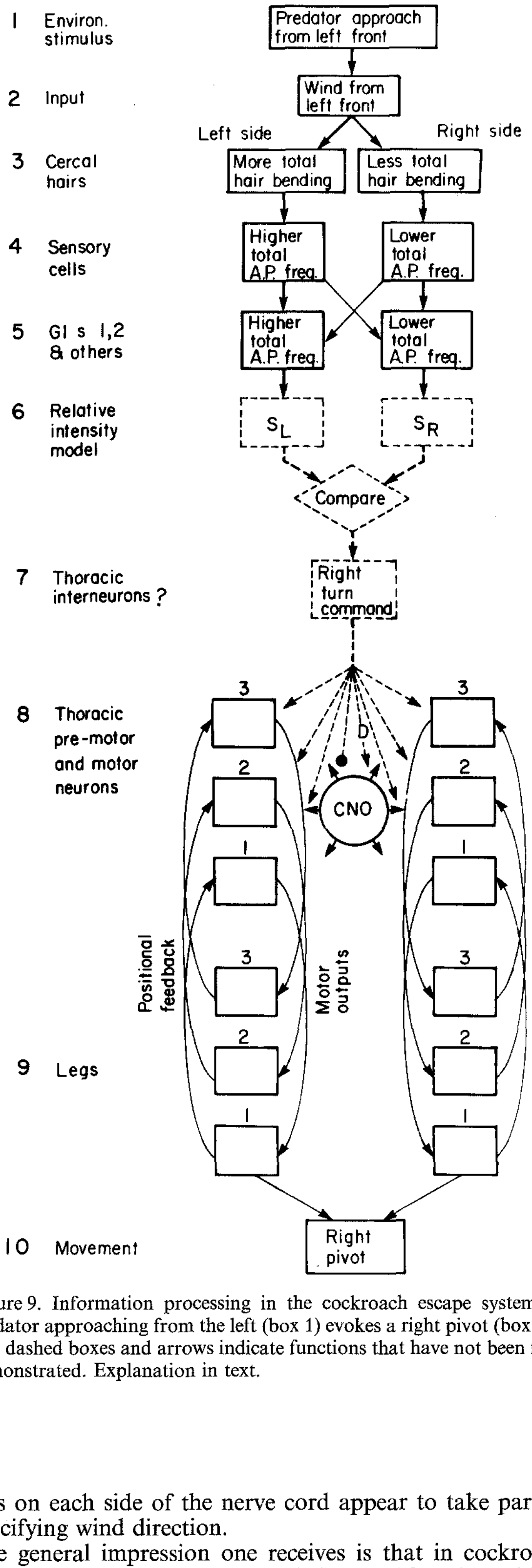

Figure 9. Information processing in the cockroach escape system. A predator approaching from the left (box 1) evokes a right pivot (box 10). The dashed boxes and arrows indicate functions that have not been fully demonstrated. Explanation in text.

GIs on each side of the nerve cord appear to take part in specifying wind direction.

The general impression one receives is that in cockroach escape, responsibility for a given behavioral function is highly shared among groups of neurons, rather than being focussed in single cells like the crayfish LGI. It remains possible that single LGI-like cells will be found among the thoracic ganglia (box 7 of fig. 9). By recordings from the thoracic connectives in animals pinned to a slick surface, it should be possible to clarify this possibility. These recordings are currently in progress.

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1 Callec, J. J., Guillet, P. C., Pinchon, Y., and Boistel, J., Further studies on synaptic transmission in insects. II. Relations between sensory information and its synaptic integration at the level of a single giant axons in the cockroach. J. exp. Biol. *55* (1971) 123–149.

2 Camhi, J. M., The escape system of the cockroach. Scient. Am. *243* (6) (1980) 158–172.

3 Camhi, J. M., Neuroethology: Nerve Cells and the Natural Behavior of Animals. Sinauer, Sunderland, Massachusetts 1984.

4 Camhi, J. M., and Comer, C. C., Modeling the information in groups of identified cells: Giant interneurons and cockroach escape behavior. Soc. Neurosci. Abstr. *12* (1986) 58.9.

5 Camhi, J. M., and Levy, A., Leg movements and their control in the escape turns of cockroaches. Neurosci. Abstr. *13* (1987) in preparation.

6 Camhi, J. M., and Nolen, T. G., Properties of the escape system of cockroaches during walking. J. comp. Physiol. *142* (1981) 331–346.

7 Camhi, J. M., and Tom, W., The escape behavior of the cockroach *Periplaneta americana*. I. Turning responses to wind puffs. J. comp. Physiol. *128* (1978) 193–201.

8 Camhi, J. M., Tom, W., and Volman, S., The escape behavior of the cockroach *Periplaneta americana*. II. Detection of natural predators by air displacement. J. comp. Physiol. *128* (1978) 203–212.

9 Comer, C., Analyzing cockroach escape behavior with lesions of individual giant interneurons. Brain Res. *355* (1985) 342–346.

10 Comer, C., and Camhi, J. M., Behavioral compensation for altered cercal position in the cockroach. J. comp. Physiol. *155* (1984) 31–38.

11 Comer, C. M., and Dowd, J. P., Escape turning behavior of the cockroach: Changes in directionality induced by unilateral lesions of the abdominal nervous system. J. comp. Physiol. *160* (1987) 571–584.

12 Dagan, D., and Camhi, J. M., Responses to wind recorded from the cercal nerves of the cockroach *Periplaneta americana*. I. Directional selectivity of the sensory neurons innervating single columns of filiform hairs. J. comp. Physiol. *133* (1979) 103–110.

13 Dagan, D., and Volman, S., Sensory basis for directional wind detection in first instar cockroaches, *Periplaneta americana*. J. comp. Physiol. *147* (1982) 471–478.

14 Daley, D. L., and Delcomyn, F., Modulation of the excitability of cockroach giant interneurons during walking. I. Stimultaneous excitation and inhibition. J. comp. Physiol. *138* (1980) 231–239.

15 Daley, D. L., Vardi, N., Appignani, B., and Camhi, J. M., Morphology of giant interneurons and cercal nerve projections of the American cockroach. J. comp. Neurol. *196* (1981) 41–52.

16 Delcomyn, F., The locomotion of the cockroach *Periplaneta americana*. J. exp. Biol. *54* (1971) 443–452.

17 Drewes, C. D., Escape reflexes in earthworms and other annelids, in: Neural Mechanisms of Startle Behavior, pp. 43–91. Ed. R. C. Eaton. Plenum, New York 1984.

18 Eaton, R. C., and Hackett, J. T., The role of the Mauthner cell in fast-starts involving escape in teleost fishes, in: Neural Mechanisms of Startle Behavior, pp. 213–266. Ed. R. C. Eaton. Plenum, New York 1984.

19 Glanzman, D. L., and Krasne, F. B., 5,7-Dihydroxytryptamine lesions of crayfish serotonin-containing neurons: Effects on the lateral giant escape reaction. J. Neurosci. *6* (1986) 1560–1569.

20 Jacobs, G. A., and Miller, J. P., Analysis of synaptic integration using the laser photoinactivation technqiue. Experientia *44* (1988) 362–368.

21 Krasne, F. B., and Wine, J. J., The production of crayfish tailflip escape responses, in: Neural Mechanisms of Startle Behavior, pp. 179–211. Ed. R. C. Eaton. Plenum, New York 1984.

22 Moiseff, A., and Konishi, M., Neural and behavioral sensitivity to binaural time differences in the owl. J. Neurosci. *1* (1981) 40–48.

23 Murphey, R. K., The myth of the inflexible invertebrate: Competition and synaptic remodeling in the development of an invertebrate nervous system. J. Neurobiol. *17* (1986) 585–591.

24 Murrain, M., and Ritzmann, R. E., Characterization of proprioceptive inputs to DPG interneurons in the cockroach. Soc. Neurosci. Abstr. *12* (1986) 236.11.

25 Nicklaus, R., Die Erregung einzelner Fadenhaare von *Periplaneta americana* in Abhängigkeit von der Größe und Richtung der Auslenkung. Z. vergl. Physiol. *50* (1965) 331–362.

26 Nolen, T. G., and Hoy, R. R., Initiation of behavior by single neurons: The role of behavioral context. Science *226* (1984) 992–994.

27 Olson, G. C., and Krasne, F. B., The crayfish lateral giants are command neurons for escape behavior. Brain Res. *214* (1981) 89–100.
28 Reichert, H., Control of sequences of movements in crayfish escape behavior. Experientia *44* (1988) 395–401.
29 Ritzmann, R. E., Motor responses to paired stimulation of giant interneurons in the cockroach *Periplaneta americana*. II. The ventral giant interneurons. J. comp. Physiol. *143* (1981) 71–80.
30 Ritzmann, R., The cockroach escape response, in: Neural Mechanisms of Startle Behavior, pp. 93–131. Ed. R. C. Eaton, Plenum Press, New York 1984.
31 Ritzmann, R. E., and Pollack, A. J., Identification of thoracic interneurons that mediate giant interneuron-to-motor pathways in the cockroach. J. comp. Physiol. *159* (1986) 639–654.
32 Spiram M. E., Parnas, I., and Bergmann, F., Histological and electrophysiological studies on the giant axons of the cockroach *Periplaneta americana*. J. exp. Biol. *50* (1969) 629–634.
33 Tobias, M. L., and Ritzmann, R. E., Responses of mesothoracic motor neurons to giant interneuron stimulation in the cockroach. J. comp. Physiol. *154* (1984) 633–640.
34 Vardi, N., and Camhi, J. M., Functional recovery from lesions in the escape system of the cockroach. I. Behavioral recovery. J. comp. Physiol. *146* (1982) 291–298.
35 Vardi, N., and Camhi, J. M., Functional recovery from lesions in the escape system of the cockroach. II. Physiological recovery of the giant interneurons. J. comp. Physiol. *146* (1982) 299–309.
36 Westin, J., Responses to wind recorded from the cercal nerve of the cockroach *Periplaneta americana*. I. Response properties of single sensory neurons. J. comp. Physiol. *133* (1979) 97–102.
37 Westin, J., Langberg, J. J., and Camhi, J. M., Responses of giant interneurons of the cockroach *Periplaneta americana* to wind puffs of different directions and velocities. J. comp. Physiol. *121* (1977) 307–324.
38 Wiersma, C. A. G., Giant nerve fiber system of the crayfish. A contribution to comparative physiology of synapse. J. Neurophysiol. *10* (1947) 23–38.
39 Wine, J. J., and Krasne, F. B., The organization of the escape behavior in the crayfish. J. exp. Biol. *56* (1972) 1–18.
40 Wine, J. J., and Krasne, F. B., The cellular organization of crayfish escape behavior, in: The Biology of Crustacea, vol. 4, pp. 241–292. Eds D. E. Bliss, H. Atwood and D. Sandeman. Academic Press, New York 1982.
41 Yost, W. A., and Nielsen, D. M., Fundamentals of Hearing. Holt, Rinehart and Winston, New York 1977.
42 Zill, S. N., Proprioceptive feedback and the control of cockroach walking, in: Feedback and Motor Control in Invertebrates and Vertebrates, pp. 187–208. Croom Helm, London 1985.

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Behavioral and neuronal mechanisms of cricket phonotaxis

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Summary. The auditory communication of crickets provides a model system for the analysis of the neuronal mechanisms underlying complex behavior. The song of male crickets attracts females. The necessary and sufficient parameter of the song for the female phonotaxis has been determined by a quantified behavioral analysis. Neuronal correlates of this pattern recognition exist in the cricket brain and give rise to a hypothesis on the mechanism of song pattern recognition. Causal relationships between the orientation of a cricket during phonotaxis and the activity of single identified neurons were found by monitoring and deactivating single neurons during behavior. The different roles of various identified neurons for sound localization have been tested by this method. The plasticity of the auditory system at both the behavioral and at the neuronal level has been studied after amputation of one ear, and a mechanism for sound localization with only one ear is proposed.

Key words. Insects; crickets; phonotaxis; auditory neurons; sound localization; song pattern recognition.

Male crickets attract their females by the calling song. If a female is sexually responsive and within the acoustic range she will approach the male. As Johannes Regen[18] showed, the phonotactive behavior is elicited only by sound, and other cues are not necessary. If the female arrives at the singing male, the behavior will continue with antennal contacts, the male courtship song, copulation and male guarding. Up to now only the initial steps of the behavioral sequence, the singing of the male and the phonotactic response of the female, have been studied in detail. The female faces two basic problems in analyzing the communication signal: the recognition of the calling song and the localization of the singing male. Both aspects will be described here from the behavioral and from the neurobiological point of view.

Recognition of the conspecific song

The phonotactic behavior of crickets can be studied during tethered flight[14] or during walking by using a walking compensator[28]. In this situation, the animal walks unrestrained on a sphere and in response the sphere is moved in the opposite direction, so that the animal is maintained at a constant position. As a result the angle and the velocity of walking can be measured for a long time. The walking compensator is placed in an anechoic chamber in which two loudspeakers are placed at different angles. With an attractive auditory stimulus the female walks in the direction of the active loudspeaker, meandering around the midline, and immediately follows each change of the sound direction (fig. 1).

Using this system Thorson et al.[27] tested different sound models for their attractiveness in phonotaxis (fig. 2). A typical cricket calling song consists of a series of chirps that are divided into single sound groups called syllables with a carrier frequency at about 5 kHz. Each syllable is about 18 ms long and is repeated in a chirp 4–5 times with an interval of about 35–40 ms. Changing all parameters systematically Thorson et al.[27] found that in *Gryllus campestris* there is no tracking of a burst (an unmodulated 5 kHz tone). Increasing the number of syllables in a chirp up to a continuous trill does not abolish a phonotractic response, and the length of the syllable and the length of the pause between syllables can be varied over a wide range. The only critical parameter was the syllable repetition interval which was phonotactically effective only between about 25 and 55 ms (fig. 5). From these results they concluded that the necessary and sufficient parameter for eliciting phonotaxis is the syllable repetition interval (SRI). Therefore, the recognition of the conspecific signal can be tested by electrophysiological methods without testing all temporal patterns which are physically possible.