Learning the Language of Insects— and How to Talk Back
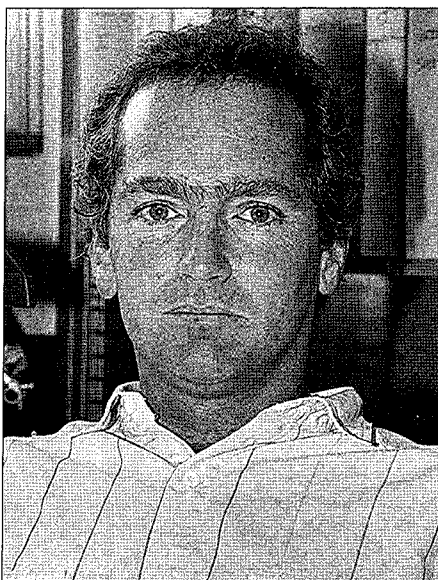
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I HAVE BEEN LUCKY over my career thus far to have been involved in research on insect pheromones, which in many ways epitomize the complexity and power of insect communication, and, for entomologists, present much promise as a means of manipulating insect behavior. However, in successfully doing our jobs as researchers, we must not only learn the language of insects, but we also should pay attention to communication between insects and ourselves, and ultimately to communication among fellow researchers and society.

I favor the definition of communication outlined by E. O. Wilson (1974), who wrote, "communication occurs when the action of or cue given by one organism is perceived by and thus alters the probability of behavior in another organism in a fashion adaptive to either one or both of the participants." Communication has sometimes been defined more narrowly, in terms of the intention of the sender—i.e., whether or not the signal that is sent was meant to benefit the sender. Apart from it being impossible to prove experimentally the teleological assumption that we can actually know the goal of the sender, in this definition only intraspecific information flow is considered to be communication. An emission from one individual, intercepted by third parties, for example, from another species nearby, and causing a behavioral response in the eavesdroppers would not be considered communication because the emission was not "meant" to be received by that third party.

I do not believe this is a particularly helpful way to view communication, because it precludes the possibility that humans can communicate with insects and vice versa. Clearly, we *do* communicate with insects, and they *do* respond so reliably to us. With Wilson's framework, insects' emissions do alter entomologists' probabilities of behavior, as do ours theirs. This is one of the things that makes entomology such an exciting discipline, and such a promising area for insect behavior research to have a positive effect on society.

I was fortunate to have begun my research career working with Wendell

Thomas C. Baker

Roelofs and Ring Cardé. Whenever a pheromone research project stalled out or reached an apparent impasse for one reason or another because the insects were not responding to our test pheromone blends, Wendell and Ring would insist upon going back through all the data with the idea that the insects were telling us something important, only we were too stupid to find the right way to listen! The lesson learned, once we got around the impasse and identified the pheromone, was that learning the language of insects requires that we do listen carefully, then, in our own halting way, persist in trying to talk back.

When communication occurs, there is information flow between sender and receiver, through a communication channel in the environment, as depicted by Shannon & Weaver (1949). Apart from the meaning, or semantic value of the information, the amount of information that reaches the receiver after the signal travels through the channel depends, in a statistical sense only, on the reduction in an observer's (receiver's) uncertainty about the occurrence of a signal, given a finite set of possible signals. The channel itself can be flooded with various amounts of noise (Fig. 1), that may influence the remaining uncertainty and

hence reduce the amount of received information. Also, even without noise the channel can, through its quirky characteristics, alter the emitted transmission and impose upon it a selective attenuation, such that by the time it reaches the receiver it has been distorted. Despite these problems, and without teleologically trying to infer the "message" in the signal, it is possible to factor out the key components—i.e., the essence—of the emission by carefully analyzing the behavior of the sender, the structure of the emission, and the behavior of the receiver. After all, many parasitoids have learned over evolutionary time to do this with many of their insect hosts. So have predators using communication signals aggressively, such as bolas spiders and fireflies that attract and kill prey by signaling in the pheromonal or light-flash "languages" of their prey. Many phytophagous insects as well have been selected to locate plant parts, or whole plants, by using a narrow range of possible emissions that indicate that a favorable host is present. Understanding the minimal set of cues that influences behavior was the essence of the ethological school of behavior studies, as exemplified by Niko Tinbergen's work on baby herring gulls' responses to the red spot on their mothers' beaks or his work on digger wasps' homing abilities using landmarks. Information flows to us from our insect subjects. Our job is to learn what it consists of.

Communication in the three major modalities—light, sound (pressure disturbances), and chemicals—has many common characteristics. There is a main carrier frequency, which is the dominant wavelength in light, the main tone in a sound emission, and the blend of chemicals in a semiochemicals emission (Fig. 2 A–C). In addition, research in all modalities has shown that it is important that the emission at a particular carrier frequency be amplitude-modulated, which means that its intensity be varied considerably for it to evoke a response in the receivers (Fig. 2 D–F). In communication using light emissions, this entails flashing or varying the intensity in some form in space and time (Fig. 2E). In sound

212

communication, amplitude modulation involves "chirping" or "trilling" with long or short periods of silence, rather than emitting a continuous tone (Fig. 2D). In chemical communication, amplitude modulation usually is provided by the turbulent shearing of the emission as it leaves the source to create filaments of odor similar to what we can visualize within smoke plumes (Fig. 2F). However, some rhythmic pulsing of chemical emissions can be imparted by the emitter, such as arctiid or lymantriid moths emitting pheromone, and these can, in some cases, stand out against the turbulence-induced modulation for a half a meter or so downwind (Conner et al. 1980). Such pulsing thus far has been found to have no extra signal value and also does not increase the response of males compared to a continuously emitted stream of pheromone.

No signal from insects has yet been found that is frequency modulated and has communication value. Frequency modulated (FM) signals would involve changing color, sweeping through a series of tones, or changing one's chemical blend. However, bats hunting for insect prey are FM emitters that with each ultrasonic chirp sweep downward from high to low tones and from the particular narrow range of tones of the reflected signal, gather information about the size and wing-beat frequency of their prey. These bats *also* modulate the amplitude of their cries by sending discrete chirps with a silent period that aids in receiving echoes, but there are species that emit AM (amplitude modulated) cries only, with no frequency sweeps. The moths that are hunted have not been shown to be responsive to the FM modulations of the cries, but rather react defensively by trying to evade the bats in response to a wide range of ultrasonic tones across the frequency range of the sweeps.

Bat–moth communication brings up the aspect of reflected versus emitted signals in the three modalities. Bats are providing their own sonic lanterns, or strobe lights, if you will, with which they peer into the darkness for moving prey items. They rely on reflected sound for information to flow to them about prey. Most visually dependent insect predators and parasitoids rely on ambient light from the sun to reflect off prey items and provide information flow. Likewise, most visual communication systems use reflected, ambient light, except in the notable cases of firefly communication, in which emitted signals are the rule. Emitted, rather than reflected, sounds are the rule for insects that communicate by means of pressure disturbances. However, some species do enhance their resonance by reflecting their emissions off of the sides of
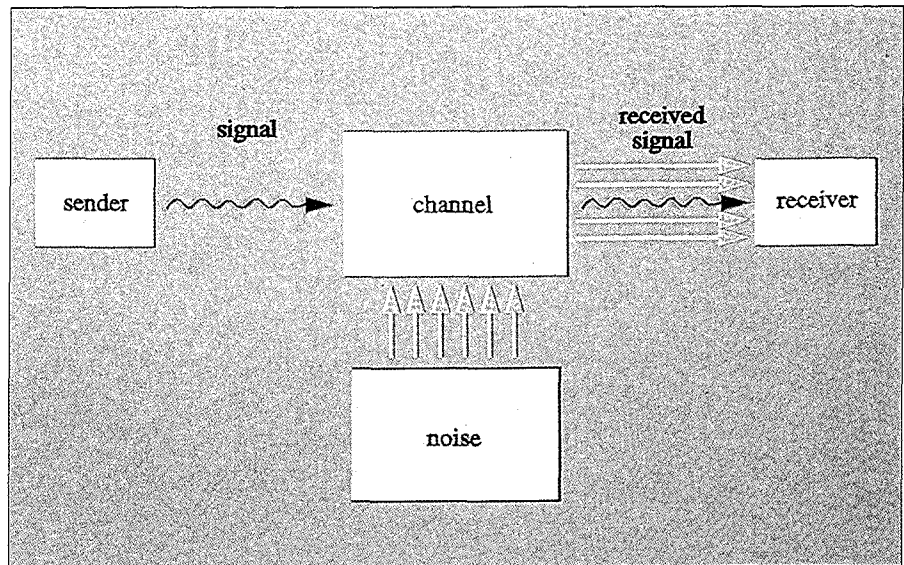

Fig. 1. Diagram of information flow that results in communication. The signal is depicted as fluctuating in amplitude (wavy purple line), whereas noise in the communication channel is depicted as being unvarying in amplitude (straight lines), but of a different carrier frequency (yellow instead of purple). The signal is able to be received and responded to even with the background noise present due to the different carrier frequency and its amplitude modulation relative to the noise (after Shannon & Weaver 1949).

specially constructed burrows, or off of leaves enlisted to increase the resonance of their emissions for the same purpose (Prozesky-Schulze et al. 1975).

Semiochemical communication in insects involves both emitted and reflected compounds. Obviously "you are what you eat" means that all atoms emitted from within one's body must have at some point been assimilated from an external source, and, therefore, could be considered "reflected." However, some molecules are ingested or adsorbed from surroundings and then reemitted as a signal in more-or-less *unaltered* form, as shown by Tom Eisner in his work on the defensive compounds of many insects (see, for example, Eisner 1970 for review). The results of many studies on courtship pheromones emitted by male moths have shown that these pheromones also are comprised of mainly plant-derived, little-altered molecules. Other semiochemicals are mainly self-generated, synthesized emissions, as exemplified by the lepidopteran sex pheromones manufactured from building-block acetate molecules, as highlighted by the work of Lou Bjostad and Wendell Roelofs (see Bjostad & Roelofs 1987 for review).

Other common properties of communication in any of these modalities include the fact that sustained reception of intact signals is affected both by background noise in the channel and by adaptation of the sensory pathways, whether the system involves light, sound, or chemicals. If some of the sensory pathways in the receiver have

been made dysfunctional from adaptation due to background noise, then the signal that reaches the brain may have been severely altered and rendered ineffective in evoking behavior.

Another major commonality among communication systems in the three main modalities is the way in which communication systems are dissected by researchers in order to distill the minimal set of signals important in evoking a response in receivers. First, the natural sequence of behaviors needs to be observed and analyzed for the researcher to get a feeling as to which parts of the sender–receiver interaction appear to be important in evoking a response, or in other words, in successfully communicating, as indicated by the response. Then the naturally emitted signal needs to be captured and played back for detailed analysis. In visual communication, relative reflectances of insect body parts such as wings can be gained by obtaining them and placing them in spectrophotometers to determine the major hues or carrier frequencies that are preferentially reflected and absorbed by pigments struck by ambient, white sunlight. The emission spectrum of fireflies can be immediately captured and measured on a spectrophotometer and displayed to find the major peak emission frequency or wavelength of light. Temporal analysis of the tempos at which wing reflectances are amplitude modulated or firefly flashes are pulsed, as well as the durations of the flashes and pulses can be recorded on film or videotape and measured during playback.
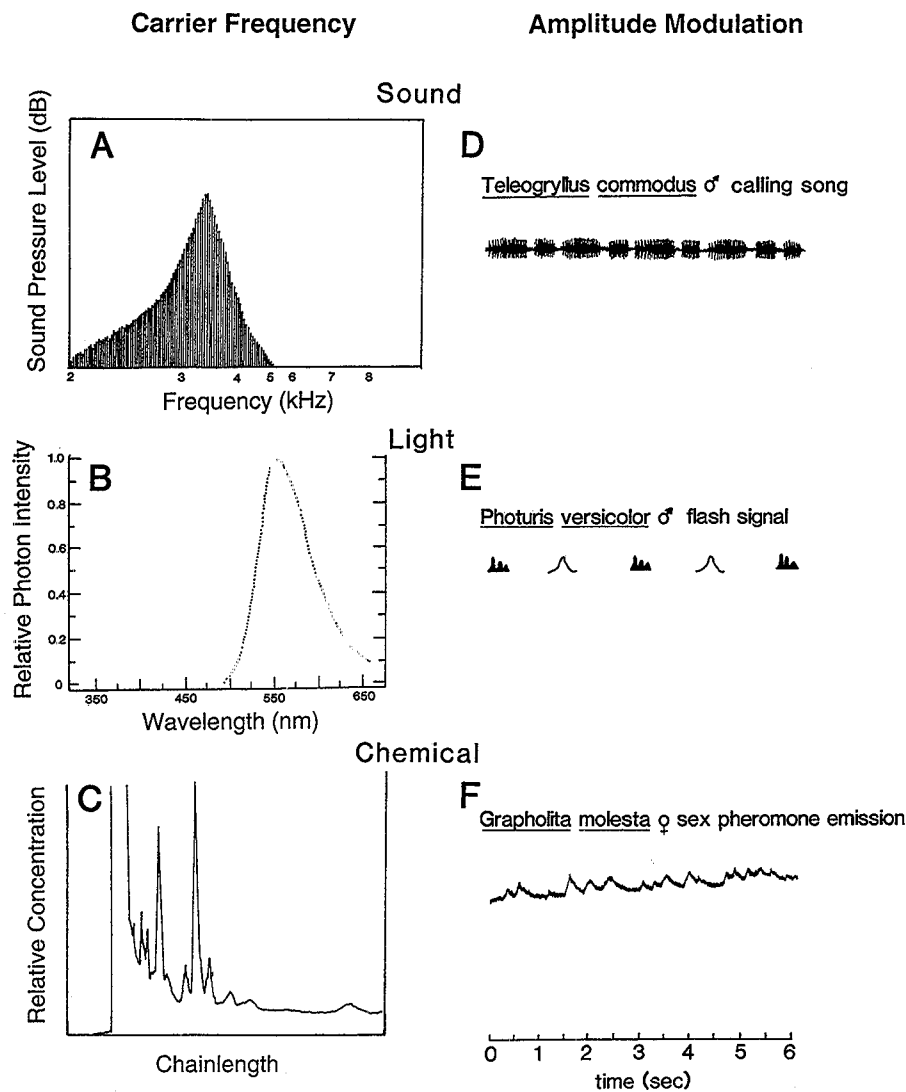
Carrier Frequency

Sound

A

Sound Pressure Level (dB)

Frequency (kHz)

2   3   4   5 6 7 8

Light

B

Relative Photon Intensity

1.0
0.8
0.6
0.4
0.2
0

350   450   550   650

Wavelength (nm)

Chemical

C

Relative Concentration

Chainlength

Amplitude Modulation

D

Teleogryllus commodus ♂ calling song

E

Photuris versicolor ♂ flash signal

F

Grapholita molesta ♀ sex pheromone emission

0   1   2   3   4   5   6

time (sec)

Fig. 2. Examples of communication signals using sound, light, and chemicals, involving the systems of Teleogryllus commodus (cricket), Photuris versicolor (firefly), and Grapholita molesta (moth), respectively. The emitted signals all have a characteristic predominant carrier frequency (A–C), and some degree of amplitude modulation (D–F). The male Photuris versicolor amplitude-modulated flashes (E) are depicted in black, and the female's answering flash in white. (A) is a sonogram section taken by Leroy (1964); (B) is a transmission spectrum from Lall et al. (1980); (C) is a gas chromatogram of emitted pheromone taken by Baker et al. (1981); (D) is an oscillogram taken by Bentley & Hoy (1974); (E) is an intensity reading taken by Lloyd (1966); and (F) is an electro-antennogram recording of a female sex pheromone plume taken in the field, 3 m downwind of the source by Baker & Haynes (1989).

In communication systems using sound, a representative example of sound analysis is that of the field crickets, Teleogryllus oceanicus and T. commodus during calling, courtship, and aggression (see Bentley & Hoy 1974). In this type of analysis, the emissions need to be recorded faithfully with a microphone and tape recorder having a flat frequency response that does not artificially deaden part of the sound at one part of the frequency spectrum, thereby making the signal appear to be more powerful in the other portions of the spectrum than it really is. The sound is then carefully dissected in space and time (that is, with regard to the carrier frequency, or major tone where most of the power lies, plus how the tone is broken up, amplitude modulated, in time). This is best viewed with a sonogram analysis, in which the frequency domain and time domain are displayed on two different axes for immediate viewing. Greater resolution of the frequency domain can be gained by viewing a section of the emission and having it displayed as a power function to see in which frequencies the different percentages of the total song energy reside (Fig. 2A). Greater resolution of the temporal aspects of the amplitude modulations in time can be gained by analyzing the emissions on an oscilloscope, in which the time sweep can be easily modified to magnify certain details of the waveforms (Fig. 2D).

In chemical communication systems, again the emission must be captured and replayed for analysis on an appropriate instrument (for olfactory communication usually on a gas chromatograph [GC] and for contact chemoreception usually on a high-performance liquid chromatograph). An example of such an approach comes from studies on courtship communication in the oriental fruit moth Grapholita molesta (Busck). First, the courtship sequence was recorded and analyzed as to what aspects seemed to be important (Baker & Cardé 1979). The emission was gathered from hundreds of hairpencil organs by extracting them in a solvent. Then the solution was injected onto a gas chromatograph and the frequency spectrum of the emission analyzed, separated first of all according to the molecular weight of the molecules (Fig. 3) (Nishida et al. 1982). Individual compounds were further dissected by breaking them apart in a mass spectrometer [MS] to measure the sizes of pieces that they fragmented into. This latter technique, the combined GC–MS system, gives important information about their structure in terms of double bonds, functional groups on the end such as alcohols, aldehydes, acetates, etc., that can be definitive when the information about the fragments is combined with the information about elution time from the GC.

For all modalities, the next major step in determining which aspects of the recorded and analyzed emissions are important to communication is to play back portions of the signal to see whether a behavioral response can be elicited, then gradually increase the numbers of portions that are recombined until a minimal set of frequencies is reconstructed that explains the successful response to the natural emission. A discriminating behavioral bioassay is crucial for success in this effort. In chemical communication research, this is called fractionation and recombination.

An example of this approach again involves the identification of the oriental fruit moth courtship pheromone. The emission was fractionated on GC (Fig. 3) and the fractions were puffed over a female antenna to see which ones might be most active on antennal receptors. From this electroantennogram (EAG) analysis, one peak seemed to have substantial activity. Then a fraction containing this peak was recombined with others during behavioral testing, in which filter papers impregnated with various combinations of this fraction plus others were held 2 cm upwind of calling females, to see if they would be attracted to the

odorous papers as effectively as they were to the natural extract. We found that the combination of two particular fractions, the EAG-active one plus another one, increased the attraction compared to the one fraction alone. Analysis of the compounds in these fractions revealed that the EAG-active one contained one compound, (E)-ethyl cinnamate. The other fraction contained two compounds that were both stereoisomers of methyl jasmonate (Nishida et al. 1982).

The verification that one of these compounds, (Z)-methyl epijasmonate, was the second pheromone component and that (E)-ethyl cinnamate was also a pheromone component came from obtaining synthetic samples of the compounds and presenting them either singly or as a blend to females who responded by being attracted to the blend. Synthetic samples of other compounds present in the emission were also obtained and presented to the females, yet even though some were much more abundant than the two pheromone components, they did nothing to influence the behavior, and were judged not to be involved in communication. Therefore, the key to proving that communication has occurred lies in the manipulation of the signal using synthesized components, along with requiring that a significant behavioral response be observed in response to the addition of any of the components. To prove that communication occurs in any modality, we must prove that we can talk back to the insects.

Interestingly, the (Z)-methyl epijasmonate was present in such small quantities that we could not get enough for GC–MS analysis. However, for months we felt that the odor from this fraction smelled so familiar that if we could locate the other source of it we might get enough to be able to identify it. This component had a slightly herbal, slightly floral, slightly fruity odor, yet we could not remember exactly where we had smelled it before! Then one day one of us, Ritsuo Nishida, sniffed a whole uncut lemon before he prepared it to squeeze it into his tea, and immediately realized that the oriental fruit moth hair-pencil coponent was in there. Eventually, after analysis of the airborne volatiles from lemons, the (Z)-methyl epijasmonate proved to be a heretofore unidentified odorant from lemon and, nanogram-for-nanogram, was the most powerful odorant yet identified from this fruit. The odor is familiar to us as the nondescript "fruit-bin" odor that we are hardly conscious of as we walk past piles of lemons, limes, and other citrus fruits in the grocery store. The fragrance industry that is involved with lemon-scented cleaning and
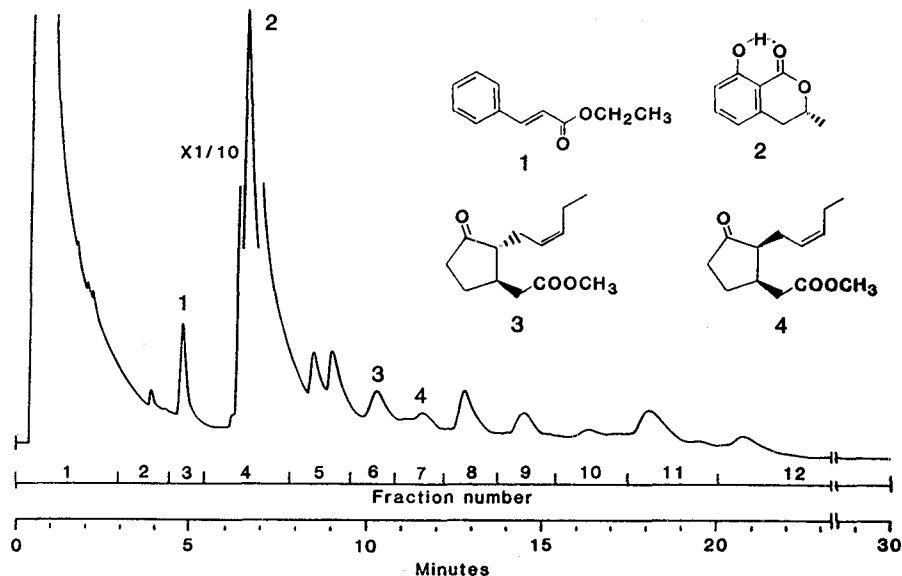

Fig. 3. Gas chromatographic recording (packed column) of male G. molesta hairpencil extract, showing the relative abundance of unknown components and the fractions taken by researchers for testing in electroantennographic and behavioral bioassays. Four compounds that were identified from the extract included two (compounds 1 and 4 (E)-ethyl cinnamate and (1R,2S)-(+)-(Z)-methyl epijasmonate, respectively), that when added together evoked significant levels of attraction of female G. molesta females in behavioral assays. Compounds 2 and 3 were behaviorally inactive, even though 2 was over 10 times as abundant as the other compounds, and even though 3 differs from 4 only by virtue of being a stereoisomer. To the human nose, 3 is virtually odorless, whereas 4 has a pleasant, herbally fruity aroma like that of an uncut lemon.

polishing agents became interested in manufacturing this epimer to add to their products for communicating to humans the sensation of "lemon-freshness."

Another interesting sidelight came when Ritsuo Nishida read that methyl jasmonate was known in the perfume industry as the "queen of aroma" and was one of the oldest and most widely used compounds by perfumers, extracted initially from jasmine plants. Further research by Terry Acree and Ritsuo Nishida revealed, however, that of the four possible epimers, only 1R, 2S-(+)-(Z)-methyl epijasmonate, the compound involved in the courtship pheromone blend and contributing to attraction, was strongly fragrant to the human nose (Acree et al. 1985). The other three stereoisomers comprising 97% of the "queen of aroma," proved to be virtually odorless! The beautiful fragrance attributed for years to the methyl jasmonate actually came from an impurity present at about 3% in the methyl jasmonate, and this impurity is the oriental fruit moth courtship pheromone component! Who would have thought that moth and human courtship fragrances would be so closely intertwined, and both could involve a signal gathered initially from plant chemicals? We found subsequently that males lacking the hairpencil compound (E)-ethyl cinnamate can imbibe it from sugar water and incorporate it into their

hairpencils for use as a pheromone, an example of a reflected chemical signal (Nishida et al. 1985, Löfstedt et al. 1989).

The responses of insects receiving sound emissions must be assessed in the same fashion to understand which elements are most critical to successful communication. First, a discriminating way to measure the response must be developed, and an example of this is with Teleogryllus oceanicus females made to walk on a styrofoam pretzel and choose whether to go right or left at choice-points during their walk. Responses to natural emissions replayed from audio tape were compared in this way and showed that the females could discriminate from among hybrid and even hybrid sibling male songs, based on slight differences in the patterns of amplitude modulation (Bentley & Hoy 1974). One useful feature of this assay is that the responder is not allowed to take itself into an area where the sound pressure level from one of the two loudspeakers becomes greater than the other, thereby biasing the choice with overall amplitude.

The rule in acoustic communication thus far, whether it be for crickets, grasshoppers, drosophilid fruit flies, and even insects such as leafhoppers and lacewings that transmit their pressure disturbances through a substrate such as a plant, has been that signals among species differ in patterns

of amplitude modulation. For example, leafhoppers, *Graminella nigrifrons* send vibrations through plants and then wait to hear an answer. Males then begin moving up the plant, and by a type of trial and error with regard to walking up one branch or another, they arrive at the answering female who is stationed near the top (Hunt et al. 1992). In their work, Hunt et al. used a Kay sonograph from the audiology and speech therapy department at University of Kentucky. To learn the language of an insect, entomologists used an instrument affecting our own ability to communicate. They determined that only a small fraction of amplitude-modulated vibrational pressure disturbances is actually important in attracting mates.

In a similar way, the parts of firefly emissions that are important to communication were discerned by using synthesized signals, in this case generated from flashlights. In the classic work of James Lloyd (1966), he determined that the carrier frequency, or color, of the light emitted by flying males was not that critical for evoking a response from females resting in the foliage and vice versa (Fig. 2B). However, the way in which males flashed their light—that is, modulated its amplitude—including the pulse duration and the interpulse interval, was in fact critical. The interval between the flash of the male and the (usually) single response pulse from the female was also crucial to evoking an orientation response from males, who continued to approach females that responded by flashing at the appropriate interval (Fig. 2E).

Although chemical signals are rarely in any obvious way amplitude modulated by the actions of the emitter, fluctuations in the intensity of pheromone concentration, in fact, do occur and have been shown to be crucial for sustained communication. The important fluctuations in amplitude for chemical signals come from the mechanical shearing of odor as it is released from a source such as a female gland, creating small-scale turbulence, little eddies, that downwind result in pockets of clean air interspersed with dense strands, or filaments, of pheromone. We have found with the oriental fruit moth that the intermittent contact with these filaments is essential to sustaining upwind flight of males.

How do we know this? The sex pheromone of the oriental fruit moth consists of three com-ponents 6% E8-12:Ac + 3% Z8-12:OH in Z8-12:Ac, as discovered by analyzing the emissions and responses as described earlier for this species' courtship pheromone (Fig. 2C) (Roelofs et al. 1969, Cardé et al. 1979). The carrier frequency—i.e., the blend—was then varied syntheti-

cally, along with the overall emission amplitude—i.e., the concentration—and a response profile was formed from both field trapping tests and wind tunnel studies. As in the case of sound and light communication systems, the carrier frequency that turns out to be optimal for moths is centered around the naturally emitted female blend. Also, as is typical for sex pheromones, the discrimination for carrier frequency is exquisitely and narrowly tuned in males, which differs markedly from sound systems in which there is very broad tuning and little discrimination simultaneously for both the emission quality (carrier frequency) and amplitude.

In the wind tunnel, EAG results showed that a male oriental fruit moth antenna does receive intermittent stimulation from the filaments of pheromone downwind. Even in the field, we showed that 3, 10, or even 30 meters downwind the antenna receives significant fluctuations of pheromone concentration and successfully registers them, as in the wind tunnel (Fig. 2F) (Baker & Haynes 1989). Then we showed that males do need fluctuating stimulation to sustain their upwind flight, by using a wind tunnel in which we could create a uniform cloud or fog of pheromone. We also pulsed the cloud at either one per second or one per two seconds, with a similar period of clean air between the pulses. The males flew upwind only when the cloud was pulsed. When presented with the uniform, constant fog of pheromone, however, males exhibited wide crosswind "casting" flight while keeping station momentarily after taking off. It appeared as if they adapted quickly to the uniform cloud and behaved as they would had they just lost pheromone and flown into clean air (Baker et al. 1985).

Further analysis of the behavior of oriental fruit moth males in response to quick exposures to and loss of pheromone showed that they respond within 1/7 s to either odor-on or odor-off. They reversed their course across the wind-line—i.e., zigzagged—an average of seven times per second, and with a single exposure to clean air following loss of pheromone they flew more across the wind on the very next reversal to begin casting flight. Their response to contact with pheromone on the other hand, was to fly more directly upwind on the very next reversal after contacting pheromone and reverse more frequently, to create an upwind surge. Considering that the EAG results showed that males will encounter only about two or three filaments per second if they fly straight upwind in the plume, the 1/7 s reaction time of males to either pheromone on or off meant that there is therefore time between filaments

for the males' behavior to change to cross-wind casting flight, even while "in" the time-averaged plume. There is also time for the male to react by surging upwind to each filament. We believe that what we see in a zigzagging flight track therefore is a kind of hybrid response that averages out to be zigzagging—i.e., tracks that are not fully crosswind casting or fully upwind surging—because the moth is usually in transition from one to the other due to the timing of the intermittency of the simulation (Baker 1990).

Why should such a quick and highly phasic response evolve? We think it may have to do with the challenge faced by male oriental fruit moths, as well as by males of some other insect species that must fly upwind to odor sources in quickly shifting wind fields (Baker 1990). They must respond to every filament caused by small-scale turbulence by surging upwind, because the combination of odor plus wind direction points, in many environmental situations, directly toward the source. Conversely, males must begin to stop their upwind surge and begin casting quickly to keep their station in clean air in order to avoid plunging very deeply into a large pocket of clean air caused by a large-scale wind shift; they quickly become farther and farther displaced from the new position of the odor if they proceed upwind without pheromone. Casting will also increase their chances of recontacting odor that has moved off to one side or the other due to such a shift in wind direction caused by large-scale turbulence. Thus, it behooves males to respond quickly to *every* pocket of clean air, even small-scale ones, by casting as soon as it is detected, because it may turn out to be one of the large pockets inevitably looming ahead (Baker 1990). If, on the other hand, the pocket is only one of the many little ones, the male is still in position to hit the next filament. Thus, although a male moth flying upwind in response to pheromone may appear to be in contact with the plume, it really is never in contact with pheromone for any period of time at all. The male is either encountering filaments frequently due to small-scale turbulence, in which case the upwind surges are rapidly, reiteratively elicited, or else infrequently, in which wide, infrequent reversals are made crosswind, which allow it to recontact the odor.

With regard to pheromone receptor systems, the consequence of not meeting the challenge of recovering quickly enough after exposure to intermittent pheromone stimulation is receptor adaptation. Adaptation is the reduction in a receptor cell's firing response to a stimulus with

repeated presentation of a stimulus. We can see the effects of adaptation in our own color visual system. We have three classes of receptors whose sensitivities to different wavelengths of light differ substantially from each other as sketched in Fig. 4A. One class responds optimally to short wavelength light, the second responds best to middle wavelengths, and the third fires best to long wavelengths of light. When they are presented with light from all parts of the spectrum, the three types all fire at a high rate and the 1:1:1 ratio of firing creates the sensation of white, which pinpoints the predominant carrier frequency as everywhere; there *is* no predominant frequency. However, when presented with light from one part of the spectrum or another—for instance, medium-long wavelengths—the ratio of firing sent from the three receptor types up to higher-order neurons is now different, with little or no firing from the short-wavelength receptors and somewhat equal, moderate levels of firing from the middle and long wave-length receptors (Fig. 4B). This pattern pinpoints the peak wavelength as being somewhere between the peak sensitivity areas of the two classes of receptors sensitive to medium or long wavelengths, giving the sensation of orange (Fig. 4B). Conversely, a very short-wavelength emission will cause much firing in the short-wavelength receptors, but little to no firing in the middle and long wavelength receptors. This ratio of receptor inputs, high firing, low firing, low firing, is weighed by cells farther up the line and gives the sensation of blue, which we certainly can discriminate from other carrier frequencies (Fig. 4C). Why we get the pleasant sen-sations of color is a mystery, but it certainly is fortunate that we are given this beautiful gift to discriminate wavelengths of light.

Evidence for adaptation comes from exposing our receptor cells to a particular wave-length and selectively stimulating one class of receptors. For instance, first staring intensely at the short-wavelength dot in (Fig. 4C) to the point where if one now looks at the white dot in (Fig. 4D), makes the latter appear orange. This effect occurs because the short-wavelength receptors are now deficient in their output to the brain because they have been selectively adapted. Light comes from all parts of the spectrum from the dot in (Fig. 4D), but only the middle- and long-wavelength receptors are firing equally to each other because the short wavelength receptors are adapted, and the ratio of input from the three types of receptors is interpreted by higher-order neurons as orange, a medium-long wavelength of light. Thus, even though the true
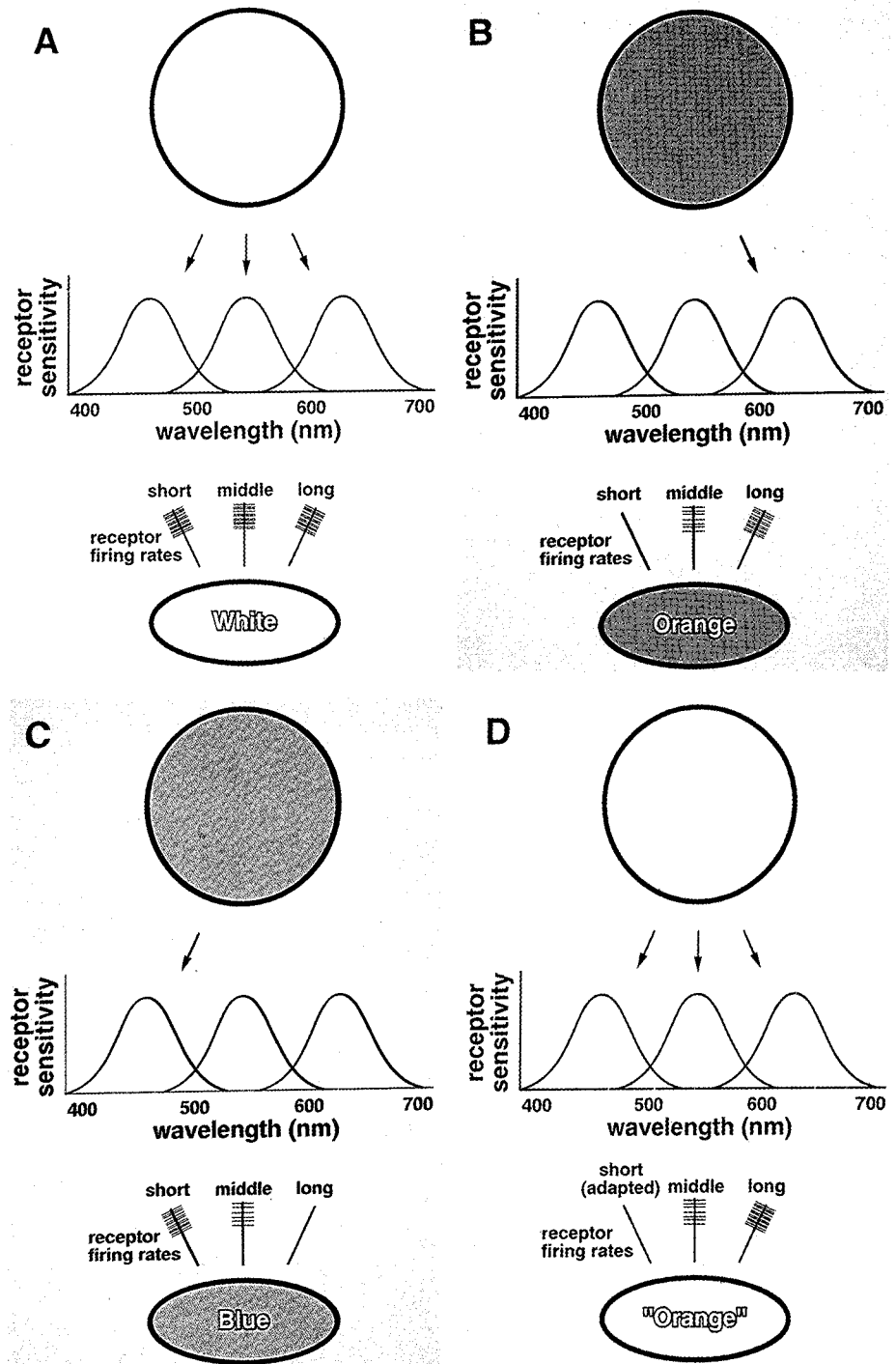

Fig. 4. How receptor adaptation can interfere with the correct reception of carrier frequency in a communication system. Stare at the blue dot in (C) under bright light for at least 10 seconds, and then quickly change your focus to stare at the white circle in (D). You should get the sensation of orange in (D) because although the ratio of energies of light from the white dot is approximately equal (A), your short-wavelength receptors have become adapted (have a reduced capacity to produce action potentials) due to the staring. Therefore they will contribute relatively little to the ratio of inputs going to the brain when you look at the white circle, and the brain will now receive the most activity from the middle and long-wavelength receptor pathways, as when presented with the orange dot in (B). See text for further explanation.

light signal, white light, is strong across all wavelengths, including the short ones (Fig. 4), the incompetence of the short wavelength receptors caused by prior, selective exposure to short wavelength light results in a wrongly received signal with a skewed

carrier frequency that does not represent reality.

Our work has shown that in sex pheromone communication, such adaptation of receptors can be a significant contributor to the reception of a wrong signal even though

the right one is being emitted. For instance in the turnip moth, *Agrotis segetum*, while working in conjunction with the pheromone group at the University of Lund, Sweden, we showed that a differential adaptation of antennal receptors can occur in response to excessive emission rates of the correct pheromone blend, and can explain the arrestment of upwind flight progress in response to excessively concentrated synthetic lures that occurs in many moth species (Baker et al. 1988). We placed single cell preparations in pheromone plumes 70 cm downwind of the source and exposed the cells to the same point sources that had earlier caused arrestment of upwind flight before the source was reached; we also exposed the cells to lower concentrations that had promoted complete flight to the source without arrestment. The highest emission rate of the correct female-emitted blend had caused males to start flying upwind, but within a few seconds, their upwind progress stopped; they became arrested while in flight and stayed flying at one distance downwind.

Recordings from single neurons on male antennae pointed out why this might have happened. First, Van der Pers & Löfstedt (1986) had shown that there are three classes of receptors on *Agrotis segetum* antennae, each tuned to one of the three pheromone components, a short chain-length, a medium chain-length, and long chain-length compound. Therefore, when a filament of the three-component pheromone blend strikes the antenna, cells of the three types residing in different hairs send a ratio of firing to cells higher up in the antennal lobe. All three cell-types need to be firing in order to register as "pheromone" in the higher centers. At the lower emission rates promoting sustained upwind flight, the cells responsive to all three components do fire consistently and repeatedly in bursts over a sustained period of time. However, at the highest emission rate, the one causing arrestment, we found that the receptor cells tuned to the major component become adapted quickly and stop firing; the cells responding to the other two components, on the other hand, keep on firing properly without adaptation (Hansson & Baker 1991). What this means is that the ratio of firing from the three cell types would now be skewed in favor of the two cell types responding to only the minor components, and the odor blend would now appear to be overloaded with those two minor components when in fact the blend in the air was still correct. Excessive concentration therefore would cause a perceived change in the quality of the odor as a result of the differential adaptation of one receptor type. As in

the example of the differential adaptation of one of our visual receptor types, higher-order cells in the brain of the male moth would judge the ratio of inputs to be something other than what was present in the real world.

The idea that by exposing insects to excessive amounts of odor we can alter their response to their own pheromone by changing the quality of the received signal through adaptation or habituation, allows us to develop new strategies for insect control. As entomologists, especially ones hired by the USDA or the Agricultural Experiment Stations in our respective states, we have an obligation to work to generate new knowledge that can be applied to improve the quality of life for the citizens of our states. Taking our knowledge of noise and how it can affect receptor pathways, we can try to add noise artificially to a communication channel to disrupt communication. In this way, once we have learned the pheromonal language of a particular species, we can talk back, loudly, with very specific noise to impede possible information flow in that species.

Noise plays an important role in the evolution of communication systems. We can see the importance of natural noise in communication channels by the ways in which palatable prey insects have been selected to blend into it. In sound communication, clearly the evasive behavior of moths responding to bat cries includes turning-tail on the bat and reducing their signal to blend, as a "stealth" moth, into the background of the open air of the night. But also the behavior includes diving into the bushes and blending into the many reflective surfaces of the vegetation that create a maze of noise to the strobe-light sounds of the bats as they search and close in on their prospective prey. Likewise defensively blending into the background noise in the light often involves painting oneself in pigments that match the ambient reflective frequency of the vegetation, in the middle wavelengths that appear green to us and to prospective predators. In addition, moths that rest on bark in daylight not only have the appropriate background noise pigments, but also, as Sargent (1968) showed, have been selected behaviorally to choose the appropriate background shade, regardless of what they see painted on their bodies. Noise has had a great selective effect therefore, on the behavior of these moths in not communicating with predators such as foraging birds.

In pheromone systems there is tantalizing evidence that some pheromone blends have evolved to stand up to different kinds of pheromonal background noise in differ-

ent geographic locations that might otherwise prevent communication. Linn et al. (1984) found that in the cabbage looper moth *Trichoplusia ni*, there are components emitted as part of the blend that are redundant, and can be eliminated without significantly harming the subsequent response. They found several important redundant pairs of components that are in this way mutually replaceable in the signal to evoke the same optimal response. This redundancy can be likened to our own printed language that contains extra, redundant letters. Some can easily be dropped out without affecting the reception of the message, and in a noisy channel that contains these exact same letters, the message can still be picked out without error. If the redundancy did not exist, there would not be a buffer against noise, and now further noise in the system would fatally erode the remaining letters' reception and make the message significantly more difficult to receive.

In *T. ni*, not just any two pairs of compounds are redundant, but rather only specific pairs can fill-in for each other if one of the pair is missing. If both members of a redundant pair are missing, then the sustained upwind flight to the source is reduced. We had hypothesized that one way that one member of the pair might be caused to be effectively absent would be a result of noise in the environment from other species of calling moths that would cause the adaptation of that particular component-specific pathway (Baker 1989). Our idea was that species such as *T. ni* that are found all over the country may have a robust set of compounds because their rich blend can stand up to the different kinds of noise in different geographical regions emanating from females from different species-complexes. Such species could be successful in communicating anywhere in the country, because the redundancy would therefore serve as a buffer against environmental noise. An example of one redundant pair is 12:Ac and Z9-14:Ac, which are two minor pheromone components in *T. ni*; another is Z5-12:Ac and 11-12:Ac.

Using the cut-sensillum single cell technique to record from antennal neurons, Julie Todd in my laboratory found that the hypothesized redundant pathways are represented neuronally by cells tuned to these particular redundant pairs of compounds (Todd et al. 1992). That is, she found antennal neurons that responded to either 12:Ac or Z9-14:Ac, but not the other pheromone components. Also, she found cells that responded to either Z5-12:Ac or 11-12:Ac, but not the other compounds. We then hypothesized that cells responding to

these redundant pairs might send their axons to the same discrete centers in the macroglomerular complex in the antennal lobe of the brain. There would be four major centers in the antennal lobe, one receiving inputs from cells responsive to the major component only, and three other centers receiving inputs from particular redundant pairs of receptor cells that reflect the behavioral redundancy found earlier by Linn and Roelofs.

In collaboration with Bill Hansson at the University of Lund, Sweden, we have now begun to see if such redundant-pair-specific centers exist, by recording from the cells and finding out which compounds they are tuned to, then dying the cells with cobalt, and silver-intensifying them to follow them down to their areas of arborization in the macroglomerular complex (MGC) (Hansson et al. 1992). So far, we have found that cells specific for the major component do in fact send their axons only to one major subcompartment of the macroglomerular complex. It will be exciting to see if the other subcompartments that are found in the MGC are there for the purpose of receiving inputs from particular redundant pairs of minor components.

Natural noise does appear to have had an effect on the ability of insects to communicate, and now by artificially adding selected types of noise we know we can affect processes such as mating and oviposition, even feeding. The use of pheromones for disrupting mating has become commercially acceptable, even desirable. For instance, by placing controlled-release dispensers of three-component oriental fruit moth pheromone into the environment, the success rate of males locating calling females can be reduced to <1%. First in Australia, then California, peach growers have accepted this control measure, and a pattern that has occurred is that after three successive years of using pheromones, the moth populations plummet to the point where often no control intervention is necessary. Included among other species for which commercially available disruptants have been successful are the tomato pinworm moth, the pink bollworm moth, and grape berry moth (Ridgway et al. 1990).

Does the pheromone disruption-emitted noise work by confusing males, causing them to fly upwind, locate the inappropriate synthetic sources, and waste time investigating them instead of mating? Or does it work by adapting (habituating) the males' pheromone-specific pathways to hamper their sensory capabilities? There is evidence that it is a little of both, since pink bollworm males have been observed under field conditions visiting disruptant hollow fibers. However, evidence for the adaptation–habituation mechanism as a contributing factor comes from the experiments of Hollis Flint and coworkers in Arizona (Flint & Merkle 1984). They showed that when noise in the form of the correct 50:50 pheromone blend of the two pink bollworm pheromone components was broadcast into fields, traps emitting this same ratio were completely shut down to male attraction, as were traps emitting a different series of blend ratios of the same two components. When they used a 9:1 ratio of these components with which to disrupt communication, however, they found that disruption again was profound across all signaling frequencies, including the natural blend. However, this time traps emitting a frequency artificially enriched with the component that predominated in the disruption blend did manage to capture a small but significant number of males. This blend would never have attracted males in a noise-free environment, because it is such an extreme off-ratio. This odd result showed that males could be made to fly upwind to a bad blend as if it were an optimal one by artificially compensating for the adaptation. Enriching the blend with the component to which the adaptation had selectively occurred brought back an illusion of the correct balance to the odor.

Finally, the steps involved in learning the language of insects must include communication with other scientists. We must effectively use our language to pass on our knowledge about the insects to our colleagues and to transmit our insights about possible evolutionary patterns or about the prospects for applying our knowledge for pest management purposes. The insects do, indeed, oftentimes seem to be trying to tell us something. Once we learn what it is, we must not be lazy and let their message die by failing to publish or talk about our findings. The important feature of communication between insects and ourselves is that we must understand that *we are the channel*. The old axiom "publish or perish" is familiar to everyone. But actually, the important aspect of this statement for those involved in insect communication research is publish, or else the language of insects will perish. Their words will not merely have fallen on deaf ears, but even more tragically, they will have ended up in a mute human channel.

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