APPROACHES TO INSECT BEHAVIOR OF INTEREST
TO BOTH NEUROBIOLOGISTS AND
BEHAVIORAL ECOLOGISTS

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I. SYNOPSIS

The manifold habitat-dependent behavioral tactics insects have evolved are the common subject of research by both behavioral ecologists and behaviorally oriented neurobiologists. Behavioral ecologists prefer to study undisturbed individuals and populations in the field. They describe behaviors of different species and try to elucidate how they contribute to reproductive success. Neurobiologists concentrate on substrates and mechanisms that underly distinct and quite often simple behavioral acts, and most commonly, they do this in restrained animals. This paper is an effort by an insect neurobiologist toward a mutualistic coexistence between behavioral ecology and neurobiology by the discussion of topics of insect behavior that can enhance future cooperation, especially in the field of communication systems.

II. INTRODUCTION

Animal behavior can be investigated at various levels within its organizational hierarchy, according to the problems of interest and the questions being asked. However, quite often new insights and new ideas are achieved when scientists working at these different levels begin to talk to each other and make an attempt to exchange concepts, methods and results. This should become particularly important for behavioral ecologists and neurobiologists, especially when the latter concentrate on the neural bases of adaptive behaviors and habitat-dependent tactics that the former study in the field. But there are considerable differences in the problems being attacked and in the research strategies used to solve them.

As schematized in figure 1, both intra- and interspecific behavioral interactions provide a common source for research and could start a fruitful cooperation between behavioral ecologists and neurobiologists. Behavioral ecologists focus, for example, on how different species select their mates, compete in mate selection, hunt for prey, avoid or fool predators, forage, or take care of offspring, and how they organize social groups. They like to know how these behaviors contribute to survival and reproductive success, and how they have evolved. Their discoveries raise questions for themselves and also for neurobiologists, such as, what sensory modalities are involved in these tactics, and how do sensory, central nervous and effector systems function in order to produce the demonstrated behaviors.

Neurobiologists, by mainly working under controlled laboratory conditions and quite often with behaviorally restrained animals, search for com-

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MUTUAL INTERACTIONS BETWEEN BEHAVIORAL ECOLOGY
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Fig. 1. Common sources of research interests in behavioral ecology and neurobiology, and mutual interactions.

Components involved in sensorimotor performances that are expressed in different behaviors. It is their ultimate goal to study how visual, acoustical or chemical signals are produced and how these signals are perceived and encoded in sensory and nervous elements to provide a causal basis for intra- and interspecific interactions. Their discoveries at the molecular, cellular and multicellular levels may in turn provide feedback to behavioral ecologists and have impact on their research.

It is the purpose of this article to start a dialogue between the two groups by introducing problems of insect behavior attacked by insect neurobiologists that may guide future research in behavioral ecology, and even to enhance cooperation.

III. INSECTS AS MODEL SYSTEMS

Insects offer great opportunities for behavioral ecologists (see, Blum and Blum 1979; Thornhill and Alcock 1983; Gwynne and Morris 1983) to study the strategies and tactics of sexual selection, reproductive competition and the evolution of mating systems. For neurobiologists (see Huber 1983 a,b; Camhi 1984) insects offer a rich and complex behavioral repertoire and a nervous system that can be attacked at the single cell level, allowing the so-called “identified single cell approach” (Hoyle 1983). The topics and examples chosen in this article may help initiate some cross-talk between neurobiologists and behavioral ecologists and assist scientists working in these areas to better coordinate their research activities.
A. Neurobiological Limitations in Insect Behavior

a. Escape and Hunting

It is most critical for a prey animal to detect the predator’s attack as early and to respond as fast as possible. On the other hand, an efficient hunter must develop tactics to avoid early recognition and escape by the prey.

Toads are among natural predators of cockroaches (Camhi 1984). During the lunge of their tongue air is moved which stimulates filiform hair sensilla located on the cockroach’s anal cerci. These mechanosensitive structures are activated by air particle displacement and their spatial arrangement provides directional information to the roach (Nicklaus 1965; Westin et al. 1977; Camhi 1984). Roeder (1959) made precise behavioral measurements in the cockroach of the time course and velocity of the escape response to air puffs. He compared these measurements with data on those elements in the system that could be monitored electrophysiologically, i.e. cercal afferent fibers which originate in the mechanosensitive cercal sensillae, abdominal giant interneurons and the leg motor system. Roeder found that the quickest behavioral response expressed by movement of the body of a slightly restrained roach occurred around 20 to 30 ms after the stimulus onset, whereas the time estimated on the basis of electrophysiological data was around 16 to 20 ms. The two times agreed within an order of magnitude strongly indicating that the cockroach’s fastest escape is limited by the time courses of the underlying sensory, interneuronal and motor systems.

More recently Tautz (1977, 1978) and Tautz and Markl (1978) studied behavior of the caterpillar of Barathra brassicae (Noctuidae). This larva responds with cessation of movement to airborne vibrations caused by the wingbeat of an approaching predatory wasp. The response is lost after removal of all eight mechanosensitive filiform hair sensilla situated on the caterpillar’s thorax. The sensors are activated by air-particle displacement and are especially sensitive to wingbeat frequencies in the range of 100 to 400 Hz at unspecified amplitudes. Within this range they respond at distances of about 70 cm. Behavioral and electrophysiological data led the authors to predict that an efficient hunter can avoid early recognition by these prey larvae in two different ways: it (1) can shift its wingbeat frequency out of the sensitive range of the filiform hairs, as documented in bigger wasps parasitizing caterpillars (Rathmayer 1978), where the wingbeat frequency lies below 100 Hz; or it (2) can reduce the force of the air vibrations it produces to below the threshold of the caterpillar’s sensors. In some small wasps parasitic on the same larvae (Habrobracon sp., Braconidae), it was calculated from known mechanical and electrophysiological properties of the sensory hairs that the caterpillar will not respond until the wasp approaches closer than 4.5 cm.

b. Signalling and signal detection in the time domain

Insects display a great variety of signals for sexual communication, mate competition, territorial display and for interactions within social groups. Depending upon the species, signals may involve chemical substances (pheromones), reflected light, bioluminescent flashes, airborne sounds, and even low amplitude vibrations which are common alarm signals in ant
colonies (Markl 1967, 1968, 1970; Markl and Fuchs 1972). Here I shall concentrate on acoustic communication in which airborne sounds are used. Two signal parameters are most important; the sound frequency spectrum and the temporal organization (rhythm) of sounds. The latter is also a frequency and is important for signal detection in the time domain.

In timballing cicadas and in some stridulating katydids, trains of short and highly damped sound pulses are produced at high repetition rates. We would like to know how the sender generates such fast sound pulse rates and also whether the receiver is able to transduce such fast amplitude modulations into groups of nerve impulses which encode the rate.

Most cicadas timbal at rates of appr. 200 Hz (=Hertz=cps) (Pringle 1964; Hagiwara and Watanabe 1956). This rate is generated by an alternation of the paired timbal systems each of which signals with appr. 100 Hz (Moore and Sawyer 1966; Reid 1971; Young 1972; Simmons 1977; Simmons and Young 1978). More recently it has been shown by high speed movie pictures (Moore and Kausch 1975) and by combined recordings of sounds and timbal muscle potentials (Moore and Sawyer 1966; Young and Josephson 1983 a; b; Moore et al. in prep.) that within each timbal-motion a train of sound pulses is broadcast. The pulse rate within each train goes far beyond 200 Hz. In all timballing cicadas the timbal is not a uniform plate, but is subdivided into parts with rather soft and flexible membranes interspersed with a sclerotized plate and a series of 2-12 sclerotized ribs. When the timbal muscle contracts it pulls the timbal plate inward. This motion progresses in discrete steps then from rib to rib. Each rib produces one of the sound pulses of a train (figure 2). In the periodical cicada Magicicada cassini up to 9 of its dozen or so ribs operate in succession during a single inward click of the timbal, and this results in a sound pulse rate of 900 Hz and a sound frequency spectrum of 4-9 KHz at nearly 100 dB (decibel) at the source. Thus, the sender is able to generate fast pulse rates because of the biomechanical properties of its timbal. The number of pulses produced by a timbal may vary among sounds produced by a single male, but the pulse rate of the timbal ribs varies very little; dramatic rhythm rates at much lower frequencies are produced by turning the whole paired mechanism on and off. Frequency and amplitude modulation of carrier frequencies are also quite common among these complex sounds (Moore, pers. comm.).

The receiver, a male or female conspecific, may be able to resolve the high timbal rib pulse rates, but at present we have not performed the relevant quantitative behavioral tests in the field and laboratory which could unequivocally demonstrate such high pulse rate detection. However, indirect evidence that these cicadas may not encode pulse rates beyond 200 Hz (at signal durations of less than about 10 ms) comes from whole auditory nerve and single auditory interneuron recordings (Huber et al. 1980). The response of many auditory receptors to playbacks of conspecific songs strongly indicates that the receptors only respond to the overall timbal movement and associated rhythm of ca. 200 Hz (figure 3), and do not clearly resolve the succession of pulses produced by the ribs. Auditory interneurons of Magicicada septendecim recorded within the fused thoracic central nervous system encode only the buzzy song as a whole but not the detailed temporal structure. In the species Magicicada cassini such interneurons copy the slower tick rate but not the fast buzz rate in the calling
Fig. 2. Sound production in cicadas. Upper trace: Sequence of brief and highly damped sound pulses produced by inward buckling of the timbal in a *Magicicada cassini* male. The 4 pulses seen correspond to the inward buckling of each of 4 ribs; the subsequent and faint pulse (arrow) is generated when the timbal springs back into its resting (outward) position (Weber, T., unpublished data). Lower trace: Two consecutive muscle potentials recorded from the ipsilateral timbal muscle while the male was producing sound as shown in the upper trace, another group of sound pulses would follow the second potential. Each single muscle potential (shown) precedes muscle contraction (not shown). Each muscle contraction is followed by a fast inward movement of the corresponding timbal with the associated sounds (upper trace). Time scale horizontal, voltage scale for sound pulses, vertical (Huber, unpublished data).

song. If it turns out in future work that even single auditory receptors can not follow such fast rates, then a part of the temporal information laid down by the sender is lost at the receiver's ear, and the explanation for the occurrence of ribs may come from another context.

A quite similar problem has been reported in the very loud buzz of the katydid *Neocomocephalus robustus* (Josephson and Halverson 1971). Here the male stridulates by rubbing one forewing against the other. The wing stroke frequency and resulting pulse rate reaches to 200 Hz or even beyond, producing a very high and broad sound frequency spectrum. Also in these katydids the generation of songs with high pulse rates depends on special biomechanical and muscular properties (Josephson 1973, 1984).

The question arises: Does the receiver encode such pulse rates? Morris and Fullard (1983) investigated the discrimination power in some ticking and buzzing *Conocephalus* species in the time domain using a phonotactic assay. They found that songs or random noises that lacked a distinct amplitude modulation mimicking the pulse rate still remained highly attractive to females. This could mean that the receiver either "pays no attention" to the pulse rate of the song in conspecific recognition or its sensory system can not resolve fast rates. A comparison with electrophysiological results obtained in the genus *Gryllus* will perhaps be helpful for understanding possible limitations of the auditory system in the time domain.
Fig. 3. Time resolution in the auditory nerve of cicadas (*Okanagana rimosa*). Upper trace: Series of bursts of calling sound pulses. Lower trace: Summed activity recorded from the whole auditory nerve. Note that each sound burst is correlated with a single but summed auditory nerve signal. Each sound burst reflects 2 pulses from one timbal followed by 2 or 3 pulses from the other timbal by a single inward movement of each of the two timbals. Playback of these bursts elicited a response of similar duration in the auditory nerve after a latency of approximately 20 msec, as indicated by the arrows. Sound intensity 75 dB SPL, time scale between black bars 20 msec (modified from Huber et al. 1980).

Auditory receptors in *Gryllus bimaculatus* and *campestris* copy sound pulses of the chirped calling songs (narrow, relatively low sound frequency spectrum) with a burst of nerve impulses, and impulse frequency within each burst encodes sound intensity (Esch et al. 1980). At 90 dB the impulse frequency encoding reaches about 300 Hz. Assuming that similar intensity encoding is present in *Conocephalus*, then a sound pulse rate of 200 Hz, with an interpulse interval of 5 ms between consecutive pulse onsets, would result in a discharge frequency of auditory receptors of 200 Hz—assuming that each receptor responds with a single impulse to each single sound pulse. However, if the receptor also encodes the intensity of the sound in a manner like that of *Gryllus*, then consecutive bursts of nerve impulses would overlap and partly interfere. A consequence would be to reduce high fidelity temporal resolution of the pulse rate by the receptors. So far no auditory system studied lacks intensity encoding. Thus, *Conocephalus* is perhaps forced to make a compromise between pulse rate copying and intensity encoding. Morris and Fullard’s results suggest a change from using the high pulse rate as an important temporal parameter.

B. NEUROMUSCULAR ECONOMY AND COURTSHIP BEHAVIOR

As often reported (Hoyle 1964, 1970), the insect nervous system has rather few motor neurons and many muscles are innervated by not more than 3. In addition, several muscles serve multiple motor actions such as walking, flying or stridulating; they are called bi- or even multi-functional (Wilson 1962; Elsner 1968, 1975). The courtship behavior of the male grasshopper *Stenobothrus rubicundus* provides an excellent illustration of such “multifunction” (Elsner 1974). Two kinds of stridulation are displayed during courtship: conventional hind leg stridulation, characterized by al-
tornating up- and down-strokes at a frequency of 12 Hz (producing short bursts with a broad sound frequency spectrum); wing stridulation with the unfolded fore- and hindwings raised and lowered periodically at a frequency of 70 Hz (producing even shorter bursts with a broad sound frequency spectrum)—this rate of movement is also characteristic of flight. During wing stridulation the sclerotized veins of the hindwings are beaten against each other to produce sound (figure 4). Between leg stridulation at the start of the courtship and wing stridulation at the end, the male interposes a middle part where approximately every third downstroke of the hindleg is prolonged and subdivided into 3-10 short-lasting subpulses which follow the frequency of wing stridulation, though the wings are still folded.

Recordings of sounds and muscular activity showed that during leg stridulation other motor units within the same muscles became active than were active during the final wing stridulation. In addition, their phase relationships changed. Thus, the male has produced two different motor outputs. However, during the prolonged downstrokes of the middle part,
motor units that activate leg stridulation were superimposed with those used for wing stridulation. This indicates firstly, that the male can not suppress the second motor pattern before the first has ended, and secondly that a transition occurs at the neuromuscular level before the actual wing movements are performed. Each set of motor units is driven by its own generator network, e.g. by a limited number of neurons which may be multifunctional as well. Thus, the middle part of courtship expresses two output-specific but overlapping rhythmical processes.

Acridid grasshoppers are well known to be most responsive to the species-specific temporal structure of the song (Helversen 1972; Helversen and Helversen 1975, 1983). In Stenobothrus rubicundus it can not be excluded that the different temporal arrangement of sound pulses in the middle part of courtship is used as an important time element for male recognition, or that it is just a byproduct of sender mechanisms arising from the simplicity of neuromuscular systems.

C. Conspecific Song Recognition in Crickets: Behavioral and Neurobiological Studies

One fundamental problem in animal communication is recognition, expressed for instance in species or even individual recognition and also in tactics where one species mimics another as documented in fireflies (Lloyd 1965, 1976, 1980, 1981, 1983).

Recognition is thought to be based upon sensory and neuronal detector systems, often called ‘templates’. These are viewed as nervous machineries that match certain behaviorally relevant stimulus configurations, named ‘sign stimuli’ by the students of animal behavior. Sign stimulus detection requires a filter process within the peripheral and or central nervous system.

Recognition of conspecifics often involves more than a single sensory modality. Male butterflies are aroused by female pheromones and then find the stimulus source with the help of sensory input generated by wind and by visual cues (Preiss and Kramer 1983). Male acridid grasshoppers use sound to attract females from a distance, but courtship is elicited by a set of visual stimuli (Riede et al. 1979). In many crickets and especially katydids both airborne sounds and substrate vibrations direct the female to the singing male at closer distances (Latimer and Schatral 1983; Keuper and Kühne 1983). Corresponding to these behavioral observations, neurons identified within the auditory pathway respond both to airborne sound and substrate vibrational signals. The substrate signal increases the accuracy of the response to the temporal structure of the sound (Kalmring et al. 1983).

a. Behavioral approach to recognition

From field observations with marked female crickets we know that they approach calling males of the same species even in populations where more than one species is present (Popov et al. 1974). Other stimulus modalities such as visual targets or chemical substances may contribute (Weber et al. in prep.; Stout et al. in prep.), but the acoustic channel is sufficient.

By studying female cricket phonotaxis on a walking compensator (a spherical treadmill designed to record the walking mode and walking direction in a closed loop system) we learned about the demands for conspecific song recognition and sound source localization (Wendler et al. 1980, Weber
et al. 1981, Thorson et al. 1982, Schmitz et al. 1982, 1983, Pollack et al. 1984). Figure 5 shows a drawing of the experimental setup used and some of the results. With the female positioned on the treadmill in the dark or under homogenous light conditions in a soundproof room (neither of which reflects the natural habitat), we discovered a rather simplistic template for calling song recognition in females of *Gryllus campestris* (Thorson et al. 1982). Females were aroused and began phonotactic tracking on the treadmill if the model calling song had the natural sound frequency spectrum of 4 to 5 kHz (even without the higher harmonics present in the natural song) and was organized in syllables (pulses) spaced between 25 to 55 ms intervals, reflecting syllable or pulse repetition rates between 18 to 40 Hz. No other intrachirp and interchirp parameters were critical, except that each syllable (pulse) had a critical duration of more than 200 usec (compared with 15 to 20 ms in the natural song) and the silent intrasyllable (intrapulse) pause had a critical duration of at least 4 ms (natural values ca. 10 to 15 ms). Even playbacks of natural calling songs in reverse did not prevent female phonotaxis, that is, the receiver did not discriminate the different amplitude modulation (chirp envelope) when played forward or backward. When given a choice between similar model songs, females always chose the one that was a few decibels louder. At equal intensity, calibrated close to the female's body on the treadmill, they meandered between the two loudspeaker positions (185° separation), indicating that they were unable to discriminate. Tone bursts of similar frequencies but without syllables (pulses) of natural chirp length and chirp repetition rate did not start females of *Gryllus campestris* walking, and they were not tracked at all. When the females were given a choice between them and 'pulsed chirps' they tracked the latter, even if the sound intensity in the former was increased. However, recently different results were obtained with females of *Gryllus bimaculatus* (Doherty in prep.) Here some clear burst trackers were found.

A rather surprising result was obtained with these chirping crickets: Some females tracked model songs built of continuous trills at their natural pulse frequency, duration and repetition rates. It appears as though the receiver may not always require the chirp organization of the song at least not under treadmill conditions (but see Stout et al. 1983).

This raises the question: Is the 'simplicity' of the template in the receiver related to the particular life style of *Gryllus campestris*? This mid-European species occupies habitats of hilly grassland where individuals are often rather widely spaced, especially toward the end of their reproductive season. No other species of *Gryllus* lives in this habitat in this area. Males call in front of their burrows between late April and early July at a time when no other insect is singing. Birds sing during this time, and they can be heard by crickets, but their most abundant predators are spiders, carabid beetles, lizards and shrews. It could be that the absence of sympatric species has facilitated the evolution of a rather simplistic template.

The species most closely related to *Gryllus campestris* is the southern-European *Gryllus bimaculatus*, which does not overlap with *G. campestris*. Their relationship is documented by the fact that they can be hybridized in the laboratory (v. Hürmann-Ileck 1957). Individuals of *Gryllus bimaculatus* live alone or in smaller groups and adults fly. *Gryllus campestris* adults are
flightless. Males of the two species produce nearly identical calling songs and females of *Gryllus campestris* on the treadmill don’t discriminate between them (Thorson et al. 1982). With simultaneous playback of the two natural songs from two loudspeakers (135° apart), nearly equalized in intensity, the females meander between the speaker positions as though faced with two conspecific songs (figure 5).

Fig. 5. Phonotaxis of female of *Gryllus campestris* (1, 2) and tracking of conspecific and heterospecific (*Gryllus bimaculatus*) songs (3, 4). A. Schematic view of the sound proof room with the spherical treadmill and a female cricket positioned on top carrying a reflecting foil on the pronotum (not visible). IR infrared sensing and detecting devices; x, y positions of motors which drive the sphere; L1, L2 positions of the two loudspeakers (135 degrees apart). B. Recordings of the females’ phonotactic behavior (tracking) when stimulated with model calling chirps (1, 2) or playbacks of natural calling sounds (3, 4). (1) *G. campestris* response to pulsed chirps (4 pulses per chirp at 5 kHz) and 5 kHz tone bursts of same total duration as the pulsed chirps in a sequential paradigm. The female tracks only pulsed chirps not tone bursts. Relative loudspeaker positions (L1, L2) are indicated by straight lines superimposed over the corrective meandering during playback of sounds, and their angular position is indicated left (range 0° to 360°); symbols above and below show signal from each speaker (L1 above, L2 below), line means no signal vs four pulsed chirps, or solid tone bursts. (2) *G. campestris* response with model pulsed chirps from the left then right sides followed by pulsed chirps and tone bursts presented in a choice paradigm, and followed by pulsed chirps from the left. The female always tracks pulsed chirps. (3) *G. campestris* response with natural conspecific calling song (indicated by c on the side from which it is played) and the similar calling song of *G. bimaculatus* (indicated by b, similarly) in a sequential paradigm. The female tracks both songs equally accurately, and without sound she circles (right). (4) *G. campestris* with the same natural sounds as in (3). First the conspecific song (c) is played on the right, then the left, then both songs simultaneously three times but changing sides each time, then the heterospecific song (b) on the left. When given a choice between conspecific and heterospecific calling song at nearly equal sound intensities the female is unable to discriminate between the two and meanders between the two loudspeaker positions. (A, B composed from Weber et al. 1981, and from Thorson et al. 1982).
Popov (Popov et al. 1974, 1975) reported that the two species overlap in some part of southern Russia. There the calling songs are heard at the same time of the day, but hybrids were not recorded in the field. This suggests that in sympatric populations of these species the templates become more specific. Popov tested individuals from areas of sympatry and found that females of *Gryllus bimaculatus* were less discriminatory with respect to the number of syllables (pulses) per chirp than those of *Gryllus campestris*. Our results obtained with mid-European *Gryllus campestris* (Weber et al. 1981, Thorson et al. 1982) contradict Popov’s findings with sympatric *Gryllus campestris* but confirm his results with *Gryllus bimaculatus*. Further field and laboratory studies are needed to establish the concept that sympatry may sharpen the templates.

Crickets are poikilothermic and their body temperature follows ambient temperature. As first shown by Walker (1957) ambient temperature effects the syllable (pulse) repetition rate in trilling and chirping tree crickets (mostly *Oceanthus* spp.): it increases with increasing temperature. Similarly, in chirping crickets of the genus *Gryllus* both syllable (pulse) and chirp repetition rate change with temperature (Kriechbaum 1983, Doherty and Huber 1988, Doherty in press). Therefore, we became interested in temperature effects on female phonotaxis in order to get some insight into temperature coupling between sender and receiver. Females of *Gryllus bimaculatus* were acclimated to either 15°C, 22°C or 30°C in an incubator, and then tested on the treadmill for phonotaxis in the equally-acclimated sound-proof room. A computer-controlled program of model calling songs with different syllable (pulse) and chirp repetition rates and durations was delivered. As shown in figure 6, ‘cold’ females (15°C) shifted their preference to lower syllable (pulse) repetition rates, and ‘hot’ females (30°C) preferred higher syllable (pulse) repetition rates. These results may indicate that sender and receiver are temperature-coupled in *Gryllus* as well as in *Oceanthus*, that is, that mechanisms for song generation in the sender and those for recognition in the receiver are influenced by temperature in a similar way. How such effects are achieved within the nervous system remains to be discovered, and we need much more information on the nature of sounds produced and responses elicited at different natural temperatures throughout the ranges of several species of crickets.

b. Neurobiological approach to phonotaxis

Song recognition and sound source localization, both expressed in the phonotactic behavior of crickets, require auditory organs capable of airborne sound perception. In crickets and katydids auditory organs are located in the proximal part of each fore tibia. In crickets each ear contains 50 to 60 receptor cells arranged in a row along the crista acustica (Eibl 1978), and as recently demonstrated by Oldfield (1982, in prep.) in an Australian katydid, such an arrangement reflects a peripheral tonotopic organization. Each receptor within the whole organ is tuned to a certain sound frequency, and behaviorally important frequencies may even be represented by more than one receptor. The receptor cells are in close contact with the inner wall of the ‘acoustic trachea’, a sound conducting pathway (Kleindienst et al. 1981), which itself has close contact with the larger posterior tympanum. The smaller anterior tympanum in crickets is underlain by a thicker sheath
Fig. 6. Temperature dependent phonotaxis in females of *Gryllus bimaculatus* with model chirped sounds. Ordinate: % of female tracking time per stimulus time; abscissa: Sound pulse rates (SP), ranging from 20 to 90/1000 secs (11 to 50 pulses or syllables/sec). Open triangles are mean values for several females that tracked at 15°C (chirp period 700 msec), open squares are mean values for several females that tracked at 22°C (chirp period 500 msec), open circles are mean values for several females that tracked at 30°C (chirp period 350 msec). Hatched bars at the bottom diagram proportionate syllable interval periods for the natural males' songs at the listed temperatures (modified from Doherty, in press).

...of cells and is not in direct contact with the acoustic trachea and the receptors. However, both tympana add to hearing (Huber et al. in press), but most effective is the posterior tympanum (see Larsen and Michelsen 1978). Airborne sound reaches the tympana directly from the outside and the posterior tympanum also from inside via the acoustic trachea that connects to a spiracular opening in the prothoracic-mesothoracic body wall. Sound induced oscillations of the tympana are required for hearing (Kleindienst et al. 1983, Huber et al. 1984). These oscillations depend on sound pressure differences and phase differences of the sound waves impinging on the tympanum from both sides (Hill and Boyan 1977, Kleindienst et al. 1981, 1983). Such a 'pressure gradient receiver' (Michelsen and Nocke 1974) can be considered as a novel evolutionary design in animals with small body sizes whose behaviorally relevant sound waves are proportionally much greater in length relative to overall body length than for large vertebrates, and whose diffraction by the body is therefore minimized.

Female *Gryllus* with one auditory organ destroyed are still able to 'recognize' their conspecific song. In the field (Klopflleisch 1973) and on the treadmill (Huber et al. 1984) they begin to walk as soon as a normal calling song is broadcast. They generally circle toward the side of the intact...
ear according to the rule 'turn toward the ear most strongly stimulated'. During this circling they also exhibit short episodes of tracking with typical meandering, however, at an unexpected erroneous angle with respect to the sound source. This meandering is thought to be associated with 'lateralization' or 'binaural comparison' (Rheinlaender and Blätgen 1982) in two-eared crickets. But peripheral binaural comparison is not available in one-eared crickets, so the persistence of meandering in one-eared crickets demands a new evaluation of the assumptions and data regarding the underlying mechanisms of meandering (Huber et al. in 1984).

Females who lose a foreleg during postembryonic development, even if subsequently regenerated, lack both tympana on a regenerated leg. Histological examination shows that within this leg the tracheal organization and the auditory receptor arrangement necessary for audition are also missing. Nevertheless, these females track calling songs nearly as precisely as those with both ears intact (Huber et al. 1984). There is no doubt that binaural information normally guides the female most correctly to the singing male; but even with monaural input some form of localization remains. Phonotactic orientation in one-eared females is even 'improved' after an initial period of monaural hearing deficit. This points to previously unrecognised plasticity within the auditory pathway.

In a search for the neural mechanisms underlying sound source localization, especially conspecific song recognition, we first turned our attention to the functional capacity of the ears. When recording from single and partly identified auditory receptors at the axonal level we found some axons 'tuned' (i.e. most sensitive) to the calling song sound frequency spectrum of 4 to 5 kHz (figure 7), others tuned to the courtship song sound frequency spectrum of 13 to 16 kHz, and still others sensitive to a broader range of frequencies (3 to beyond 30 kHz) (Esch et al. 1980, Hutchings and Lewis 1981). Thus, the spectral domain of the cricket ear is not just designed for intraspecific demands. It also has the capacity to perceive sound signals outside the range produced by that species such as songs of other species or sounds emitted by predators, sometimes even hunting bats (Popov and Markovich 1982). Indeed, negative phonotaxis (interpreted as avoidance) was reported in Teleogryllus by Moiseff et al. (1978) and by Pollack and Hoy (1981).

Bioacousticians discovered rather early that many cricket species, even those living sympatrically, emit calling songs comprised of a narrow band of carrier frequencies within a rather limited overall range of sound frequencies, usually between 2 and 7 kHz (Popov et al. 1974). The small overall range may be associated with the biomechanical properties of the wings that radiate sound (Michelsen and Nocke 1974). This prospect raises the question: Is the ear able to discriminate sound frequencies within this overall narrow band? The best example known to us is that of the two partly sympatric species, Teleogryllus oceanicus and commodus. Males of T. oceanicus call in the range of 4.2 to 4.7 kHz, those of T. commodus in the range of 3.3 to 3.7 kHz (Hill 1974). Their sound spectra are separated by only 300 to 500 Hertz. Hill (1974) showed by behavioral studies that females can discriminate model songs that differ only by these frequencies.

One mechanism by which discrimination of sound frequencies can be improved beyond that already available at the receptor level involves
Fig. 7. Song encoding capacities of one primary auditory fiber in females Gryllus campestris, and central projections of that fiber. A. Model chirps with 4 pulses (syllables) at three different sound pressure levels (upper traces) and responses of the same single identified primary auditory fiber tuned to 4.5 kHz (lower traces), recorded semi-intracellularly. Its threshold curve is shown in the inset of B. Note that this fiber copies the sound pattern by bursts of nerve impulses, and encodes sound intensity by an increasing number of spikes per burst, and by slightly increasing spike frequency. B. Left half of the prothoracic ganglion seen in the horizontal plane with the central part of the auditory fiber stained with the fluorescent dye Lucifer yellow. The terminations of the fiber cover the area called the auditory neuropile. AC, PC, anterior and posterior connectives respectively; ML, midline of the ganglion; LN, prothoracic leg nerve that contains the bundle of 55 to 60 auditory fibers (modified after Huber 1983).

'sharpening the tuning' (narrowing the sensitivity range) of neurons by side-band inhibition. Sound frequencies outside the best excitatory frequency of the cell elicit an auditory input to the cell which has an inhibitory effect. Side-band inhibition was demonstrated in cricket auditory pathways using two-tone stimulation techniques and by recording from identified central auditory neurons (Boyan 1981, Oldfield and Hill 1983, Hutchings and Lewis 1984, Boyd et al. 1984). Thus, cricket auditory pathways are in principle capable of discriminating sounds which differ in pitch by a few hundred Hertz. It is quite possible that such a mechanism—which deserves studies at the network level—not only has evolved in interspecific contexts separating
mate selection from predator avoidance, but also in the context of individual song differences as in male/male aggressive signals etc. (Alexander 1961, Lloyd 1980b).

The following discoveries, probably of adaptive significance, should be evaluated in this context. In females of *Gryllus bimaculatus*, Boyan (1980, 1981) recorded and identified central neurons in the brain that were tuned best to the conspecific courtship song carrier frequency (figure 8). When the female’s ear was stimulated simultaneously with two tones, these neurons exhibited a clear suppression of synaptic potentials and spike responses to the courtship song frequencies if the second tone was near the calling song carrier frequency.

An example of behavioral correlate in a field situation is that females approaching a calling male by phonotaxis receive only input from receptors tuned to the 4 to 5 kHz band at a distance, because the song’s sound energy is greater in this band and is less attenuated by the surrounding vegetation (Popov et al. 1974). Upon closer approach the ear will also receive higher harmonics of the male’s call (8 to 10 or 15 kHz). Some auditory receptors are also tuned to lower and higher sound frequencies in addition to middle ones; when close to the male the high frequency pathway is activated in addition to the low frequency pathway, though less so because of the lower energy of the higher harmonics. On the treadmill, when stimulated with model calling songs of the natural pattern but at carrier frequencies higher than 8 kHz, females tracked the sound source with an “erroneous” angle as though they were orienting to a male at a location other than the speaker (Thorson et al. 1982). This angle is carrier frequency dependent and has a value of more than 90 degrees at frequencies above 12 kHz. Such frequencies are present in the male’s call when a female has approached closely. Since we never observed a change in the phonotactic course in the field, it is reasonable to postulate that a suppression of responses in neurons sensitive to these higher frequencies which mediate “erroneous” angle tracking—or even negative phonotaxis—improves the accuracy of phonotaxis and is of adaptive significance, and/or is overridden by tactual, visual, or chemical cues at such close ranges.

Bioacousticians have further shown that calling songs of different species could easily be discriminated by their different temporal pattern, including intra- and interchirp parameters (Alexander 1961; Popov et al. 1974, Otte and Alexander 1983). At the level of the ear, electrophysiological recordings provide no clear-cut evidence of a species-specific temporal tuning of auditory receptors. In other words, none of the 50 to 60 auditory sense cells responded preferentially or exclusively to the conspecific pattern. Instead, the receptors copy in their impulse discharge all kinds of patterns, including chirps and trills, bird songs, and tones as well as other environmental noises broadcast within their relatively broad sensitive range. In the temporal domain, then, the ear is designed to fit intraspecific demands; however, the acoustic channel is open also for interspecific interactions.

Searching for ‘temporal template properties’ in the central neurons requires an experimental strategy which is based upon results of behavioral studies such as those reported earlier. We may discover neurons tuned to conspecific song carrier frequencies that in addition encode the rhythm
Fig. 8. Local brain auditory interneuron response suppression in females of *Gryllus bimaculatus*. A. Right half of brain viewed from front with camera lucida drawing of the interneuron inside (IN); NC, cell body; arrow points to intracellular recording site; ON, lateral ocellar nerve; OT, optic tract; AN, antennal nerve; CEC, circumesophageal connective. B. Suprathreshold response of the neuron in the range of 2 to 20 kHz, equal sound pressure levels, with optimal response to the sound frequency band of the courtship song (COS) and a much weaker response to the band of the calling song sound frequency spectrum (CS); points on curve represent means, bars standard deviations. C. Response to an artificial courtship sound alone and with a second lower frequency sound played simultaneously at different intensities. The neuron is first stimulated with a control-tone (CT, 15 kHz, dashed line = 100% of response) in the range to which the cell is optimally responsive. Subsequently adding a tone of either 1 kHz (closed circles) or 10 kHz (open circles, upper curve) only weakly suppresses the response relative to that at 15 kHz; however, if the added tone (TT) is 5 kHz (in the range of the carrier frequencies of the calling song, open circles, lower curve) the response to 15 kHz is significantly suppressed especially at increasing intensities of the TT. CT, control tone only; CT = TT, sound intensities of CT and TT are equal; TT+5, +10, +20, TT was delivered with 5, 10 or 20 dB higher intensity than the CT. With TT+20 db at 5 kHz, mimicking the natural situation, the response to 15 kHz is reduced more than 80% (modified after Buyau 1981).

pattern of that conspecific song. Only then can we call such neurons part of the 'recognizer template'.

We started our experimental strategy within the prothoracic ganglion and continued toward the brain. Using intracellular recording and marking
Fig. 9. Morphology and physiology of the prothoracic intraganglionic Omega-neuron in *Gryllus campestris* females. A. Lucifer yellow fill of one member of the mirror-image pair of the Omega-neurons type I. The faint autofluorescent stripe in the middle marks the midline of the prothoracic ganglion. IPSI, the half of the ganglion where the neuronal cell body, neurite and ipsilateral field of arborizations are located (input area of the neuron); CONTRA, axon traversing from ipsilateral to contralateral side of the ganglion and terminating in the contralateral field of arborizations (output area of the neuron). B. Response of the neuron to monaural stimulation by a model calling song with a central carrier frequency of 5 kHz at 80 dB SPL, of 4 chirps. CB IPSI, patterned discharge of burst of nerve impulses riding on top of depolarization waves with ipsilateral stimulation, each burst reflects the response to one syllable (pulse). CB CONTRA, contralateral stimulation shows syllable related inhibitory postsynaptic potentials (downward directed deflections). BOTH, binaural stimulation (input from both ears simultaneously) gives patterned discharge bursts with a slight reduction in the number of impulses per burst due to contralateral inhibition. These recordings were obtained intracellularly at the input region of the neuron (modified after Wohlers and Huber 1982).

of neurons with the fluorescent dye Lucifer yellow (see figures 9 and 10) we delimited a family of mirror-image nerve cells which responded to the calling song stimulus (Wohlers and Huber 1978, 1982). Among them were several cells tuned to the carrier frequency of 4 to 5 kHz that repeated the pulse and chirp rates by bursts of nerve impulses, figures 9 and 10. One pair of cells, called Omega-neurons (figure 9), forms a two cell network
Fig. 10. Morphologies and responses of two types of plurisegmental ascending prothoracic auditory interneurons in *Gryllus campestris* females. A. Lucifer yellow fill of one member of the mirror-image pair of the ascending neuron type I (AN1); seen in the horizontal plane with cell body, neurite crossing the ganglionic midline, and densely packed arborization field with axon passing to the head ganglion on the contralateral side. B. Lucifer yellow fill of one member of the mirror-image pair of ascending neuron type II (AN2); seen in the horizontal plane with cell body, thin neurite which crosses the ganglionic midline and arborizes in the larger dendritic field that extends to the entrance of the auditory nerve, and with axon passing to the head ganglia on the contralateral side. In both A and B the autofluorescent stripe marks the midline (ML) of the prothoracic ganglion. C. AN1 is tuned to the calling song carrier frequency in the range of 4 to 5 kHz, as seen by the threshold curves (solid and dashed lines). It copies the syllable pattern within each calling chirp with high fidelity at all sound intensities, as seen in the poststimulus response pattern histogram. Each single histogram correlates to one syllable of the four pulses (syllables) at 4.5 kHz and 70 dB SPL. D. AN2 is more broadly tuned and sensitive below 60 dB SPL in the range between 3 and 16 kHz, as seen by four threshold curves (solid lines). The response pattern histogram is shown also and documents that AN2 copies the calling chirp as a whole. Stimulus was presented with 5 kHz, 4 pulses and 70 dB SPL. Threshold curves in C and D: Ordinate, sound intensity in dB SPL to elicit a response just above threshold; abscissa, sound frequency range covering 2 to 16 kHz. Histograms in C and D: Ordinate, number (n) of nerve impulses (spikes) sampled consecutively for each 2 ms time period during a stimulus series of 20 model calling chirps; abscissa, time in msec where 0 means onset of the first syllable (pulse) of the chirp. (A, B, modified after Wohlers and Huber 1982; C, D, modified after Stout and Huber 1981).

with reciprocal inhibition (Wohlers and Huber 1978, 1982; Silverston et al. 1985). Each cell receives excitatory input from only one ear and is inhibited by input from the other ear conveyed by the mirror-image partner cell. Since the terminals of the primary auditory fibers end within the prothoracic ganglion in what is called the ipsilateral neuropile, with no
crossing to the contralateral side, binaural reciprocal inhibition by the Omega-cells is one mechanism by which a cricket may enhance directional information processing in the calling song range (Kleindienst et al. 1981). In principle, such a network is also able to assist pattern recognition (Wiese 1978, 1983, 1984), if the dynamic properties of the network are such that only phonotactically effective patterns are copied and transmitted with fidelity. Recently, Selverston et al. (1985), killed one Omega-cell in female crickets by photoinactivation, and thus withdrew it from the interaction network. Under these conditions the remaining Omega-cell received and transmitted excitatory input from 'its ear' but the inhibitory input from the contralateral ear was missing. With another single test on our walking compensator a female with one Omega-cell killed was expected to change direction finding during phonotaxis, because a part of binaural comparison was lost. This female exhibited clear and precise tracking of the sound source before Omega-cell killing, and after killing showed only a slight asymmetry in tracking to the expected side of the intact Omega-cell. We have a hint, but many more such behavioral experiments are needed to draw firm conclusions.

Two other pairs of mirror-image central neurons with axons ascending to the brain (figure 10) are particularly interesting in our context of song recognition. One pair, the AN1 type cells, are best tuned to the calling song carrier frequency and copy the natural song pattern at all intensities. Each member of the pair receives auditory input from only one ear, from the ear whose primary auditory fiber terminals overlap with the dendritic field of the AN1 cell. It is conceivable that this cell is involved in one-ear song recognition, however, it can not be called an intrinsic element of the 'recognizer template' because it is not selectively tuned only to the pattern of the conspecific song (Stout and Huber 1972; Schildberger 1984). Another pair of ascending neurons—AN2 type cells——(figure 10) is equally or more sensitive at higher sound frequencies and responds to the calling chirp with a rather continuous discharge of impulses throughout the whole chirp. This neuron does not copy the pulse repetition rate but encodes the chirp rate. It could play a role in those females which track bursts, as well as function in negative phonotaxis and in avoidance of predators.

There are several possibilities for the manifestation of a 'recognizer template' at the neural level. Perhaps there are neurons present at higher levels of the auditory pathway that are tuned to the conspecific temporal pattern and thus reflect phonotactic demands, or the template may be more widespread, perhaps laid down in a multiganglionic network, which due to cooperation of its members represents the 'recognizer' etc. We favor the first possibility because very recently Schildberger (1984) identified a class of brain neurons that showed a clear correlation in their response (evaluated by the number of spikes per chirp) to the phonotactically effective range of pulse repetition rates. These neurons have band-pass properties and it is such a class of brain cells which we consider at present to be the most intimate part of the 'recognizer template' (figure 11).

Further studies will show how these brain neurons are connected to each other within the auditory pathway, and how their band-pass properties are achieved. We expect to unravel mechanisms at the cellular and synaptic levels that provide a basis for temporal tuning, and furthermore, to get
information about how these neurons elicit walking and orientation characteristics known to be present in phonotaxis (Weber et al. in prep., Stout et al. in prep.). On a longer scale, other questions can be attacked. For instance, are the neurons providing the substrates for recognition affected by temperature in much the same way as shown for phonotaxis? Are there sex-dependent similarities and differences, including temperature matching within sender and receiver? Is temperature matching merely a function of chance and eventual close proximity? A further step may even deal with 'trade-off' phenomena recently studied in phonotaxis of Gryllus bimaculatus (Doherty in prep.) with the outcome that at the limits of effective neural functional ranges different temporal parameters are weighted by the females. We finally hope to contribute as neurobiologists to bridging the gap that still exists between us and behavioral ecologists in this most fascinating field of communication strategies.

CONCLUDING REMARKS

I have tried to outline mutual interests and ways for future cooperation between behavioral ecologists and neurobiologists by discussing examples of adaptive behaviors and the present state of knowledge concerned with their neural bases. What the reader should understand is that the time has come when these two fields would greatly benefit from cross talk and cooperation with each other. Insect neurobiology has yet a rather limited influence on insect behavioral ecology because many of the behavioral strategies studied by ecologists are too complex to be attacked by neurobiologists with the present day technical know how and expertise. But this will change as neurobiologists become better able to study behaviors at the neuronal level in freely moving animals, and important beginnings in this were made during the last decade (Huber 1983 a,b).

But there is still another reason for the existing gap between behavioral ecology and neurobiology, which is of mental origin. There is a limited cross-talk between the two groups, too little "looking across the fence into each others flowering garden". We must experience each others problems, must find a common language to discuss possible ways to solve them, and no longer only step side by side. One way toward this desired goal is for neurobiologists to try to become apprentices in behavioral ecology, and, vice versa, behavioral ecologists should not hesitate to dive a bit deeper into the pond where neurobiologists play. This needs patience and open minds on both sides.

What behavioral ecologists and evolutionary biologists could perhaps gain from neurobiologists—aside from the problems they are interested in—is to learn to look for tactics that can be used experimentally to make predictions which can be falsified or verified. At present, neurobiologists are confronted with and suffer from a plethora of speculations and hypotheses formulated by behavioral ecologists, often without a thought for an experimental solution. On the other hand, what neurobiologists could gain from behavioral ecologists is to become open to the diversities in strategies and tactics animals have evolved, and to be confronted with field work and the comparative method. Then perhaps we can all gain a closer understanding of the real biological questions. This is a big challenge for both, let's start.
Fig. 11. Temporal selectivity of brain neurons in females of *Gryllus bimaculatus* in relation to song recognition, and generalized phonotactic tracking range for both *G. bimaculatus* and *G. campestris* (hatched area). Upper: Diagram of model calling chirps (arranged vertically), chirp energy equal (nearly equal length of chirps, chirp repetition intervals 500 msec). Within each chirp the duty cycle was kept 50%, that is the individual syllable (pulse) durations were equal to the intersyllable (interpulse) durations. The model chirps were presented at 5 kHz and 80 dB SPL. They differed in the number of syllable (pulses) per chirp (from 25 at the left to 3 at the right), in syllable (pulse) duration (length of the black bars) and intersyllable (interpulse) duration, and most importantly in syllable (pulse) repetition interval (ranging from 8 to 98 msec). Lower: Phonotactic response range (hatched area) of females to these chirps (listed above). 100% = maximal phonotactic (right ordinate) or maximal neuronal response (left ordinate in terms of spikes recorded from any female per chirp duration). The phonotactic range was replotted from Thorson et al. 1982, and from Doherty in prep. Superimposed on the hatched area are data points that represent responses of identified brain neurons. Open and closed triangles represent recordings from brain neurons that respond maximally to short syllable (pulse) repetition intervals (range 8 to about 50 msec.
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with above 75% response), open and filled squares represent recordings from neurons that respond best to longer syllable (pulse) repetition intervals (range 34 to 98 msec above 75% response). Open and filled circles represent neurons that match in their response most closely the range of phonotactically effective syllable repetition intervals (26 to 60 msec above 75% response). Each symbol at every syllable (pulse) repetition interval is a data point from a different animal. Chirp diagrams lie directly above their proportionate syllable (pulse) repetition intervals (after Schildberger 1984).


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