Cricket Auditory Communication

The female's ability to recognize the male's calling song and to seek out the source of the song can be used to study how nervous-system activity underlies animal behavior

by Franz Huber and John Thorson

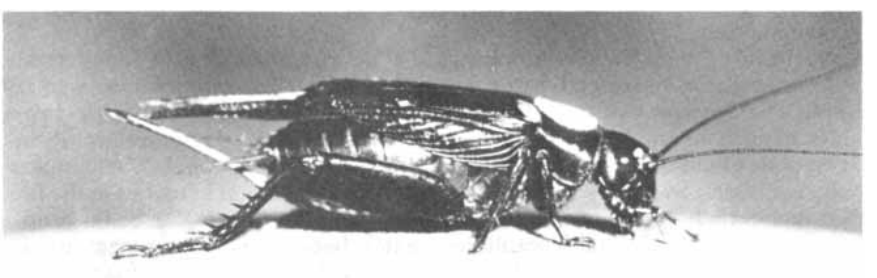
The male cricket sings by scraping his wings, and the female tracks him down. Traces of this interpretation of cricket mating behavior go back to antiquity, but it was not until 1913 that Johann Regan, a high school teacher in Vienna, tested it experimentally. He arranged for a male to sing to a female over the recently developed telephone. The experiment succeeded: when the chirps of the male were broadcast, the female approached the telephone earpiece. Nonauditory stimuli such as chemical signals could therefore be ruled out as cues for her response.

With more modern electronic and physiological methods one's questions can go deeper. What features of the male's song cause the female to seek its source? How do the neurons, or nerve cells, in the female's central nervous system distinguish the song from other songs and sounds? Given the curious arrangement of the cricket's auditory receptors—the cricket's ears are situated below the knees—how does the female determine the direction of the song? More than a dozen laboratories around the world are now attempting to find the answers. Here we shall try to convey the flavor of some of the recent progress.

The answers are well worth the effort. A central aspect of the neurosciences is the attempt to explain the behavior of an animal in terms of the operation and interactions of individual neurons. Often such work is done with invertebrates to take advantage of their stereotyped behavior, the relative paucity of their nerve cells and the fact that many of the largest neurons can now be identified readily in all members of a species, much as a particular tooth is readily identified in person after person. So far the greatest successes have come on the output, or motor, side of neuronal organization. For example, investigators have established that complex bodily movements are orchestrated by particular sets of neurons in leeches, arthropods and mollusks. Neuronal events at high levels on the input, or sensory, side have been more elusive. One such event is a subtle "decision": the neuronal recognition of the cricket calling song and the initiation of the tracking behavior of the cricket in the direction of the source of the song.

It is precisely this "decision" that the work we shall describe here is intended to probe. First we shall summarize the male field cricket's song and what is known about the cricket's auditory organs. Then we shall focus on behavioral and neurophysiological experiments that begin to suggest in detail what happens in the brain of the female when the song is being recognized. Much of the work was done at the Max Planck Institute for Behavioral Physiology in Seewiesen, West Germany. It was done in close collaboration with our colleagues, in particular Theo Weber, Hans-Ulrich Kleindienst, Klaus Schildberger, David W. Wohlers, Dietmar Otto, George Boyan, Eckehart Eibl, Harald Esch and Leslie Williams.

The calling songs we study are those of the chirping crickets, which include European field crickets such as *Gryllus campestris* and *G. bimaculatus*. In males of these species each of the two front wings includes what amount to a file and a scraper, so that when the wings are closed, and hence rub together, the wings are set briefly into oscillation at a frequency of about five kilohertz (5,000 cycles per second). The result is that each time the wings close there is a pulse of almost pure five-kilohertz sound, often called a syllable, lasting for from 15 to 20 milliseconds. Heard close up, it can be painfully loud. The reopening of the wings is silent, but subsequent closings and the syllables generated by each of



SPHERICAL TREADMILL makes it possible for a walking female cricket (*above*) to have a free choice of speed and direction while nonetheless being kept at a fixed distance from loudspeakers emitting various test sounds. The cricket walks on top of a sphere 50 centimeters in diameter mounted in an anechoic chamber (*right*), with a disk of reflective foil stuck to her back. The foil reflects infrared light from an overhead source to photodetectors that sense her position and send corrective signals to motors driving the bearings of the sphere; the motors counterrotate the sphere to keep the cricket near its top. The corrective signals yield continuous records of her speed and intended direction of motion. Loudspeakers broadcast sounds (calling songs of the male cricket or specially altered "songs" synthesized by a computer) from particular directions within the chamber. As she walks, the female cricket expresses her apparent recognition or rejection of the features of such test sounds by tracking or by ignoring the loudspeakers from which the test sounds are emitted. The photographs were made by Theo Weber in the laboratory of one of the authors (Huber) at the Max Planck Institute for Behavioral Physiology in Seewiesen, West Germany.

them follow at intervals of about 35 milliseconds, so that the syllable-production rate is about 30 syllables per second. The commonest kind of chirp emitted by the male cricket is a train of four syllables, which is followed by a brief silence. The chirps are usually repeated at a rate of from two to four chirps per second.

How does the female cricket hear the chirps? In broad outline the auditory apparatus resembles the human arrangement: a sound-transduction system including tympana, or eardrums, excites an array of auditory receptor cells, which in turn excite auditory neurons. In the cricket, however, the ears are below the knee of the foreleg on each side of the body. There a pair of tympana on the surface of each tibia overlie an array of from 55 to 60 auditory receptor cells.

The axons, or nerve fibers, emerging from the cells run up the leg as a bundle, the auditory nerve. Their destination is the prothoracic ganglion, in the central nervous system. Recordings of the electrical activity carried by the nerve (or of the activity of the prothoracic neurons receiving signals from the nerve) establish that the auditory receptor cells respond to airborne sounds ranging from about three kilohertz to what would be, for human hearing, ultrasonic frequencies. Evidently a major population of the receptors responds best at about five kilohertz, the carrier frequency of the male calling song.

Remarkably, the ear on one side of the body is coupled to the ear on the other side by the lower branches of an air-filled tracheal tube that no longer serves only for respiration. Each of the two upper branches ends in a spiracle, a portal to the air surrounding the cricket, on each side of the body. As a result sound pressure reaches each tympanum both directly (at the outside surface of the tympanum) and indirectly (at its inside surface, by way of the air-filled tube). These relations are hard to examine by direct measurement: the small size of the tracheal tube (it ranges from .1 to .3 millimeter in diameter) means one must reason by inference. Still, many studies, in particular the laser-vibrometry measurements made by Axel Michelsen and Ole Naesbye-Larsen at the University of Odense in Denmark, have revealed some of the properties of the arrangement. In such measurements a surface (in this case a tympanum on the foreleg of a cricket) is illuminated by a laser and the velocity of the surface is calculated from the Doppler shift of the frequency of the light that is reflected from the surface.

The results are somewhat surprising. For example, five-kilohertz sound entering, say, the left spiracle proves to be more efficient at deflecting the left tympana (by back pressure from within the tracheal tube) than five-kilohertz sound of the same intensity broadcast just outside the tympana. Apparently the tracheal tube has a resonance near five kilohertz. Of what value is this complex system of tubes? As a female seeks out a singing male, she characteristically follows a zigzag path. It is as if she were obeying a simple rule: turn toward the ear currently receiving the loudest sound.

The problem the cricket faces is that her forelegs, and hence her ears, are only about a centimeter apart, whereas the wavelength of a five-kilohertz tone is about seven centimeters. Under those circumstances the difference in intensity between the sounds arriving from any one source at the outer surface of each ear is at most a few decibels, which is not enough to guide the

female's search for a singing male. The tube system evidently ensures that the sound differences at the two ears are much enhanced by wave phenomena of cancellation and reinforcement due to travel times, resonances and phase shifts in the tube. In sum, it appears most likely that the tube system, with its resonance near the carrier frequency of the male calling song, evolved as an aid to directional hearing.

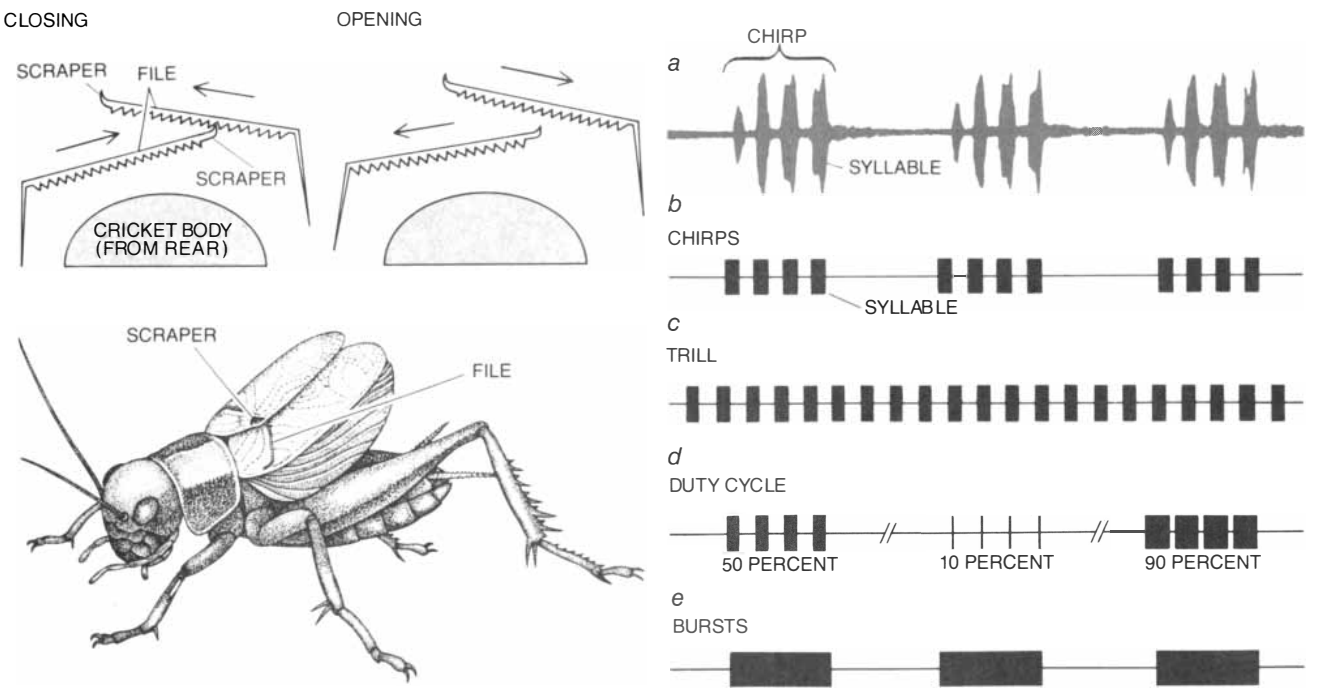
The understanding of the contribution the tracheal tubes make to a cricket's hearing remains incomplete. Until recently, for instance, it was not known which of two distinct phenomena, tympanal deformation or the internal sound pressure in the tracheal tube, actually excites the auditory receptors. (Those quantities can vary grossly from each other in amplitude and phase as the frequency and angle of incidence of the sound change.) The question has now been clarified by Kleindienst and Wohlers at Seewiesen, in collaboration with Naesbye-Larsen at Odense. They separated the two variables by means of sound-cancellation experiments.

A cricket's foreleg is encased in a small, soundproof broadcast chamber called a legphone, so that a sound can be made to impinge exclusively on the tympana of that leg. Within the cricket's body the sound gets pumped through the tracheal tube and thus to the tympana on the opposite leg. Meanwhile sound of adjustable amplitude and phase is broadcast externally to this opposite leg. A laser vibrometer monitors the motion of the posterior tympanum, while a microelectrode monitors the excitation of the auditory receptors by recording the activity of an auditory neuron in the prothoracic ganglion [*see illustration on page 64*].

The idea is to adjust external pulses of five-kilohertz tone so that when matched internal and external pulses are both delivered, the vibrometer detects no tympanal motion. Under those circumstances the findings are unambiguous. When pulses are delivered only internally or only externally, the tympanum moves, the auditory receptors fire volleys of nerve impulses (spikelike electrical signals in the nerve fiber) and the auditory neurons respond by producing several impulses of their own. When, however, the internal and external pulses coincide, so that the tympanum is motionless, the auditory neurons are silent. Yet the internal tracheal sound pressure at such a time can be as great as 80 decibels. Evidently it is tympanal deformation and not local tracheal sound pressure that activates the receptors; direct mechanical effects are presumably implicated in the transduction process.

Behavioral scientists generally study crickets and their auditory abilities by observing what the female does when various sounds are played to her over loudspeakers. In the classical experiment the female is released in a Y-shaped maze or on a flat surface called an arena, and loudspeakers broadcast selected sounds from various directions. One difficulty with such experiments is that the female must be recaptured and repositioned after each walking trial. Moreover, when an animal is to choose between sources of sound, a chance start toward one of the sources makes that source louder simply because it is nearer than it was before the animal moved.

These difficulties are avoided if one arranges to keep the female in place during the tests, on top of a sphere that rotates to compensate for her movements. The cricket can then have a free choice of speed and direction of walking and yet remain more or less stationary with respect to sources of sound. The cricket can be tested continuously, often for hours; extensive sequences of sounds can be presented, including some trials to test the reproducibility of her responses and other

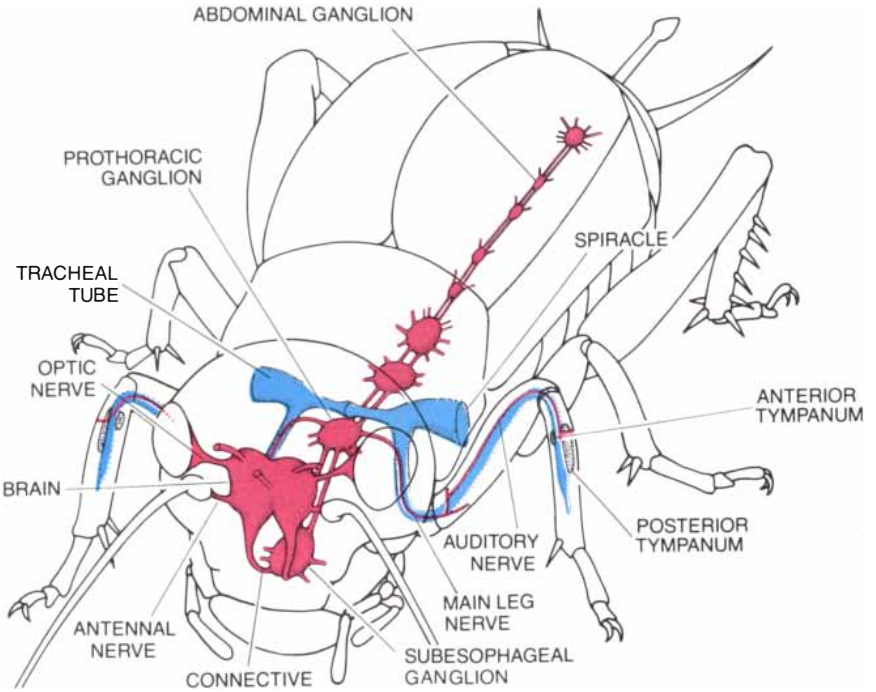


CRICKET SONG is produced by the male when he rubs his wings together. The highly schematic diagrams at the upper left show the sound-making mechanism: each wing incorporates a scraper and a file, so that every time the wings close they are set in brief vibration at a frequency of about five kilohertz (5,000 cycles per second). The diagram at the lower left shows how the wings of the cricket are raised and scraped together when the sound is made. The song (*a*) is therefore made up of "syllables" of five-kilohertz tone. Typically there are four syllables per chirp, and the syllables come at a rate of 30 per second. The temporal patterns of some computer-synthesized songs are schematized below the temporal pattern of the natural song. One synthesized song (*b*) reproduces the principal features of the natural song. Another (*c*) is a "trill": it fails to divide the song into chirps. Others (*d*) preserve the chirps and syllable rate but expand or contract the duration of each syllable, thus varying the duty cycle, or ratio of the sound to the silence within a chirp. Finally, one test pattern (*e*) is made up of "bursts" of five-kilohertz tone of the correct chirp duration but not separated into syllables.

trials to check on whether the order in which sounds are presented is affecting the results. (Methods for studying hearing in tethered flying crickets, developed by Andrew Moiseff, Ronald R. Hoy and Gerald S. Pollack of Cornell University, offer some of these advantages.)

Our device, which is essentially a spherical treadmill, was designed by Ernst Kramer and Peter Heinecke at Seewiesen and is now in use in several laboratories. The cricket walks freely on top of a plastic sphere 50 centimeters in diameter. A small disk of light-reflecting foil is stuck to her back, and infrared light at 963 nanometers, a wavelength invisible to the cricket, arrives from an overhead source. When the cricket moves away from the precise top of the sphere, photodetectors sense her motion by means of the reflected light and motors rotate the sphere so as to compensate for her motion and keep her near the top.

For the cricket, of course, walking on the treadmill is not quite the same as natural walking: the corrective accelerations imparted to the sphere unavoidably alter the inertial forces the cricket may detect by way of sensory receptors within her legs. Still, we can adjust the responses of the motors to the commands they receive in such a way that the cricket gets no farther than about half of her body length from the very top of the sphere, and yet her motions do not look awkward. By keeping track of the position and velocity signals sent from the photodetectors to the motors we gain a continuous record of the direction in which the cricket is trying to walk and also of her walking speed.



TRACHEAL-TUBE ARRANGEMENT (*blue*) dominates the cricket's peripheral auditory system. It connects the two "ears," which are curious structures below the knee of each foreleg. On each side of the body a large, funnel-shaped upper branch of the roughly H-shaped tube leads to an opening called a spiracle at the body surface; the tube's lower branch descends through the foreleg to a position between the ear's two tympana, which are auditory membranes overlying an array of receptor cells. Hence sound reaches each ear not only externally, from the enviroment, but also internally, by way of sound pressure within the tracheal tube. The cricket's central nervous system (*red*) consists of a sequence of ganglia (aggregates of neurons), which are linked by pairs of connectives, or bundles of the fibers sent out by the neurons. The frontmost ganglion is the brain, with its optic and antennal nerves. Next comes the subesophageal ganglion, followed by three thoracic ganglia and several abdominal ones. Sensory signals from the array of receptor cells under the auditory tympana enter the prothoracic ganglion, which is the frontmost thoracic ganglion.

The behavior of female crickets on the spherical treadmill is often quite unambiguous: it routinely gives us yes or no answers to questions about her proclivities. For example, when computer-simulated chirps are played from loudspeakers at various positions around the sphere, the female tends to respond in a characteristic way. In a series of short episodes of walking she tracks the loudspeaker emitting the sound. Her accuracy increases as the intensity of the sound is raised from 50 to 70 decibels. When we switch speakers, she switches direction appropriately. (The experiment is conducted in an anechoic chamber so that the only effective sounds reaching the cricket are the ones coming directly from the speakers.) On the other hand, most females ignore bursts of five-kilohertz tone that last for as long as a chirp would last but are not divided into the sequence of syllables that constitute a natural chirp.

Given this powerful means of assaying the female cricket's responses to sounds, we have asked in detail what features of the temporal pattern of the male calling song appear to be critical for initiating the female's tracking of the song. Candidate features include the chirp rate, the syllable rate and the number of syllables per chirp. Earlier studies had already suggested that the syllable rate is important. Guided in part by those studies, we began with the working hypothesis that the natural syllable rate—approximately 30 per second—is the only feature the female needs in order to recognize the song and begin to seek its source.

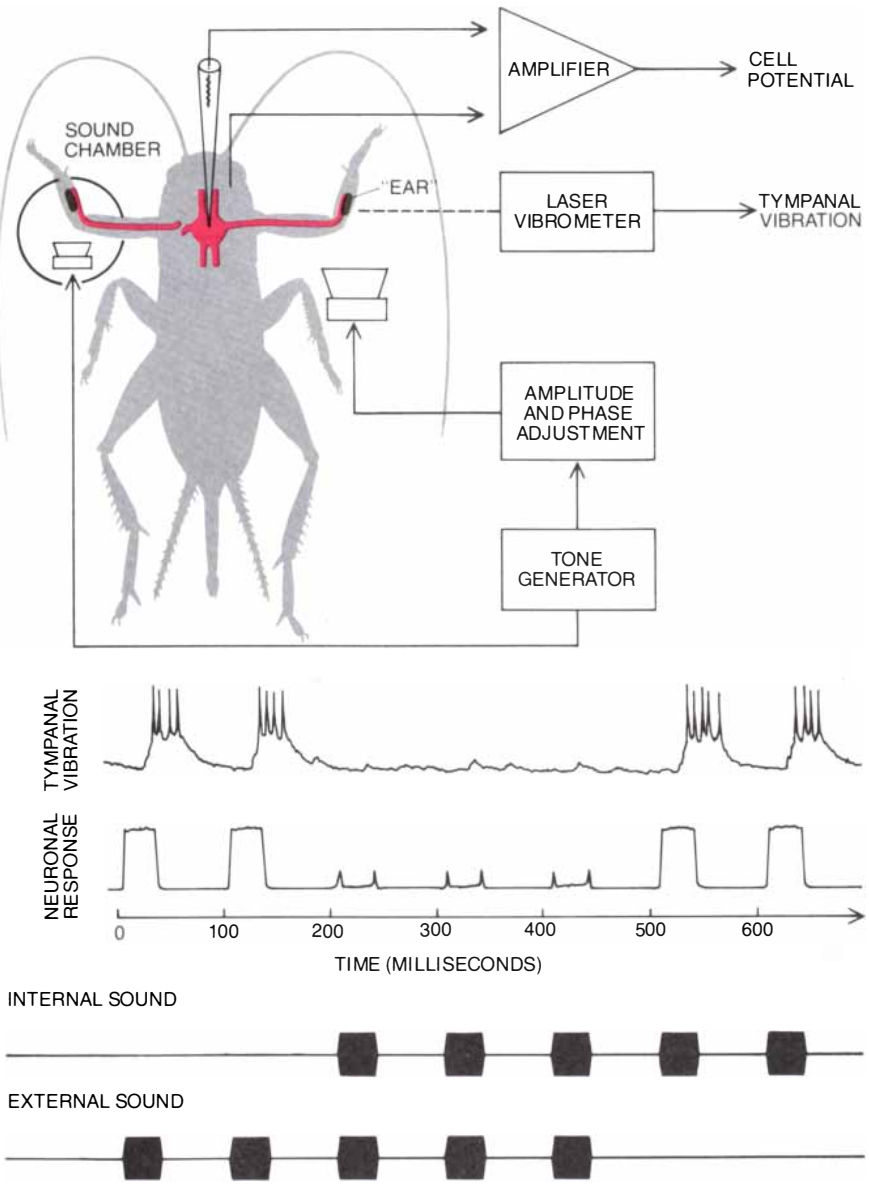
In the case of the European field cricket *Gryllus campestris,* the working hypothesis survives a surprising number of tests. For example, the females ignored single-syllable chirps but tracked chirps of three or more syllables when the syllables were presented at the 30-per-second rate. In other words, the syllable rate is crucial; the number of syllables is not.

In a further set of experiments we varied the ratio of tone to silence in each chirp. In a natural chirp the syllables take up about half the time of the chirp, for a "duty cycle" of 50 percent. By synthesizing chirps consisting of four brief pulses of five-kilohertz tone at a 30-per-second rate, we reduced the duty cycle to 10 percent; by synthesizing chirps consisting of four long pulses of tone at a 30-per-second rate, we increased the duty cycle to 90 percent. The female tracked both kinds of synthesized songs. Again, the syllable rate is evidently crucial; the duration of each syllable is not. Test songs with such departures from the natural duty cycle tended, however, to require presentation at greater volume than natural songs require, as expected from the reduction in 30-hertz power that accompanies unnatural duty cycles. Finally, we synthesized continuous "trills" of five-kilohertz syllables at the 30-per-second rate, with no subdivision into chirps. Although earlier reports had suggested that trills are not attractive to female crickets unless the crickets have first been primed by hearing normal chirps, we found that a majority of the females tracked a trill even when it was the first song of the day. The 30-per-second syllable

rate appears to be the principal cue.

Our pursuit of the 30-hertz recognition hypothesis has been in the spirit of Alfred North Whitehead's celebrated advice, "Seek simplicity; and distrust it." And indeed there are interesting complications. A minority of the females we tested would not track trills at all but began to track immediately if the trill was interrupted periodically, giving rise to chirps. Moreover, John Doherty, working with our treadmill at Seewiesen, has examined the behavior of female crickets of the species *G. bimaculatus,* which is closely related to *G. campestris.* Although some of the females track trills, a minority will track asyllabic bursts of five-kilohertz sound—a clear refutation of our working hypothesis that the syllable rate of 30 per second is the sole crucial feature of the male calling song.

It is not yet clear whether such findings are occasional glimpses of a complex recognition process or simply reflect an abnormal lack of sensory selectivity within the central nervous system of certain individual crickets. Such differences do, however, highlight an important procedural point: When one "gets to know" individual females during long runs on the treadmill in many experimental conditions, consistent differences among individuals—even in qualitative ability—are found. These are not always discerned in the usual statistical summaries of such experiments.

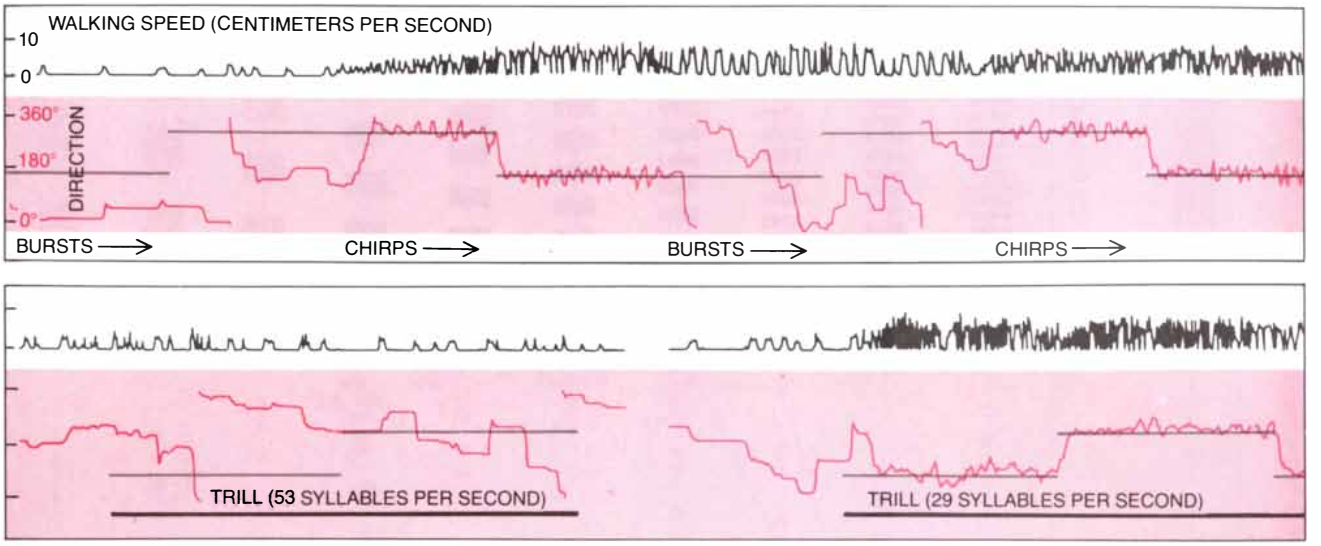


SOUND-CANCELLATION EXPERIMENT developed by Hans-Ulrich Kleindienst at Seewiesen clarified the role of the tympana in sound transduction. One of the cricket's forelegs is enclosed in the small chamber shown at the left in the diagram. Brief five-kilohertz tones are delivered within the chamber; the sound propagates through the tracheal tube and excites receptors on the opposite leg by exerting internal pressure on the tympana. External sound is delivered simultaneously to the leg at the right in the diagram. The motion of the posterior tympanum on the latter leg is monitored by a laser vibrometer. The phase and amplitude of the external sound can be adjusted in such a way that it cancels the effect of the internal sound, whereupon the tympanal motion ceases. Auditory signals from the ear on the leg in the chamber are eliminated by cutting the auditory nerve. An intracellular microelectrode measures the response of an auditory interneuron in the prothoracic ganglion. The results of one experiment are shown. When either internal or external sound is delivered to the ear on the right, the posterior tympanum moves and the neuron is excited. When tympanal motion is canceled by presenting the two sounds together, the neuron is not excited, even though the internal tracheal sound pressure can be substantial. Thus the experiment shows that tympanal deformation is critical for the transduction of sound; the sound pressure inside the trachea does not suffice to activate the receptor cells in the ear.

It is clear, in any event, that the modulation of five-kilohertz sound at the characteristic natural syllable rate is the most reliable way to call a female cricket. In the next stage of our research we undertook, again in collaboration with Weber, to capitalize on this finding by designing a stimulus program for a search for song-recognizer neurons in the central nervous system of the female. The fundamental problem in such a search is that most of the auditory neurons in the central nervous system of the female cricket respond not only to the male calling song but also to sounds we know the female does not track.

One must therefore test each candidate neuron (during the period, sometimes frustratingly brief, when a microelectrode is in place and is recording the activity of the neuron) with a range of songs including some that elicit tracking and others that do not. To this end we employ a sequence of computer-synthesized songs that systematically varies the syllable rate while keeping the duration, energy and repetition rate of the chirps nearly constant. The female's behavior when she is stimulated with this sequence amounts to a band-pass response: for syllable rates near 30 per second she tracks almost flawlessly, whereas for rates of less than 20 per second or more than 40 per second her performance worsens dramatically.

The next question is how the central auditory neurons respond to such sequences of correct and incorrect songs. Here a description of some of the neuroanatomy of the cricket is essential. The auditory nerve runs through the knee joint of the foreleg from the tibia into the femur. There it joins the main leg nerve. Nevertheless, its constituent axons continue to form a distinct, com-



TRACKING OF SYNTHESIZED SONG by a female cricket on the treadmill is demonstrated in typical recordings of speed and direction. For each of two experiments the upper trace (*black*) gives the female's walking speed. When she tracks, she usually follows a zigzag path, sometimes pausing and sometimes walking as fast as six centimeters per second. There are two sets of lower traces (*in colored bands*): horizontal line segments (*gray*) show the direction of the sound source, which is changed by switching from one loudspeaker to another; wiggly curves (*dark color*) show the direction in which the female is walking. In one experiment (*top*) trains of bursts of five-kilohertz tone were alternated at about two-minute intervals with trains of four-syllable chirps simulating natural song. The female ignored the bursts but tracked the source of the chirps avidly, changing direction appropriately when the sound direction changed. In another experiment (*bottom*) two trills were presented, one at a syllable rate of 53 per second and the other at a rate of 29 per second that is found in nature. The female ignored the "wrong," 53-per-second trill but tracked the source of the 29-per-second trill.

pact bundle, distinguishable from the rest of the nerve, until they enter the prothoracic ganglion, a neuronal complex that is (among other things) the first central processing station for auditory input.

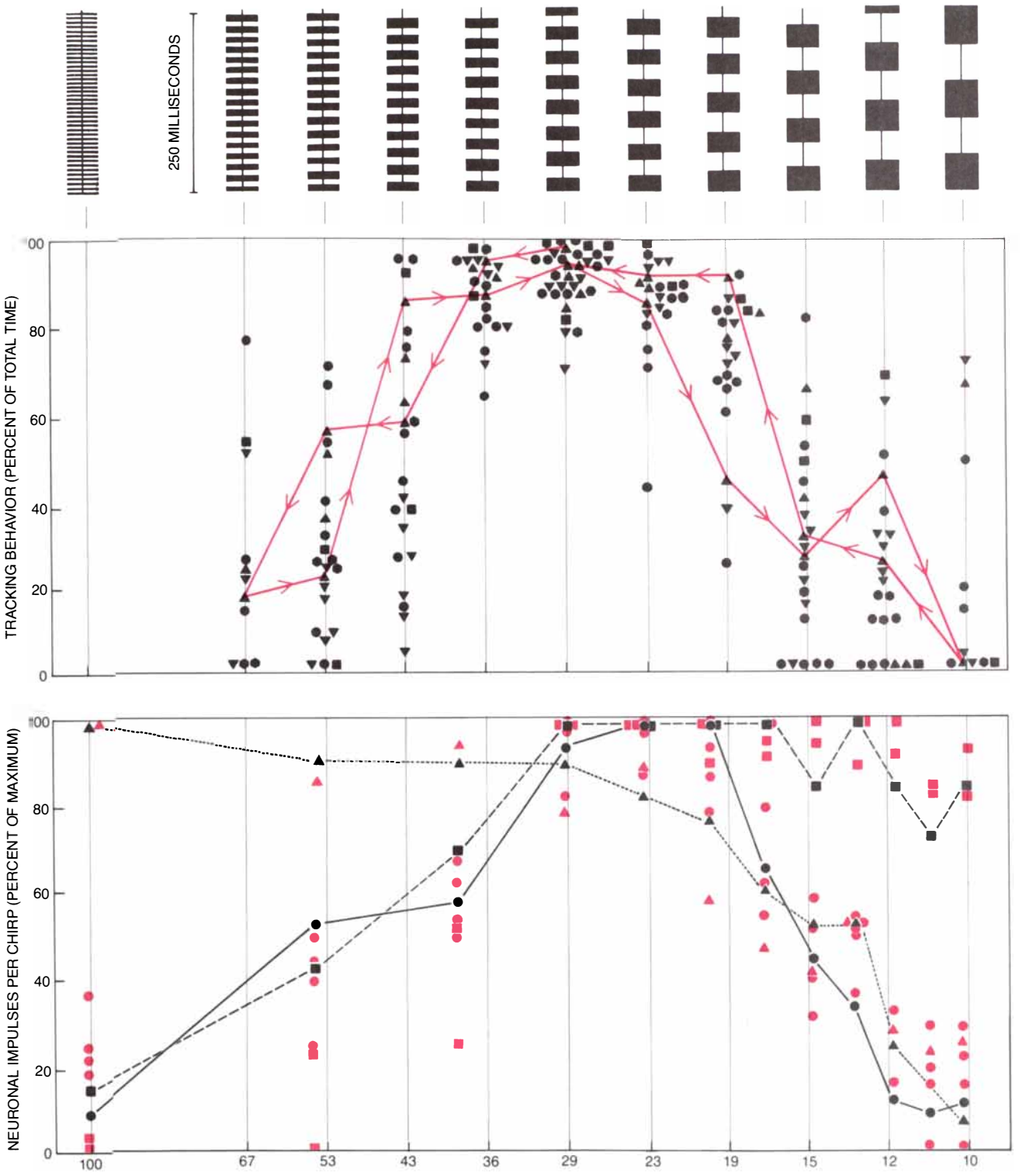
To determine the precise field of distribution of the auditory fibers one cuts the auditory nerve and exposes the cut to a cobalt salt, which travels up the fibers. The precipitation of the salt then reveals that the fibers branch and terminate inside the ganglion on the same side as the leg from which they come, without crossing the midline. The restricted region of the ganglion in which they terminate is known as the auditory neuropil. There the terminal branches of the fibers make synapses with interneurons: nerve cells that process and relay information within the central nervous system. In recent years a number of such cells have been identified. "Identified" is in fact a technical term with a twofold meaning. First, the cells have been shown to be characterized by a particular pattern of electrical activity and a particular anatomical structure. Second, the cells have been shown to be present consistently in many individuals of a species.

Two of the most prominent identified auditory neurons in the prothoracic ganglion, studied by several investigators, are the omega-1 neurons, or ON-1 neurons, named for their resemblance in shape to the Greek letter omega (Ω). They are present as a bilateral pair, each the mirror image of the other. Each ON-1 cell confines its arborizations (the bushlike branchings of the protrusions over which a neuron dispatches or gathers signals) to the two neuropil regions of the prothoracic ganglion. Each ON-1 cell receives excitatory input only from the ear ipsilateral to (on the same side as) its cell body. That is, the ON-1 cell whose cell body occupies the right half of the prothoracic ganglion receives excitatory input only from the ear on the right foreleg. Although it responds over a broad range of frequencies, the ON-1 cell "copies" the male calling song briskly. That is, it generates a train of impulses closely mimicking the temporal pattern of the song. In less than a millisecond such trains are conducted to the other side of the ganglion along the omega-shaped trajectory of the axon of the ON-1 cell.

Curiously, stimulation of the ear contralateral to the cell body of each ON-1 cell inhibits the cell, and the inhibition of each ON-1 turns out to be exerted by its mirror-image partner—as suggested by Wohlers' work and demonstrated recently by Allen I. Selverston of the University of California at San Diego in collaboration with Kleindienst in Seewiesen. Hence the inhibition is reciprocal. In principle, therefore, the inhibition could serve to sharpen differences between auditory signals from the two ears, enhancing the sensitivity to the direction of sounds above and beyond the enhancement the tracheal tube provides. Other neuronal interactions in the prothoracic ganglion are less easy to analyze. For one thing, a second pair of omega neurons, called ON-2 cells, are closely apposed to the ON-1 cells but have a different pattern of sensory activation. Moreover, numbers of smaller neurons remain unstudied.

The output lines emerging from the prothoracic ganglion seem to have a coherent pattern—perhaps deceptively so. In particular several large, identified prothoracic neurons have axons that travel upward to the brain. Among these "ascending neurons" two prominent types, the AN-1 and AN-2 cells, occur as mirror-image pairs. The AN-1 cells are highly sensitive to the five-kilohertz calling-song carrier frequency, whereas the AN-2 cells are sensitive predominantly at higher frequencies. Unlike the omega neurons, the AN-1 cells receive input from the contralateral ears; they show no sign of receiving input from the ipsilateral ones. The dendritic (input-gathering) arborizations of each AN-1 cell overlap with the axonal (output-transmitting) arborizations of an ON-1 cell.

It is interesting that among all these identified prothoracic cells (the omega neurons and the ascending neurons) we find no candidates for neurons that recognize the male calling song. We find only neurons that copy chirps—and other sounds—and convey their temporal pattern to the brain (or, in



BEHAVIOR AND BRAIN-CELL ACTIVITY on the part of female crickets show closely related responses to synthesized songs that have varied syllable rates. Females on the treadmill heard a series of chirps (*top*) that varied the syllable rate but minimized the variation of certain other features of the song. The preference of females for syllable rates near 30 per second emerged from their tracking behavior (*middle*), which showed a band-pass pattern: a sensitivity to a particular range of syllable rates. Several female crickets (*geometric symbols*) were tested in a number of experiments; the data from one of the experiments are connected by colored arrows to show the back-and-forth sequence of the tests. In the brain of the cricket specific neurons (*bottom*) prove to respond to songs (in terms of the number of nerve impulses that are elicited by each chirp) in ways that closely parallel the female's behavioral response. Some cells have a band-pass response (*circles*), that is, they respond best at syllable rates near 30 per second. Other cells have a low-pass response (*squares*), that is, they respond best at or below 30 syllables per second. Still others have a high-pass response (*triangles*). Line segments connect the data for one of the neurons of each type. The behavioral data are from *Gryllus campestris;* the neurons were studied by Klaus Schildberger of Seewiesen in the closely related species *G. bimaculatus,* which shows behavior similar to *G. campestris.*

some cases, in the opposite direction, to lower thoracic ganglia). For these cells the presentation of a range of computer-synthesized songs that systematically varies the syllable rate elicits no preference for the rates near 30 syllables per second: the rates that lead the female to track the source of the male's song.

The search for the song-recognizing neurons moves on, therefore, to the brain. Here the end branches of the axon sent out by each of the AN-1 cells produce dense terminal arborizations (first demonstrated by Boyan and Williams), which overlap the arborizations of a population of brain interneurons (found on each side of the brain) identified by Schildberger. The interneurons are known as BNC-1 (brain neuron, class 1) cells. In turn the arborizations of the BNC-1 cells overlap the arborizations of another bilateral population of brain interneurons, also identified by Schildberger, called BNC-2 cells.

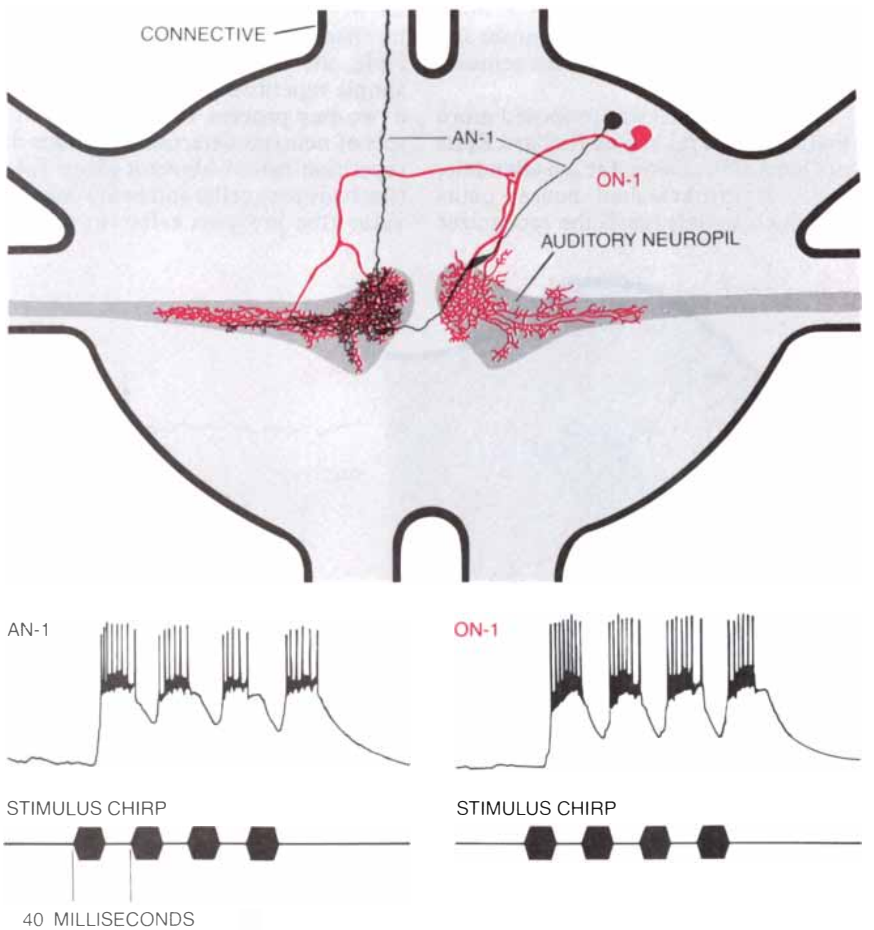
The overlaps suggest that auditory signals ascending to the brain by way of the axon of an AN-1 cell first reach the BNC-1 cells, from which they are relayed to the BNC-2 cells. In this regard it is notable that when the male calling song is presented to the female while the electrical activity of BNC-1 and BNC-2 cells is being monitored, the activity generated by the BNC-1 cells proves to copy the temporal pattern of the chirp less accurately than the neurons of the prothoracic ganglion do. The copying done by the BNC-2 cells is even less accurate: the impulses generated by them are seldom detectably synchronized with the syllables of the chirp.

The BNC cells are small, so that extended recordings of their electrical activity are hard to make. Moreover, the recordings must be followed by the injection of a dye so that the cell can be identified anatomically. Nevertheless, a picture is emerging from Schildberger's work. There is a subpopulation of BNC-2 cells in which each neuron responds (in terms of the number of impulses it generates per chirp as the syllable rate is varied) in a band-pass manner closely reminiscent of the band-pass behavior of the female. That is, the neuron responds preferentially to songs with syllable rates near 30 per second—the rates that most reliably activate the female's tracking. To our knowledge, Schildberger's finding is the first discovery of an unambiguous central neuronal correlate of a temporal pattern-recognition process in an insect.

The BNC-2 population also includes neurons that respond only to signals that have syllable rates in or above the recognition band. In brief, they are high-pass cells. Moreover, the BNC-1 population includes neurons that respond only at syllable rates in or below the recognition band. In brief, they are low-pass cells. The discoveries are a striking parallel to the band-pass, high-pass and low-pass neurons found recently among the auditory neurons in the brain of the frog by Gary Rose and Robert R. Capranica of Cornell.

What the band-pass cells among the BNC-2 population in the brain of the female cricket do when they have recognized the male calling song is still not known. The close relations between their particular sensitivities and the band of syllable rates that elicit tracking behavior encourage the hypothesis that the BNC-2 cells activate rather directly the central mechanisms responsible for tracking. Perhaps the activity of the BNC-2 cells leads in some way to release of a neuropeptide (a short amino acid chain), which serves as a chemical messenger activating the tracking behavior. Or perhaps the BNC-2 cells act by means of descending neurons, which Schildberger has also identified. In any case, Schildberger's discoveries stimulate speculation about the details of the recognition process itself.

How might a neuronal recognizer of simple temporal patterns work? Three quite different ideas have been proposed. One of them emerges from suggestions made over the past two decades by a number of investigators. They include Masakazu Konishi of the California Institute of Technology, who studied bird song; Richard D. Alexander of the University of Michigan and Hoy and his colleagues at



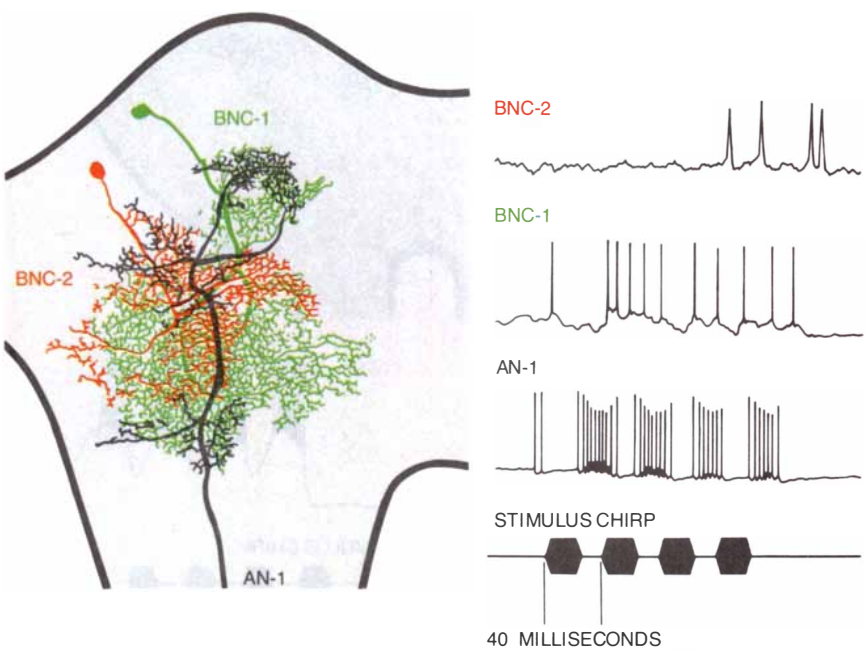
PROTHORACIC GANGLION includes auditory neurons that constitute the first central processing station for signals arriving from receptors in the cricket ear. Fibers of the auditory nerve (*gray*) distribute their signals in a region of the ganglion called the auditory neuropil. A nerve cell called the omega neuron, or ON-1 cell (*color*), picks up the signals. Its omega-shaped axon, or nerve fiber, crosses to the auditory neuropil on the opposite side of the ganglion. There an ascending neuron, or AN-1 cell (*black*), dispatches its axon upward toward the brain. Recordings of the electrical activity of the two kinds of cell (*bottom*) demonstrate that both the ON-1 cell and the AN-1 cell copy the temporal pattern of the calling song of the male cricket. Mirror-image ON-1 and AN-1 cells (not shown) have similar structures that emanate from cell bodies on the left side of the ganglion. Cells were stained by injecting the dye Lucifer Yellow through the intracellular recording electrode.

Cornell, who studied cricket song, and H. Carl Gerhardt, Jr., and Doherty of the University of Missouri, who studied frog calls.

In essence the idea is that the female has a built-in pattern generator that produces a template to be compared with the patterns of sensory signals arriving in the central nervous system. In the case of the cricket the idea is particularly compelling. Insects are known to have neuronal "pattern generators" for rhythmic behaviors such as walking, flying and singing. To be sure, the female cricket does not sing. Nevertheless, she shares with the male the relevant neuronal and motor apparatus; sometimes when she becomes aggressive, she moves her wings in the same way the male does when he sings. On the other hand, it is unclear how a template could be compared with an arriving male song, given the latter's arbitrary arrival time with respect to template timing. Apparently one must postulate a triggering mechanism for template generation. The idea remains speculative.

The second idea was proposed more than two decades ago by Richard Reiss of General Precision, Inc., in Glendale, Calif. It invokes dual neural paths by which signals reach the recognizer mechanism. Suppose one path delays signals more than the other path, by a predetermined amount of time. Suppose further that the recognizer requires the temporal coincidence of signals from both paths. The recognizer will then respond only to certain temporal patterns, namely the ones in which the delay matches a periodicity in the pattern. Here too the idea remains speculative. One problem is that in its strict form the recognizer accepts syllable rates that are multiples of the rate it is designed to recognize. Such pseudorecognitions are apparent neither in our behavioral data nor in Schildberger's recordings of cricket auditory neurons.

The third idea depends on the recent discoveries, in both the cricket and the frog, of band-pass neurons in close association with high-pass and low-pass neurons. Perhaps, as Schildberger has pointed out, these cells are trying to tell us something about the recognition mechanism. Perhaps, as a general principle, the nervous system recognizes simple repetitive patterns of sounds in a two-step process. In the first step two sets of neurons determine whether the repetition rate is above a given value (the high-pass cells) and below another value (the low-pass cells). In the second step a set of band-pass, or recognizer, cells become active only if both the low- and the high-pass cells are active. In mathematical logic or computer circuitry the sequence corresponds to the operation called logical AND. The anatomical data are not inconsistent with this idea. The low-pass BNC-1 cells appear to deliver signals to the band-pass BNC-2 cells. Often, moreover, the BNC-1 cells respond to sound stimuli before the BNC-2 cells respond. It would be interesting to know whether comparable relations obtain in the brain of the frog.

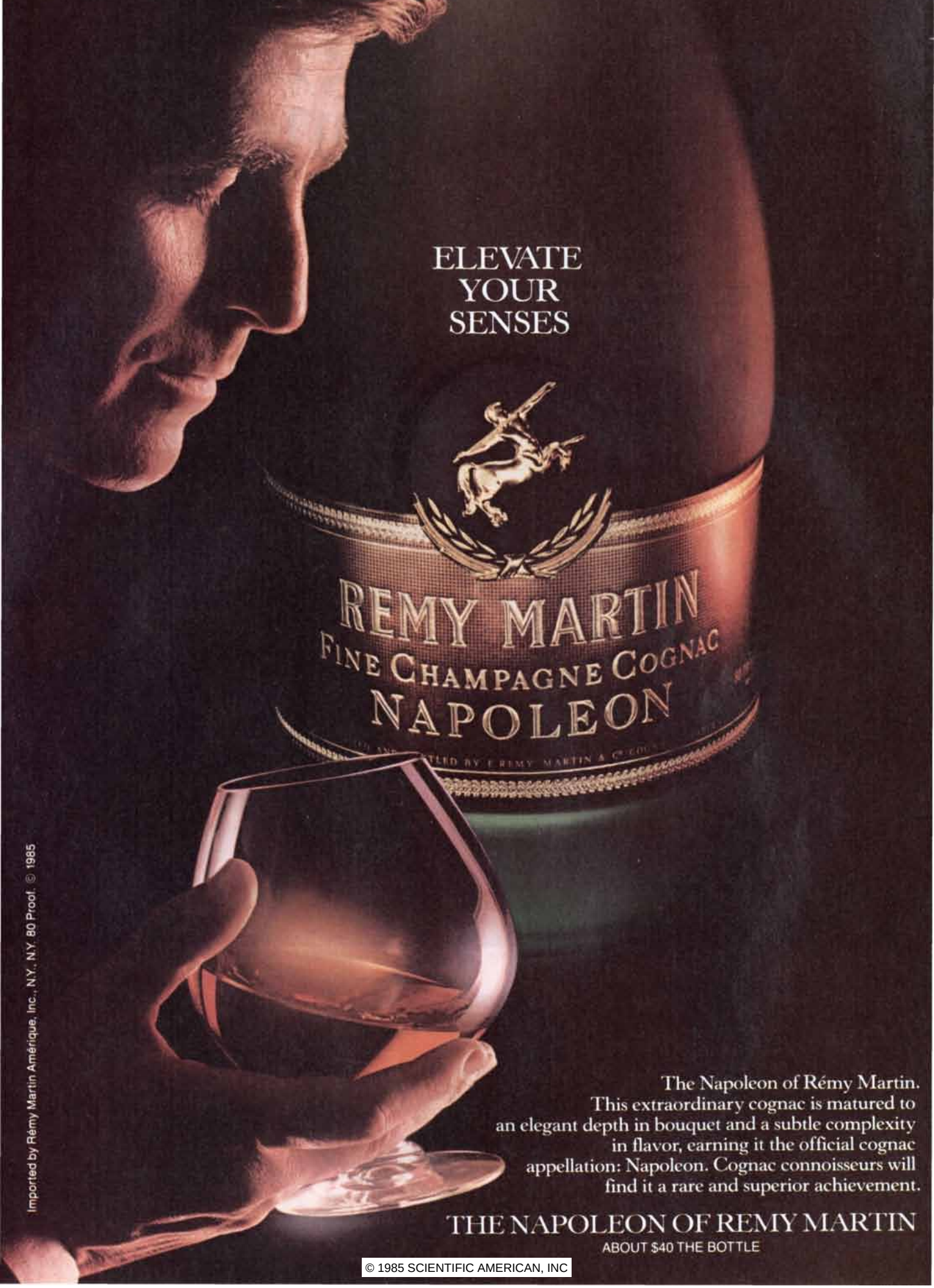


BRAIN of the cricket includes neurons that appear to participate in recognizing (and not simply in copying) the temporal pattern of the male calling song. Here the left side of the brain and two of the neurons within it are drawn as they would be seen from above the head of the cricket. The axon sent out by the AN-1 cell in the prothoracic ganglion (*black*) arrives from below. Its most forward synaptic terminals overlap the forward branchings of a population of neurons designated BNC-1, one of which is shown (*green*). In turn, branchings of the BNC-1 cells overlap those of another neuron type, designated BNC-2 (*red*). Recordings of the electrical activity of the neurons (*right*) show that they do not simply copy the temporal pattern of the male calling song. Instead some BNC-1 cells make low-pass responses to the range of synthesized songs (*see illustration on page 66*); some BNC-2 neurons make band-pass responses and some make high-pass responses. The findings suggest that the neurons take part in recognizing the male calling song and that they activate tracking.

A further step in the quest from the cricket's behavior to the neuronal machinery underlying it would be to determine how the interactions among neurons can produce high- and low-pass responses to sensory signals. Here we face an embarrassment of riches: the known interactions among neurons in fact explain too much. To put it another way, the basic neuronal properties of excitation and inhibition readily yield a wide range of bases for elaborate computations. For example, the well-known phenomenon of temporal summation, in which the rapid arrival of signals excites a neuron whereas slower arrivals do nothing, provides a high-pass filter. Let us say only that the details of the interactions among identified neurons in the brain of the cricket are now being evaluated in light of the computational possibilities. We all know how difficult it is to understand undocumented software written by someone else.

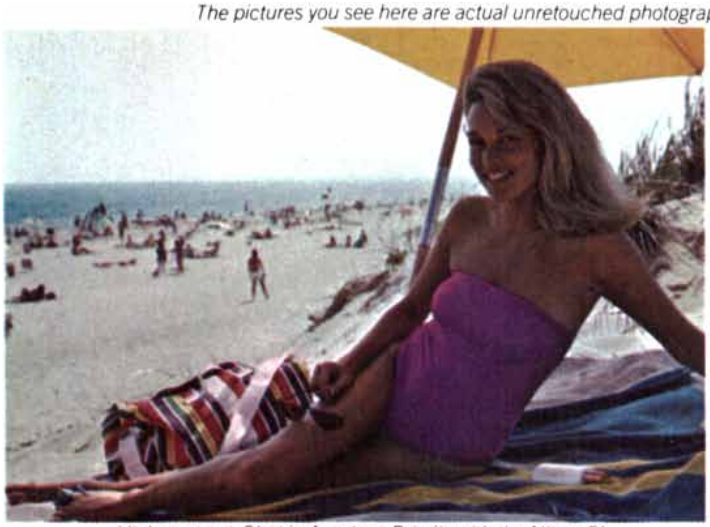
In the meantime studies of cricket behavior on the spherical treadmill continue to produce surprises. For example, Weber and we have now found that if calling songs are synthesized at unnatural carrier frequencies, the female is fooled into tracking an illusory male at an angle to that of the actual source of sound. Moreover, it has emerged that females maturing with only a single ear because of faulty development can often track sound quite accurately. Such findings are fundamentally affecting our ideas about directional hearing in crickets.

Two centuries ago the German artist August Johann Roesel von Rosenhof became so fascinated with insect behavior that he turned from painting human portraits to painting and studying insects. He offered a vivid account of cricket behavior: the male's "lust keeps him singing with scarcely a pause, until finally he gets his wish; if a female is nearby, she goes after the song." The female's performance continues today to offer special challenges to students of acoustics, behavior and neurophysiology.



Presenting a camera with the human eye than See.

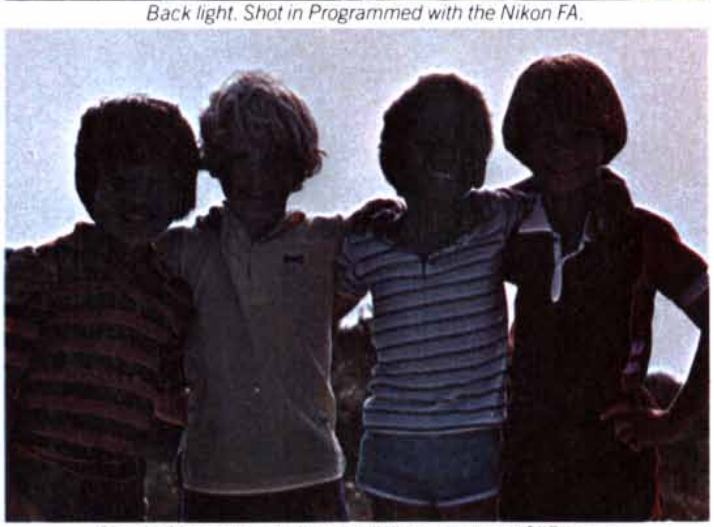
The pictures you see here are actual unretouched photographs, shot simultaneously without any exposure compensation.



High contrast. Shot in Aperture-Priority with the Nikon FA.

Back light. Shot in Programmed with the Nikon FA.

Shot in Aperture-Priority with a leading multi-mode SLR camera.



Shot in Programmed with a leading programmed SLR camera.

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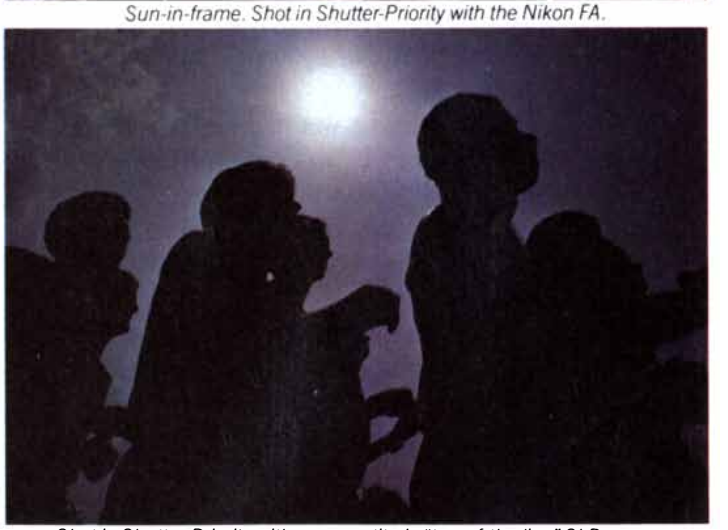
that has more in common with other cameras.

Available light. Shot in Programmed with the Nikon FA.

Sun-in-frame. Shot in Shutter-Priority with the Nikon FA.

Shot in Programmed with the biggest selling SLR camera.



Shot in Shutter-Priority with a competitor's "top-of-the-line" SLR camera.

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