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The tuning of moth ears

J. H. Fullard

Department of Zoology and Erindale College, University of Toronto, 3359 Mississauga Road, Mississauga (Ontario, Canada L5L 1C6)

Summary. The simple ears of months have responded evolutionarily to the varied levels of selection pressure exerted upon them by insectivorous bats. While frequency-matched (syntonic) bats exert the primary pressure that determines where a sympatric moth's best frequency (BF) lies, there are bats that echolocate in mismatched (allotonic) bandwidths forming selection pressures strong enough to warrant increased secondary sensitivity at these frequencies. It is unknown what neural mechanism is used by these insects to broaden their audiograms but for some neotropical moths, external hearing aids provide a mechanical means of obtaining this sensitivity. Recent studies have uncovered social uses for auditory systems in certain moths and these requirements may provide additional selection pressure. Auditory conditions exist in certain moths that should provide a means to study the evolution of this sensory system from its mechanoreceptor origins to its degeneration in the absence of bat predation.

Key words. Moth auditory characteristics; defensive behaviour; bat echolocation frequencies; predation pressure; evolutionary adaptation.

Introduction

Most moths possess ears that alert them to the echolocation calls of hunting bats[29,30]. Although simply designed, they provide the moth enough information about the bats in their environment to allow these insects a considerable advantage in staying alive[31].

Bats (Chiroptera) are the world's second largest order of mammals with over 900 described species and co-incident with this taxonomic diversity is a wide array of echolocation designs. Bats employ specialized forms of biosonar to accomplish their nocturnal tasks and there are specific relationships between their echolocation cells and foraging ecologies[3,7,14,24]. Many bats are insectiovorous and the various communities of these predators around the world present considerably different selection pressures on moths. If the ears of moths are specifically tuned to the calls of bats, these pressures should be reflected in their auditory designs[13].

There are three lines of evidence that support the assumption that bat predation forms the main selective force on moth ears. First, moths, with some exceptions[1,19,32,34], do not produce sounds (and therefore do not require ears) during their social interactions. Moths that use social sounds belong to geographically and taxonomically distant groups, and acoustic intraspecific communication likely represents a secondary adaptation for ears. Second, the neural simplicity of moth ears differs from those used for social communication. The multineuronal ears of Orthoptera appear to function in frequency discrimination[22,26], a superfluous task for moths concerned only with detecting the presence of bats. Of interest in this regard is *Teleogryllus oceanicus*, a cricket that apparently uses a single interneuron for bat-detection[23]. Third, bats form the only source of nocturnal sound with frequencies matched to the sensitivities of moths' ears. For instance, figure 1 illustrates the spectra of sounds that could be construed to influence moths and indicates that bats alone generate the frequencies that moths are best able to hear.

Moth ears and defensive responses

Lepidoptera are either deaf or have independently evolved ears according to their superfamilial affiliation (table), a rule that has held, to date in all areas studied (nine countries, four continents). Although ears provide an effective anti-bat defence, the table suggests that not all Lepidoptera have adopted this particular strategy. The ear of a moth represents the

The anti-bat defensive behaviours (studied and speculated) of some Lepidoptera. Primary defence[27] refers to actions taken before a bat is aware of the moth's presence while secondary defences occur after the bat begins active pursuit.

Superfamily	No. auditory receptors	Defensive behaviours Primary	 Secondary
Papilionoidea	0 (?)	Diurnal flight	(not required)
Hesperoidea	0 (?)	Diurnal flight	(not required)
Cossoidea	0 (?)	Reduced flight (?)	Large size (?)
Bombycoidea	0	Reduced flight (?) Flight close to ground (?)	Large size (?)
Notodontoidea[a]	1	Negative phonotaxis	Evasive flight
Noctuoidea	2	Negative phonotaxis	Evasive flight Sound production[b]
Geometroidea	4 (?)	(?)	(?)
Pyraloidea	4 (?)	(?)	(?)
Sphingoidea[c]	(?)	(?)	Evasive flight

[a] Superfamilial status unclear, some authors place into Noctuoidea.
[b] Only in certain Arctiidae.
[c] Only in certain species.
(?) unknown or putative.

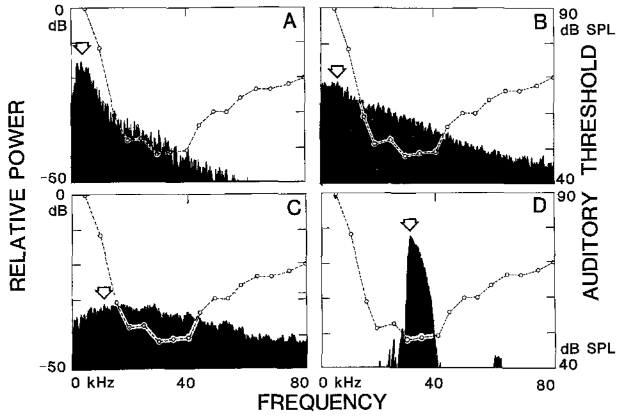

Figure 1. The spectra of sounds suggested to influence the ears of moths. *A* Breaking twigs (oak); *B* rustling leak litter (oak and maple); *C* crackling underbrush (various grasses); *D* echolocation call of the big brown bat. The median audiogram accompanying each average spectrum is taken from a sample of 52 sympatric noctuoid moths. The peak frequencies of each spectrum are indicated by arrows.

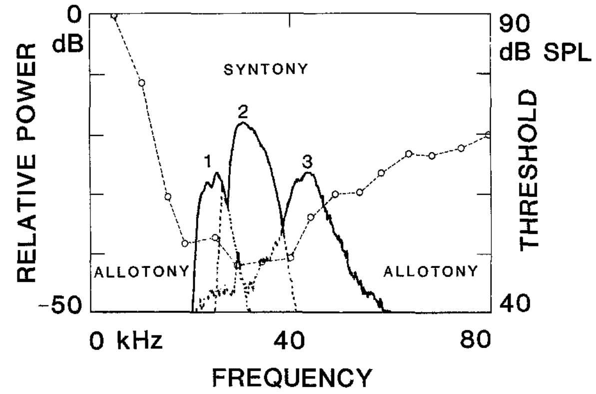

Figure 2. A closer examination of the acoustic relationship between moth ears and bat echolocation calls. The median audiogram of 52 Nearctic noctuoid moths is plotted against the average echolocation spectra of three common sympatric bats (1 – *Lasiurus cinereus*; 2 – *Eptesicus fuscus*; 3 – *Myotis lucifugus*). This figure suggests that moths are influenced not by individual bat species but by the echolocation assemblage (outlined in bold) of their sympatric predatory community.

ultimate in sensory simplicity with only one, two or four auditory receptor cells (A_1–A_4). As a result of this neural economy, moths cannot discriminate frequencies and depend solely upon their ears' temporal resolving powers to detect bats. Moth auditory threshold curves (audiograms) indicate their most sensitive receptor (A_1) is broadly tuned with low Q_{10dB} values[9, 33] and a best frequency (BF) at 20–50 kHz (fig. 2). Frequencies within (i.e., matched to) the moth's BF are termed syntonic while those outside of the BF (i.e., less detectable) are called allotonic. In the absence of additional receptors selection has molded the moth's ear to certain frequencies that it needs to hear best.

Auditive moths use the information transmitted to their central nervous systems (CNS) to mediate a graded series of responses (table). There have been numerous studies on the sensory physiology of moth ears but little is understood of the neural circuits that underlie the defensive behaviours these structures initiate. Recent work on the CNS auditory processing in the tobacco budworm moth, *Heliothis virescens*[6], has now provided a model for these circuits. Regardless of how these interneuronal pathways operate, the moth must rely upon a scant peripheral nervous complement for activating its defence. For this paper, I assume that negative phonotaxis accounts for a moth's greatest survival (cf. Roeder[28]) and it is, therefore, the physiological characteristics of its most sensitive auditory receptor, the A_1 cell, that determines the moth's main chances of staying alive.

Sensory ecology of moths and bats

In areas of low bat diversity (e.g., Canada) the range of echolocation frequencies that moths are exposed to covers a comparatively narrow bandwidth. By contrast, the bat faunas of equatorial regions emit considerably more echolocation frequencies that sympatric moths must contend with[25]. Figure 3 compares the median audiogram of a sample of moths from southeastern Ontario to that of moths from a site in tropical western Zimbabwe and indicates that African moths have ears significantly more sensitive to all frequencies tested (5–110 kHz). I suggest that increased sensitivity in African moths is a result of their requiring ears more broadly tuned to the greater bandwidth of echolocation frequencies they must detect to stay alive.

Although threshold differences exist, figure 3 illustrates that the moths' BF's are similar in both sites. BF convergence may be due to the fact that physical constraints (e.g., atmospheric attenuation[18, 20]) place limits on the lowest and

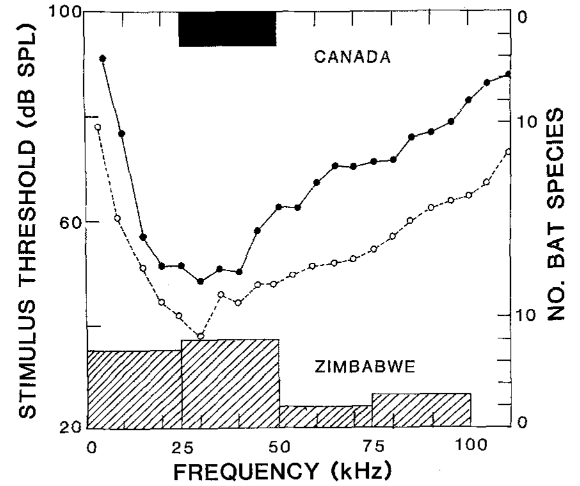

Figure 3. A comparison of the median audiograms of a sample of North American (eastern Canada) and African (western Zimbabwe) moths in response to the diversity of bats (commonly captured species) they are sympatric with. Although in both sites most bats echolocate at 25–50 kHz, Zimbabwe differs from Canada in possessing echolocation frequencies considerably above and below this bandwidth. Zimbabwean moths respond to their greater selection pressure with more allotonically sensitive ears.

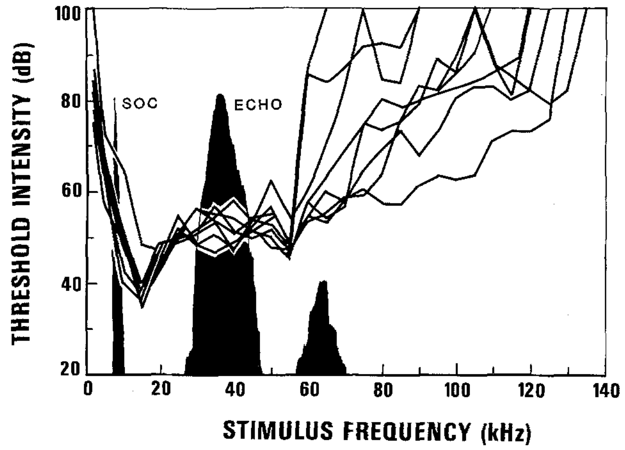

Figure 4. The auditory response of the Kauaian noctuid moth, *Elydna nonagrica,* to the sounds emitted by its sole chiropteran predator, *Lasiurus cinereus semotus.* The audiograms of all individuals examined are plotted against the spectra of this bat's social (SOC) and echolocation (ECHO) signals. The moths' audiograms reveal their highest sensitivities and lowest threshold variabilities at frequencies syntonic to the bat's vocalizations.

highest frequencies that can be used in echolocation. As a result, most bats (particularly those that require long-range resolution) have congregated their calls around the favoured bandwidth of 20–50 kHz and this is where the average moth has evolutionarily tuned its BF. Although BF's are similar in different habitats, the presence of allotonic bats accounts for the greater sensitivity in moths exposed to diverse bat faunas such as those found in Africa. Unable to discriminate frequencies, it is unlikely that moths identify particular species of bats when they hear them. Instead, moths should react to sympatric assemblages of predatory bats as represented by their echolocation frequencies[9] (fig. 2). The frequency spectrum of a predatory assemblage includes all the echolocation sounds emitted by moth-feeding bats and represents both primary and secondary predators. The relative impact of individual bats on the audiograms of sympatric moths depends on their particular level of selection pressure and the echolocation frequencies that correspond to this pressure. Increased auditory sensitivities in African moths such as those illustrated in figure 3 occur at bandwidths where lepidoptivorous bats emit allotonic echolocation frequencies (e.g., *Hipposideros caffer* (150 kHz)[8]. One does not need to compare moths from such ecologically distant areas to detect auditory differences. Within a Nearctic zone, western Canadian moths are more sensitive than their eastern counterparts[16] due, we believe, to the different echolocation assemblages of the two areas.

Since ears allow for increased survival, it is expected that moths will exploit any acoustic cues that warn of hunting bats. Not all of these signals, however, need be bat biosonar. Figure 4 illustrates the audiograms of a sample of noctuid moths from the Hawaiian island of Kauai audiograms differ from those of Nearctic and African moths in increased low frequency (5–15 kHz) sensitivity. There is only one bat species on Kauai that these moths face, the Hawaiian hoary bat (*Lasiurus cinereus semotus*), a lepidoptivorous species and it is only the sounds of this bat that will influence their ears. From the audiograms of figure 4, I suggest that Kauaian moths may listen not only for the 29 kHz echolocation call of the hoary bat but also the 10 kHz agonistic vocalization it emits while repelling intruding conspecifics[5]. Since the agonistic chirp is regularly heard from aggregations of hunting bats, I suggest that the moths of Kauai may 'eavesdrop' on the social activities of *L. c. semotus* and use the sounds emitted during its aggressive interactions to avoid predation. The heightened allotonic sensitivities of African and Hawaiian moths are examples of an echolocation assemblage's effects on the audiogram characteristics of sympatric moths. An assemblage that accurately represents the selection pressure on moths must include information about the relative population levels and dietary preferences of the bats that comprise it. A community of strictly frugivorous bats may present a definable echolocation assemblage but the actual selection pressure confronting sympatric moths is nil since none of these bats prey on moths. Quantifying the selective impact of an assemblage, however, is not simple given the diversity of bats' foraging habits and diets[4,17,24].

The neotropical island of Barro Colorado (BCI) in Panama has 56 known species of bats, 38 of whose echolocation calls we have recorded. The individual frequencies of these bats range from 40 kHz to 106 kHz[15] and their foraging and dietary characteristics are equally diverse[4,17]. By combining the frequency spectra of all the species recorded on BCI, it is possible to construct a total habitat echolocation assemblage (fig. 5)[15]. This spectrum represents the acoustic output of all the island's 38 recorded species without regard to their relative population levels or dietary preferences. By limiting this composite spectrum to the calls of only lepidoptivorous species (fig. 5), a new spectrum is created with its peak more closely matched to the ears of sympatric moths. This spectrum further predicts that the frequencies maximally influencing the ears of moths (i.e., primary selection) fall in the range of 30–60 kHz. Frequencies above or below this will affect moths less but if these allotonic pressures are sufficiently intense we should see audiograms reflecting increased secondary sensitivities. One adaptation to such pressures is seen in two BCI notodontids, *Antaea lichyi* and *Hapigia curvilinea*[11]. These moths possess external auditory modifications resembling pinnae and when these structures are interfered with the moths' sensitivities are reduced to frequencies above 70 kHz. Playback experiments with pre-recorded echolocation calls of sympatric bats indicate that the structures provide a selective advantage for these moths by increasing their secondary sensitivities to certain allotonic lepidoptivorous bats in the family, Phyllostomidae[12].

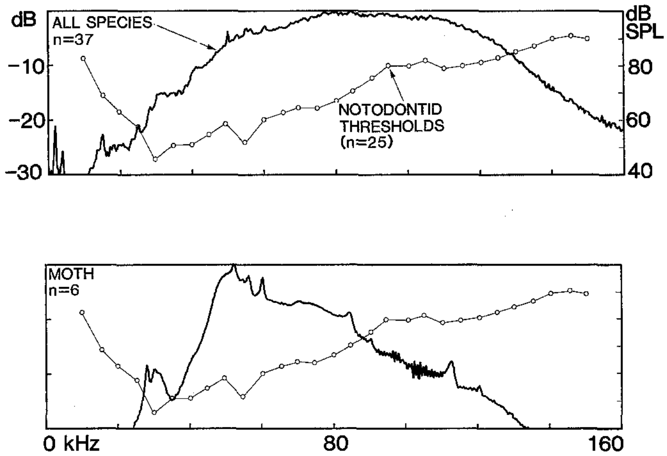

Figure 5. The hypothetical frequencies that influence the ears of Panamanian moths. Top: The composite spectrum of all the bats recorded on Isla Barro Colorado (total habitat echolocation assemblage). If moths were listening for all of the bats in this habitat, their audiograms (represented by the median audiogram of 25 notodontid moths) would be syntonic with this sectrum. Bottom: The echolocation assemblage spectrum of those species that feed heavily on moths. This spectrum represents the habitat's pertinent predation pressure and is more closely matched to the moth's audiogram.

The escape from bat predation

Islands form suitable regions for testing the prediction that an absence of bats will result in moth auditory degeneration. Two conditions must exist for this to occur, however. First, there must be sufficient reduction in bat predation pressure and second, the island must experience enough genetic isolation for the radiation of endemic moth species uninfluenced by bats. This hypothesis was first tested on the extremely isolated island of Kauai (endemic moth fauna = 79% of total[38]) since I initially believed that its simple bat fauna would have resulted in a sufficiently decreased predation pressure to produce deaf moths[10]. The presence of neurally responsive ears in Kauaian moths combined with field observations of their defensive reactions to attacks by the bat, *L. c. semotus*[5] confirmed that even a one-species bat fauna can exert enough pressure to warrant the retention of adaptively functional auditory defences in sympatric moths. To further simplify the effects of bat predation, Surlykke[33] studied the auditory characteristics of moths from a reputedly bat-free habitat, the Færøerne Islands of the north Atlantic. Surprisingly, these moths have ears similar to those mainland species exposed to resident bat faunas, a phenomenon explained as a remnant from times when ears were required by Færøerne moths. Another, perhaps more likely explanation is suggested by the islands' absence of endemic moth species. It appears that although these islands are geographically removed from the nearest landmass this distance is not great enough for sustained genetic isolation to exist and occasional intermixing occurs with mainland moths. Wolff[37] describes numerous wind-assisted moth migrations, some originating in eastern Europe and stretching as far westward as Iceland. Ear-bearing participants of these dispersions may repeatedly replenish conspecific gene pools on the Færøerne.

Geographic isolation is not the only evolutionary tactic that Lepidoptera have used to avoid bats. Temporal isolation (activity during times when bats are less of a threat) was suggested as the reason for why spring arctiid moths, emerging before most bats arrive from their hibernation sites, do not possess the secondary defence of sound-production in response to bat calls[14]. Diurnal butterflies and skippers do not, as a rule possess ears (but see Swihart[35]) while the ground-hugging flight of lasiocampids, the large size of saturniids and the rapid flight of sphingids may be non-auditory modes of protection for these moths[30]. The phylogenetic organization of ears (table) suggests that these defensive preadaptations existed in ancestral lepidopteran superfamilies before bats became volant and acoustic. The appearance of bats would have generated the need for ears only in small, nocturnal Lepidoptera with vigorous flight while those protected from bats by other means would not have experienced a sufficiently high selection pressure to warrant the evolution of ears. Once bats were established, however, lepidopteran defences would have become fixed. The deafness of bombycoid moths combined with the conservatism of insect nervous systems now provides a convenient opportunity to study the putative evolutionary origins of moth ears and their CNS processing circuits (fig. 6).

Deafness in certain Lepidoptera raises the question of whether the absence of a structure indicates it never evolved or that it has completely degenerated. A moth with a pronounced sexually dimorphic life history may provide answers to this problem (Cardone and Fullard, in preparation). The gypsy moth, *Lymantria dispar,* is a destructive forest insect with volant males and flightless females. Since males actively fly in response to female pheromones they should require ears during the evening[2] but the sedentary nature of females renders them behaviourally concealed from aerially-

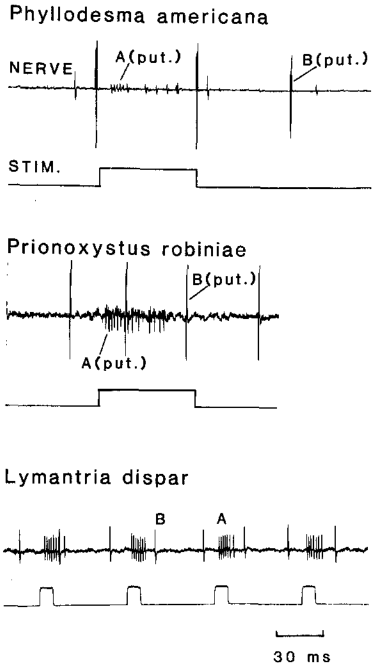

Figure 6. A possible neurological insight into the evolution of moth ears. Each of the three neural traces were taken from the respective moth's IIIN1b nerve that, in auditive noctuid moths, serves as the auditory nerve. *Phyllodesma americana* (Lasiocampidae) belongs to the deaf superfamily, Bombycoidea, and bears no external signs of tympanic organs. The neural response was elicited by an intense (>90 dB) 5 kHz tone and may represent the mechanoreceptor precursors to auditory cells. *Prionoxystus robinae* (Cossidae) is a moth from a family also reported to be inauditive but which appears to possess a rudimentary external tympanic membrane. The response was generated by an intense 5 kHz tone and this may represent one of a moth that possesses vestigial ears. As a comparison, *Lymantria dispar* (Lymantriidae) is a noctuid moth with a typical auditory response to bat signals (35 kHz, low intensity pulse-train). All three moths exhibit a spontaneously-firing and acoustically-activated cell. Further research will determine if these neurons are homologous (J. Yack, unpublished data). A, A cell; B, B cell; A(put.), putative A cell; B(put.), putative B cell.

feeding bats. Examinations of the auditory characteristics of *L. dispar* indicate that females possess neurally responsive ears but tuned to significantly lower (non-bat) frequencies than those of males. Our explanation for this auditory dimorphism is that females have only recently lost the ability to fly (females in certain populations are still sporadically volant[21]) and have commenced a process of evolutionary auditory degeneration. Other possibilities include the existence of low-frequency, female-specific acoustic predators or male-generated acoustic social signals, phenomena not likely for this well-studied moth. Perhaps the most obvious indication that the ears of females are degenerate is the observation that sounds played to them produce no behavioural effects[2]. This suggests a CNS neural uncoupling of the defensive behaviour in this moth. Acoustically-activated interneurons described in another noctuoid[6] may provide relevant circuit components to search for the point where uncoupling has occurred.

Other uses for moth ears

Although it is unlikely that gypsy moths use social sounds, studies have demonstrated the existence of these signals in other moths[1, 19, 32 34] although, for most species reported, their precise functions are unknown. If moths do listen for conspecific songs these sounds will form another selective pressure on their auditory characteristics. The audiograms of the acoustic European noctuid, *Thecophora fovea,* describe this moth's ears with typical anti-bat BF's and Surlykke and Gogola[34] suggest that acoustic moths first evolved ears for bat-detection and later used them, already tuned to an echolocation bandwidth, for intraspecific acoustic communication. This hypothesis predicts that the sounds that moths use will have the same frequencies as in the bats' calls. For moths flying in times of high bat activity, however, acoustic behaviour poses a number of questions. Most notably is: how do these moths discriminate between conspecifics and bats? Have they eliminated their need for bat-directed ears by some means of behavioural isolation (e.g., sluggish flight) or have they evolved mechanisms for discerning bat sounds? Since moth ears peripherally encode any syntonic sound, the neural circuitry for identifying 'bat' from 'non-bat' sounds, if it exists, should lie within the insect's CNS[13]. Another problem for acoustic moths comes from bats that locate their prey by using their social sounds (e.g., the frog-eating bat, *Trachops cirrhosus*[36]). Certain neotropical bats use the calling songs of katydids to locate them[4] and a similar hunting tactic may be used by bats sympatric with calling moths. The Australian pyralid moth, *Syntonarcha iriastis* which emits male social sounds for long-range communication[19] and which also appears to sing during times of bat activity will prove useful in addressing these questions.

Conclusion

Moths and bats form a uniquely simplified interaction that allows for the quantification of the selective forces acting upon the physiological design of a sensory structure. Although much is known about the neural mechanisms of moth ears, most of the relevant questions regarding their adaptive functions remain untested. Ears form only part of the lepidopteran defensive repertoire and appear to be available for uses above and beyond keeping out of the way of hungry bats. The diversity of functions for these 'simple' structures reminds us of the danger of searching for single answers to complex questions and also serves as an invitation for neuroethologists to leave their laboratories and enter the natural world of animals to better understand these questions.

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Invertebrate neuroethology: Guiding principles

F. Huber

Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen (Federal Republic of Germany)

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Pillars upon which neuroethology should rest

Nervous systems are computational structures designed to produce behavior in natural surroundings. For neuroethological research, natural behavior serves as the substrate for which an understanding has to be obtained of sensory, central nervous, and effector events that underly behavioral strategies shaped by nature's abiotic and biotic forces to improve survival and reproductive fitness of animals during the course of evolution[1, 9].

According to the dual roots of neuroethology, concepts, methods and results derived from studies of behavior, and those emerging from the entire field of neuroscience, have to be incorporated. Neuroethologists have to concentrate on molecular (subcellular), cellular, and network (circuitry) levels, which form the building blocks for hard- and software computational operations[3]. Our everyday work should focus on animals which are suitable for bridging the gap between distinct behavioral tactics and their underlying neural basis.

A call for quantitative and comparative field studies

Progressive neuroethology needs quantitative field work that teaches how behavior is executed and modified under the constraints of habitat conditions and optimized through intra- and interspecific interactions between animals and between animals and plants. Quantitative studies should reveal how behavioral components are coordinated and timed, when exposed to the relevant stimulus configurations in daily life. Such studies, especially when subsequently transferred to and simulated within the laboratory, require sophisticated methods adapted to the animal's design to pose questions that the unrestrained (or partially restrained) individual can answer, even when confined by the strait-jacket of a microelectrode.

Questions of principle should guide our research[1, 9]. At the behavioral level, we might focus on how animals orient within their environments to terrestrial and astronomical cues using different forms of locomotion, how they select and find their mates, defend their territories, avoid predators, hunt for prey or cooperate as members within a social group. Such strategies demand from the nervous system at the input side, that it should detect and recognize signals produced by con- and heterospecifics, to discriminate and localize them in a noisy habitat. On the integrative and output side, the nervous system has to decide among different behaviors, how it triggers, generates and times its components, and how it controls behavior by peripheral and central feedback devices. Moreover, we should consider actions of the nervous system that are not dependent, or are only weakly dependent on external stimuli – actions which reflect the nervous system's internal world. We should engage in a search for neural and humoral factors that determine the behavioral state and look for the causes.

Such fundamental questions often arise from, or are brought into better focus by, comparative studies. They elucidate species-specific and even individual solutions, and they open our eyes to general principles that govern larger taxonomic groups. Let us not forget, even when searching for the most basic principles, that a snail differs from a cockroach, and a frog from a bird in its demands. Thus, the exploration of an animal's natural behavioral repertoire, and the comparative study of species with different specializations, are indispensable guides for the conception of meaningful physiological experiments, particularly when approaching integrative central nervous mechanisms.

How to select a proper model system?

Comparative and evolutionary studies provide the framework for a search for those model systems which best address the desired question. But even deeper insight into the behavior in question does not necessarily help to select the best 'system' to work with on the neural level. Evolution is indifferent to the needs of students of animal behavior and to neurobiologists and it is rare that animals are equally suitable for both behavioral and nervous system analysis. Quite on the contrary, the most fascinating strategies we observe in the field are at present, and perhaps for a long time, out of reach for cellular and network analysis. The signal code of a flashing firefly and its mimicking potential are as interesting as the acoustic code of a frog, but the former is much harder to crack than the latter, when considering the neuronal implementation.