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Processing of Auditory Information in Insects

R.M. HENNIG,[1]* A. FRANZ,[1] AND A. STUMPNER[2]
[1]*Abt. Verhaltensphysiologie, Institut für Biologie, Humboldt Universität zu Berlin, 10 115 Berlin, Germany*
[2]*Institut für Zoologie und Anthropologie, Abteilung Neurobiologie, 37 073 Göttingen, Germany*

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ABSTRACT Insects exhibit an astonishing diversity in the design of their ears and the subsequent processing of information within their auditory pathways. The aim of this review is to summarize and compare the present concepts of auditory processing by relating behavioral performance to known neuronal mechanisms. We focus on three general aspects, that is frequency, directional, and temporal processing. The first part compares the capacity (in some insects high) for frequency analysis in the ear with the rather low specificity of tuning in interneurons by looking at Q10dB values and frequency dependent inhibition of interneurons. Since sharpening of frequency does not seem to be the prime task of a set of differently tuned receptors, alternative hypotheses are discussed. Moreover, the physiological correspondence between tonotopic projections of receptors and dendritic organization of interneurons is not in all cases strong. The second part is concerned with directional hearing and thus with the ability for angular resolution of insects. The present concepts, as derived from behavioral performances, for angular resolution versus lateralization and serial versus parallel processing of directional and pattern information can be traced to the thoracic level of neuronal processing. Contralateral inhibition, a mechanism for enhancing directional tuning, appears to be most effective in parallel pathways, whereas in serial processing it may have detrimental effects on pattern processing. The third part, after some considerations of signal analysis in the temporal domain, demonstrates that closely related species often use different combinations of temporal parameters in their recognition systems. On the thoracic level, analysis of temporal modulation functions and effects of inhibition on spiking patterns reveals relatively simple processing, whereas brain neurons may exhibit more complex properties. *Microsc. Res. Tech. 63:351–374, 2004.* © 2004 Wiley-Liss, Inc.

INTRODUCTION

The auditory pathway of insects serves to process and extract information about the acoustic environment. Within the auditory pathway, the information about the "who, what, and where" (Pollack, 2000) that is relevant for a particular species has to be extracted from the receptors that carry the information about an acoustic event or signal in their spiking responses. These two terms; "relevant for a particular species" and "extracted from the receptors that carry the information" constitute the two pivots of the present review.

In order to extract information, the spiking response has to be processed under various aspects: (1) Beyond detection, which is largely limited by the physical properties of the peripheral structures of the ears, the information provided by auditory receptor fibers should be sufficient to analyze sounds with a high signal-to-noise ratio. Hence, among the first questions to address is how these tasks are fulfilled at the level of lower order interneurons directly connected to receptors. Much of this is related to processing of frequencies (FREQUENCY PROCESSING); (2) Information about the "where" of an acoustic event requires a binaural comparison of receptor activities by auditory interneurons (DIRECTIONAL HEARING); and (3) most information about the "what," that is the signal content (Pollack, 2000), then may be extracted from the envelope of an acoustic signal (TEMPORAL PROCESSING). This review will also summarize how, along these 3 distinct steps of processing, the patterns of excitation and inhibition interact to extract and refine information. Due to the relatively small nervous systems of insects, as compared to the parallel computing power of a vertebrate nervous system, insects face particular constraints in their processing tasks.

In terms of auditory processing, research in insects is confronted with a trade-off that is related to the above phrase: "relevant for a particular species," which is, on first glance, a trivial viewpoint for a sensory and behavioral ecologist. However, hearing in insects has evolved many times independently (Stumpner and von Helversen, 2001; Yager, 1999) under specific environmental and historical constraints. In consequence, the solutions realized within auditory pathways of insects depend on the task that is to be fulfilled and lead to a wide diversity that begins with the design of the ears and continues throughout the steps of auditory processing in the auditory pathway. There are two major consequences from this trade-off: (1) On the one hand,

*Correspondence to: Dr. M. Hennig, Abt. Verhaltensphysiologie, Institut für Biologie, Humboldt Universität zu Berlin, Invalidenstr. 43, 10 115 Berlin, Germany. E-mail: matthias.hennig@rz.hu-berlin.de

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*TABLE 1. Processes of auditory computation and elements identified to contribute to these processes in insects.**

Process		Grasshoppers	Crickets	Bushcrickets	Cicadas	Moths
Presynaptic inhibition of sensory cells	S	n.i.[d]	n.i.[d]	n.i.[d]	n.d.	n.d.
Frequency-dependent inhibition	S	SN1, TN1[e]	ON2?[f]	DUM?[g]	n.i.[h]	n.d.
	T	TN1, AN1,3[e]	AN1,2 brain-IN[j]	AN1,2,5 TN1, DUM[k]	Many[h]	n.d.
Contralateral inhibition	S	n.i.[a]	ON1[b]	ON1 + n.i.[c]	n.d.	n.i.[u]
	T	BSN1, AN1,2[a]	ON1, AN1,2[b]	ON1, AN1,2 TN1, AN5[c]	n.d.	n.i.[u]
Summation of left and right inputs	T	AN6, AN10, TN3[s]	(AN2)[t]	AN3, DUM[g]	n.d.	n.i.[q]
Temporal inhibition	S	n.i.[m]	ON1?[n]	n.i.[o]	n.i.[p]	n.i.[q]
	T	AN3,4,12[m]	"L3"[n]	AN2, TN1?[o]	Several[p]	Extra[q]
Separate ascending channels for frequency (F), pattern (P), direction (D)		P, F, (D)	F	F, (D?)	F	

*Only representative references are given for each identified neuron or class of neurons. S = source; T = target; ? = potentially; extra: no morphological identification; n.i. = exists, but elements not yet identified; n.d. = no data. References: [a]e.g., Kalmring (1975), Römer et al. (1981), Römer and Dronse (1982), Stumpner and Ronacher (1991); [b]e.g., Moiseff and Hoy (1983), Selverston et al. (1985), Horseman and Huber (1994); [c]e.g., Hardt (1988), Stumpner (1997; 1999a), Römer and Krusch (2000); [d]Hardt and Watson (1999); [e]e.g., Kalmring (1975), Römer et al. (1981), Römer and Marquart (1984), Marquart (1985b), Römer et al. (1988); [f]Stiedl et al. (1997); [g]A. Stumpner unpublished data; [h]Münch (1999); [j]e.g., Boyan (1981), Schildberger (1984), Hardt and Watson (1994); [k]Schul (1997), Stumpner (1997; 1999b), A. Stumpner unpublished data; [m]e.g., Römer and Seikowski (1985), Ronacher and Stumpner (1988), Stumpner et al. (1991); [n]Wiese and Eilts (1985), Henley et al. (1992); [o]Schul (1997), A. Stumpner unpublished data; [p]Huber et al. (1990), Münch (1999); [q]e.g., Roeder (1966; 1973; 1976); [s]Kalmring (1975), Stumpner and Ronacher (1991), Boyan (1992); [t](weak but consistent in *Acheta domesticus*), A. Stumpner unpublished data; [u]Roeder (1973; 1976), Boyan and Fullard (1986).

an understanding of central processing requires detailed knowledge about the behavioral performance on the species level and possibly even on the individual level, since even interindividual variability is "ultimately" a result of neuronal processing (Balakrishnan et al., 2001; Schildberger, 1994; von Helversen, 1979). (2) On the other hand, trying to extract principles about information processing and attempting to generalize, one faces the danger of referring to model systems such as "the" grasshopper, "the" cricket, "the" fly, "the" bushcricket, or—the most legendary of all— "the" moth. Being very well aware of the dangers of this trade-off, in the present review we try to illustrate the three levels of processing in the auditory pathway of "insects" in a comparative manner, that is the processing of frequency, directional information, and temporal pattern, by reference to the behavior, on the one hand, which will tell us "what" the task is that has to be accomplished within the auditory pathway, and, on the other hand, by comparing model systems from which sufficient information about central processing is available from which we hope to learn "how" the task is accomplished within the auditory pathway. Since, however, the knowledge about central pathways in many hearing insects is limited, we will pay much attention to the Orthoptera, the group from which the majority of data is available (see also Table 1).

FREQUENCY PROCESSING
General Aspects and Behavior

Carrier frequency of a signal may transport information about a conspecific singer or enemy, about the sex of a conspecific, and even about differences (e.g., in size) between individuals. Accordingly, behavioral responses to signals with different spectral content are quite divergent among insect groups or species. On the other hand, in many species behavioral tuning and hearing threshold do not differ markedly (except, maybe, in overall sensitivity) indicating that little or no frequency processing occurs. In these cases, the ear may be adapted for just one task, as is the case for recognition of bat echolocating calls in many noctuid moths (Fullard, 1998) or mantids (Yager, 1999). In other cases, one may find behavioral tuning curves, which represent only a section of the hearing range, which can be calculated from the hearing threshold curve. In these cases, it is unknown what the remaining frequencies audible to the species are used for and why hearing is not restricted to the behaviorally effective range of frequencies [e.g., a low-frequency sensitivity in some parasitic flies (Köhler and Lakes-Harlan, 2001), and some mantids, (Yager, 1999)]. In other species, hearing threshold curve and behavior indicate that two behaviorally relevant frequency ranges exist, e.g., in crickets that perform positive phonotaxis to low-frequency sounds of appropriate temporal pattern and negative phonotaxis to high-frequency sounds (Moiseff et al., 1978). Grasshoppers also evaluate spectral content and use the ultrasonic part as indicator for sex of a conspecific (von Helversen and von Helversen, 1997). The most elaborate frequency dependence of behavior was found in certain bushcrickets. They have behavioral thresholds tuned to the (sex-specific) carrier frequency, and additionally show frequency dependent response functions (Dobler et al., 1994). These intensity response functions at different frequencies do not only differ by their absolute thresholds, but also by their steepness and relative optima. This indicates the ability of much better frequency discrimination than is known for crickets and grasshoppers. Actually, this might be topped by cicadas, which show the most complex songs of all insects in terms of carrier frequency modulation (e.g., Gogala, 1995). Unfortunately, behavioral studies with cicadas in the laboratory are hard to perform, but those that are available indicate that various carrier frequencies within the hearing range may be discriminated in some species (Fonseca and Revez, 2002) but not in others (Daws et al., 1997).

In principle, the structure and organization of the hearing organ provides the majority of insect groups with at least some ability of frequency discrimination (see chapters by Yack, pages 315–337, and Mason and Faure, pages 338–350, in this issue). Prominent exceptions are those insects that have either just one audi-

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tory sensory neuron in each ear like certain moths (Surlykke, 1984) or that have a set of auditory sensory neurons that are all tuned to the same frequency, which seems to be the case, e.g., in tiger beetles and many mantids (Yager, 1999). However, recent results in cicadas revealed that the apparently uniform tuning of the ears found in many different cicada species by means of summed recordings of the tympanic nerve just reflected the activity of the majority of the many hundred sensory neurons. The tuning of individual interneurons in one species demonstrated that there must be sensory neurons tuned to other frequencies than those picked up in summed recordings (Fonseca et al., 2000; Münch, 1999), and it is quite likely that this applies to other cicadas as well. On the other hand, a set of sensory neurons with different best frequencies does not necessarily imply that the central processing (and therefore the behavior) has the ability of fine frequency discrimination. Rather, a categorical perception of frequency has been found, e.g., in crickets (see above and Pollack et al., 1984; Wyttenbach et al., 1996).

Tonotopy

Where details of sensory neuron tuning and central projection areas are known (grasshoppers and bushcrickets), a clear tonotopic representation is found, as is known from vertebrates (e.g., Halex et al., 1988, Stölting and Stumpner, 1998; see also Mason and Faure, pages 338–350, this issue). Therefore, a correspondence of interneuronal tuning and dendritic overlap with respective sensory neuron terminals is observed (Fig. 1A,D; Römer, 1985; Römer et al., 1988; see also the cercal systems of crickets, e.g., Jacobs and Theunissen, 2000; Paydar et al., 1999). The projection sites of interneuron dendrites, however, are typically much larger than those of single sensory cells and sometimes also larger than one would expect based on the neuron's tuning (Fig. 1B,C; Stumpner, 1997, 1999b). This then is due to inhibitory processes (see below).

A morphological comparison of overlap in arborization of interneurons and sensory cells allows estimating the number of sensory neurons over which an interneuron integrates. Physiologically, the same is possible from frequency threshold curves (given that no frequency specific inhibition exists or that it was pharmacologically eliminated; Stumpner, 1998). For the bushcricket *Ancistrura nigrovittata* (Phaneropteridae), it has been estimated that out of on average of 37 sensory neurons, approximately 8 to 10 (certainly cells no. 10 to 17 of the crista acustica) excite the ascending interneuron AN1, which is tuned to the male song frequency around 16 kHz (A. Stumpner, unpublished data). The omega neuron in the same species obviously is excited by many more sensory neurons, since its tuning curve largely matches the threshold curve of the whole hearing organ and its dendrites project into all areas of the auditory neuropile. As was described for the omega neuron in Tettigoniidae, it apparently lacks inputs from certain low-frequency receptors (Römer, 1985, Römer et al., 1988).

Sharpness of Frequency Tuning and Frequency-Specific Inhibitions

Sensory neurons with different best frequencies allow sharpening the tuning of interneurons by central inhibition. Such a frequency-dependent inhibition is found in many auditory interneurons of insects (crickets: e.g., Atkins et al., 1989; Boyan, 1981; Boyd et al., 1984; Moiseff and Hoy, 1983; Schildberger, 1984; bushcrickets: Römer, 1987; Schul, 1997; Stumpner, 1997; grasshoppers: Römer et al., 1981; cicadas: Münch, 1999; see also Table 1). Such inhibition often was demonstrated in two-tone paradigms, but may also be seen as IPSPs in dendritic recordings. A frequency specific inhibition has several effects on the physiological characteristics of an auditory interneuron: (1) it sharpens the tuning, although typically not exceeding that found in single sensory neurons (Fig. 1B; see also Fig. 4), (2) it reduces the dynamic range of interneurons (Stumpner, 1998, 2002), and (3) it affects the timing of spikes for temporal processing (e.g., Römer and Seikowski, 1985; Stumpner, 1997, see also TEMPORAL PROCESSING of this review). Although only the first effect may be the "desired" one, the others inevitably accompany such inhibitory processes. The source of these effects can be tracked if the inhibitions are eliminated by blocking the channels that mediate inhibition, e.g., by application of picrotoxin (see Fig. 4; Römer and Seikowski, 1985; Stumpner, 1998, 2002). When the inhibitions are eliminated, not only does the frequency tuning become considerably broader, but also the dynamic range increases and the temporal spiking patterns change drastically to a primary-like response. Interestingly, picrotoxin does not affect all inhibitions in the same way, indicating that different inhibitory pathways use different transmitter substances (Stumpner, 1998). The broad effect of frequency-specific inhibitions imposes constraints on the evolution of inhibitory processes. For example, spiking patterns of neurons to conspecific signals arriving from various distances are expected to be quite different (see Römer, 1987). At close distance, due to their optimum type response curves and prominent inhibition at higher intensities, such neurons probably will not present valuable information about the song (e.g., Römer, 1987; Stumpner, 1997). As a solution to this problem, insects might use different channels for coding different information like carrier frequency and temporal pattern. However, for crickets it seems that single interneurons like AN1 carry information about carrier frequency as well as temporal pattern although they receive frequency-specific and directional inhibitions (e.g., Schildberger, 1984; Horseman and Huber, 1994; Stumpner et al., 1995; see also Serial or Parallel Processing of Directional and Pattern Information). This may be tolerable since the effect of the inhibitory influence seems to be less strong than in certain bushcricket neurons (e.g., AN1 of *A. nigrovittata*, the homologous neuron to AN1 of crickets; Stumpner, 1997).

For an attempt to weigh the benefits and limitations of frequency-dependent inhibition, it is important to ask how effective the sharpening of frequency through central processing really is as compared to sensory neurons. One of the widely used identifiers for the quality of frequency tuning is the Q10dB-value that is derived from the best frequency divided by the frequency range 10 dB above threshold. Figure 2 and Table 2 give an overview of Q10dB-values of sensory cells and interneurons of different insect groups. In general, sensory neurons have Q10dB-values between

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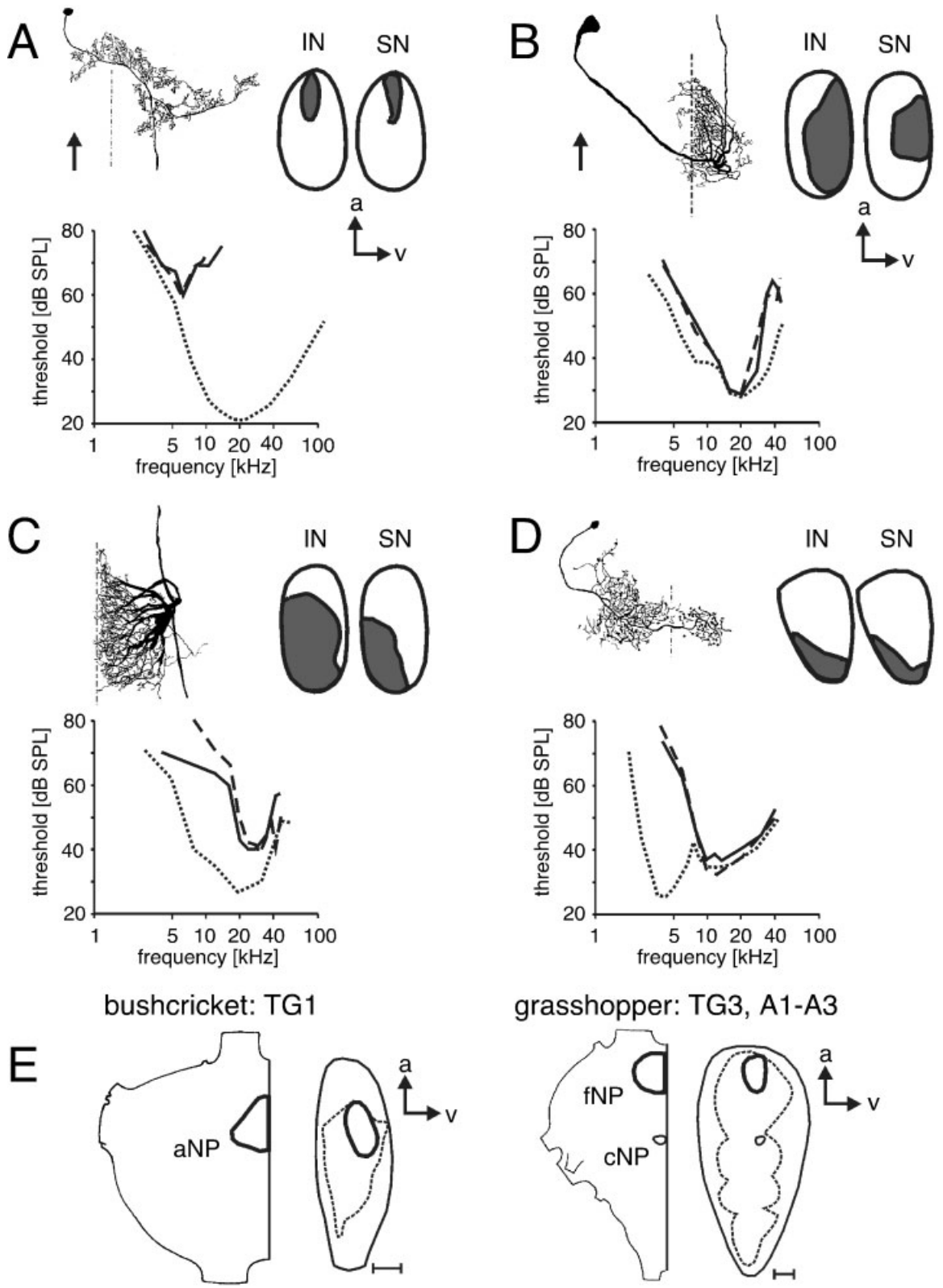

Fig. 1.

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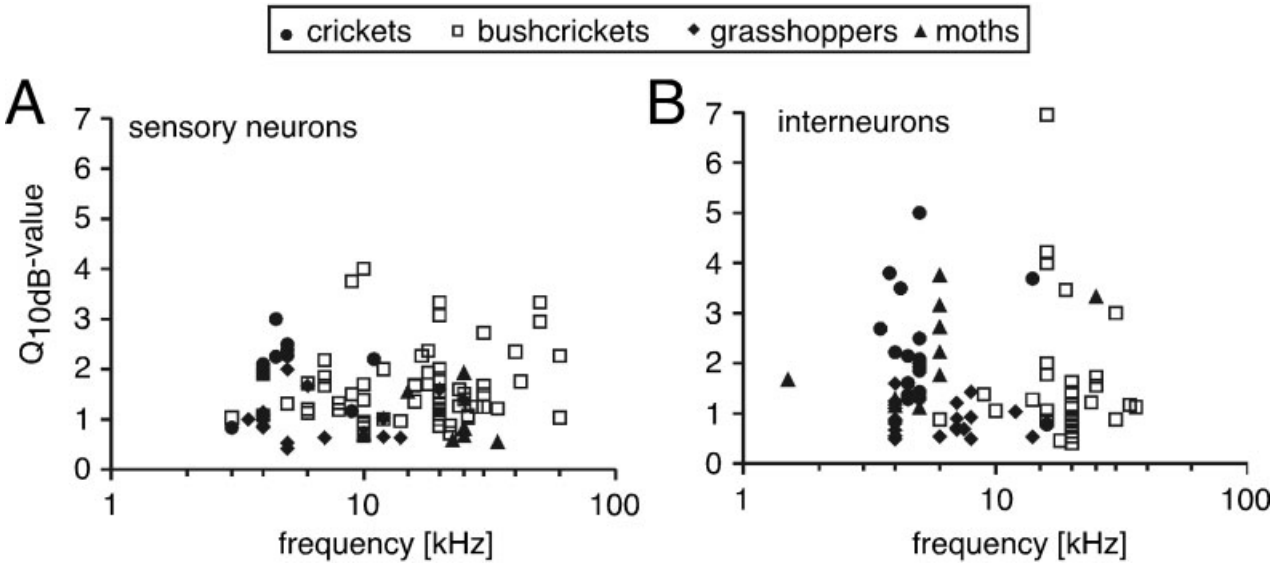

Fig. 2. Q_{10dB}-values of various groups of insects for (**A**) sensory neurons and (**B**) interneurons. Values are calculated mostly from published tuning curves: Crickets: *Gryllus bimaculatus*, Esch et al. (1980), Schildberger (1984), Oldfield et al. (1986), Schildberger et al. (1986), Horseman and Huber (1994), Watson and Hardt (1996); *G. campestris*, Wohlers and Huber (1978), Boyd et al. (1984); *Acheta domesticus*, Stout et al. (1988), Stumpner et al. (1995); *Teleogryllus oceanicus*, Atkins and Pollack (1986), Atkins et al. (1988, 1989); *T. commodus*, Ball and Hill (1978), Hennig (1988). Molecrickets: *Scapteriscus borealis*, Mason et al. (1998). Haglidae: *Cyphoderris monstrosa*, Mason and Schildberger (1993). Bushcrickets: Tettigoniidae: *Caedicia simplex*, Oldfield (1982), Oldfield and Hill (1983); *Pachysagella australis*, Römer et al. (1989); *Mygalopsis marki*, Oldfield (1984), Römer (1987), Römer et al. (1988; 1989), Kalmring et al. (1995); *Gampsocleis gratiosa*, Lin et al. (1993); *Tettigonia cantans*, Zhantiev and Korsunovskaya (1983), Hardt (1988); *Tettigonia viridissima*, Römer et al. (1988), Schul (1997); *Decticus verrucivorus*, Kalmring et al. (1978), Nebeling (2000); *D. albifrons*, Sickmann (1996), Nebeling (2000); *Pholidoptera griseoaptera*: Stölting and Stumpner (1998). Phaneropteridae: *Leptophyes punctatissima*, Hardt (1988); *Ancistrura nigrovittata*, Stumpner (1996, 1997, 1999b), Stumpner unpublished observations. Grasshoppers: *Locusta migratoria*, Römer (1976), Marquart (1985a), Halex et al. (1988), Römer et al. (1988); *Schistocerca gregaria*, Halex et al. (1988); *Chorthippus biguttulus*, Wolf (1984), Stumpner unpublished observations. Praying mantis: *Mantis religiosa*, Yager and Hoy (1989). Cicadas: *Tettigetta josei*, Münch (1999). Moths: Noctuidae: *Caenurgina erechta*, Roeder (1966); *Agrotis segetum*, Surlykke and Miller (1982); *Elydna nonagrica*, Fullard (1988); *Barathra brassicae*, Madsen and Miller (1987); *Hecatesia thyridion*, Surlykke and Fullard (1989); *Ascalapha odorata*, Fullard (1998); Notodontidae: *Xenorma cytheris*, Fullard (1998).

Fig. 1. Tonotopic representation of information by sensory neurons and corresponding projections and tuning of interneurons. Top left drawing in each subfigure shows a whole mount view of the respective neuron; top right drawing shows a sagittal section through the auditory neuropile of the pro- (A,B,C) or meta- (D) thoracic ganglion close to the midline with the termination areas of the interneuron (IN) and the sensory neuron (SN). For orientation within the ganglion, see E). The diagrams show the frequency tuning of the whole hearing organ (dotted line), of the sensory neuron (stippled line), and of the interneuron (solid line). **A:** Low-frequency descending neuron in a bushcricket (*Mygalopsis marki*, Copiphorinae). **B:** Ascending neuron (AN1) of the bushcricket *Ancistrura nigrovittata* (Phaneropteridae). **C:** T-shaped fibre in the prothoracic ganglion (actually a neuron ascending from the abdomen, AN5–AG7) in *A. nigrovittata*. **D:** A local high-frequency neuron (SN5) in the locust (*Locusta migratoria*, Acrididae). Note that the projection areas of SN and IN in A as well as in D are very similar, while the interneuronal projections in B and C are much larger than the respective sensory neuron projection. In B, the tuning of sensory neuron and interneuron match closely, despite the difference in projection areas. The reason is frequency-specific inhibition of the interneuron (see text). In C, the neuron's projection area is larger and its tuning is broader than in the sensory neuron despite the existence of frequency dependent inhibition. **E:** A whole mount view of one ganglion half and a sagittal section in a bushcricket and in a grasshopper. The strong line shows the auditory neuropile (aNP) or the frontal auditory neuropile (fNP), respectively, the stippled area delimits the cortex with somata. In the grasshopper, also the caudal auditory neuropile (cNP) in the first abdominal ganglion is shown. Modified after (A) Römer (1987), (B) Stumpner (1996, 1997), (C) Stumpner (1999b), (D) Römer (1976), and Römer et al. (1988), (E) (grasshopper) Marquart (1985a).

0.5 and 2.5, only rarely up to 3.5 and consistent differences between species are not apparent. The highest Q10dB-values were found in bushcrickets, which may also be due to the fact that by far the largest amount of data exists from bushcrickets. There are also no consistent differences between sensory neurons tuned to low or high frequencies, neither within one group nor between groups. Especially, within one species there is no indication that sensory neurons tuned to the species-specific song frequencies are more sharply tuned than other sensory neurons. When compared to vertebrates, afferent neurons of the inner ear in general have higher Q10dB-values. In various lizards and birds, the values range from below 1 to 10 or higher (e.g., Manley, 1990), in mammals from 1 to 20, rarely up to 30, and in specialized bats up to 400 at some frequencies (Suga et al., 1976; auditory interneurons in such bats may have Q10dB values even above 500 as a result of frequency dependent inhibition, e.g., in *Rhinolophus*; Behrend and Schuller, 2000).

The question then arises whether auditory interneurons in insects show higher Q10dB-values due to central sharpening of frequency than single sensory neurons. Surprisingly, this does not seem to be the case (Fig. 2B). Even though there are some reports of interneurons that show Q10dB-value above 3, the majority of interneurons possess Q10dB-values below 2. High

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TABLE 2. Q_{10dB}-values of sensory neurons (SN) and interneurons (IN) of 5 groups of hearing insects

Q10dB-values		Mean ± SD	min	max	n values	n species
Crickets	SN	2.1 ± 0.6	0.8	3.0	10	1
	IN	2.1 ± 1.1	0.6	5.0	26	6
Bushcrickets	SN	1.6 ± 0.7	0.7	4.0	65	9
	IN	1.6 ± 1.3	0.4	7.0	34	10
Grasshoppers	SN	1.1 ± 0.6	0.4	2.7	19	3
	IN	0.9 ± 0.4	0.5	1.6	22	2
Moths	SN	1.1 ± 0.6	0.6	2.0	10	7
Cicadas	SN	1.0 ± 0.4	0.4	1.6	6 (tymp nerve)	6
	IN	2.2 ± 1.0	1.1	3.8	9	1

*Given are the mean and standard deviation (SD), the minimal and maximal value, the number of values, and the number of species. The sensory neuron data in cicadas are from tympanic nerve recordings, which most likely represent the tuning of one group of low frequency receptors. For references see Figure 2.

Q10dB-values were found (1) in cicadas (Münch, 1999), for which no tuning curves of single sensory neurons are known yet due to the very small diameter of receptor axons, (2) for unidentified interneurons in the thorax of one single bushcricket species (*Caedicia simplex*; Oldfield and Hill, 1983), and (3) for some cricket ascending interneurons (e.g., "AN3" in *Gryllus campestris*; Boyd et al., 1984) with some discussion about interindividual variability and homology of ascending neurons (e.g., Hennig, 1988). However, these cases illustrate that substantial sharpening in tuning of auditory interneurons, as compared to sensory cells, by frequency-dependent inhibition is at present rather an exception than the rule. Although such a sharpening is not uncommon, the Q10dB-values of interneurons are in most cases below 2, which is similar to or even lower than that of sensory neurons. Maybe, the "desired effect" of frequency-specific inhibitions is not sharpening of frequency in the first place?

Taking Advantage of the Gradation of Best Frequency in Auditory Sensory Neurons

At least three hypotheses have been put forward that give alternative, though somewhat related explanations for the existence of sets of sensory cells with graded best frequency (Fig. 3A). The first hypothesis follows the observation of Rheinlaender (1975) that some interneurons in the bushcricket nervous system respond like "intensity detectors." Römer (1987) was able to correlate the distance of a conspecific song with the area of excitation in the prothoracic ganglion of the copiphorine bushcricket *Mygalopsis marki*. This species produces a rather broadband song, and the further away the singer from the receiver, the smaller the activated area in the prothoracic auditory neuropile. This effect is due to a general decrease in intensity as well as an increased relative attenuation of higher frequencies with distance. An ascending interneuron (possibly homologous to AN1 in other bushcrickets and crickets) that receives high-frequency inhibition is optimally excited at song distances roughly similar to those observed in male spacing behavior (Römer and Bailey, 1986). This optimal response is caused by a restricted excitatory input and a high-frequency inhibition of the interneuron that becomes most effective with nearby singers (Fig. 3A, 4). The dynamic range of that neuron becomes smaller also due to those synaptic inputs.

The second hypothesis was expressed in most detail by Hardt (1988) who suggested that the graded tuning curves might be used for intensity range fractionation (Fig. 3A,B). In its simplest form, a range fractionation can also be achieved by sensory neurons that are tuned to the same frequencies but show different thresholds. Examples are known from crickets, grasshoppers, and bushcrickets (e.g., Oldfield, 1983; Oldfield et al., 1986; Römer, 1976). In the case of sensory neurons with different best frequencies, as in most bushcrickets, an increase in intensity at a given frequency would have the same result. Then, more and more sensory neurons with lower and higher best frequencies are "recruited" to join the common activation. Therefore, the dynamic range of the summed activity of the set of sensory neurons at a given frequency is much larger than the dynamic range of a single sensory neuron, similar to what was described for the cercal system of crickets (e.g., Landolfa and Miller, 1995; Shimozowa and Kanou, 1984). In crickets or bushcrickets, a single sensory neuron has a dynamic range of about 20 to 25 dB. Certain interneurons, however, have a dynamic range of 50 dB or more (e.g., in crickets: Schildberger et al., 1986). The omega neuron of crickets and bushcrickets, for example, is a broadband neuron and receives input probably from the majority of auditory sensory neurons. Additionally, the hypothesis presented by Hardt (1988) may be of special advantage for all those bushcricket species such as *Leptophyes punctatissima* (and other Phaneropteridae), which have a female producing an extremely short narrowband response click. For such short signals, a single sensory neuron shows nearly no intensity dependence, neither in latency nor in spike number. In such a case, an increased recruitment of adjacent sensory neurons tuned to different frequencies seems to be the only mechanism to evaluate intensity, which is indispensable for left-right comparisons during phonotactic approach. As a consequence, Hardt (1988) expected directional neurons in this species to be broadly tuned, which actually is the case for the neurons with the highest directionality known in this species, the omega cell and a T-fiber (TN1). In other bushcricket species, although not narrowly tuned, TN1 seems to have a strong bias towards ultrasonic frequencies (for a summary, see Faure and Hoy, 2000).

The third hypothesis is related to improving the signal-to-noise ratio for temporal processing (Römer and Lewald, 1992). By using periodic stimuli, Römer and Lewald (1992) showed that the variability in the spiking response of an Omega cell in a bushcricket depended on the spectral content of the stimuli. Com-

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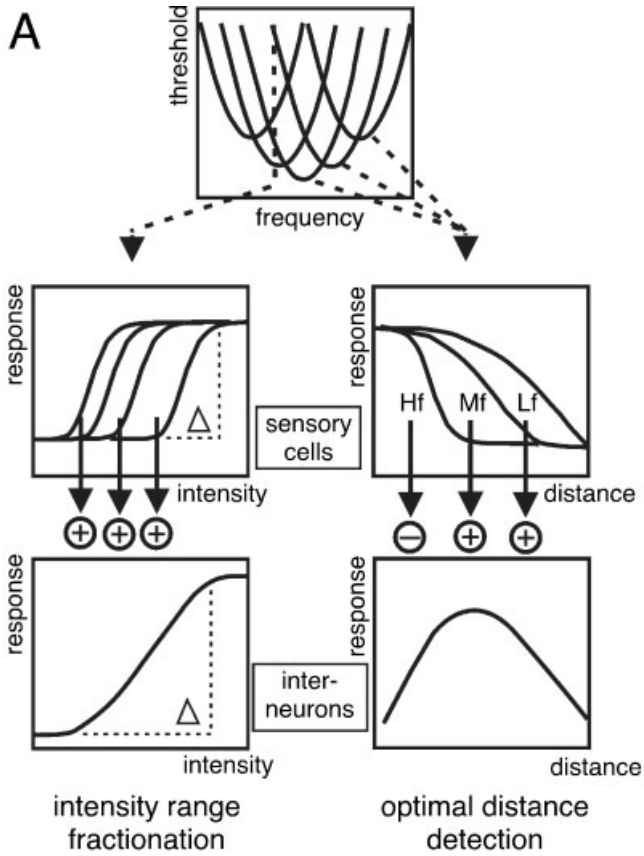

Fig. 3. Graded tuning curves of sensory neurons. **A:** The potential function of graded tuning curves. They could be used for intensity range fractionation thereby increasing the dynamic range of interneurons (**left**) or for distance detection through inhibition by high-frequency neurons (Hf) and excitation through the remaining sensory neurons (Mf, Lf) (**right**). **B:** Threshold curves of 15 sensory neurons recorded in one individual of a female bushcricket *Ancistrura nigrovittata*. Four tuning curves from sensory cells with lowest threshold at 8, 20, 38, and 50 (or higher) kHz are shown with a bold line. For two arbitrarily chosen frequencies, 10 and 30 kHz, the respective threshold values of all sensory cells responding at this frequency are marked with a cross. The crosses represent 12 values between 40 and 82 dB SPL at 10 kHz and 10 values between 38 and 83 dB SPL at 30 kHz. It should be noted that *Ancistrura* has on average 37 sensory neurons, therefore 22 more tuning curves would have to be filled in the diagram. Modified after a scheme made by Hardt (1988) for *Leptophyes punctatissima*.

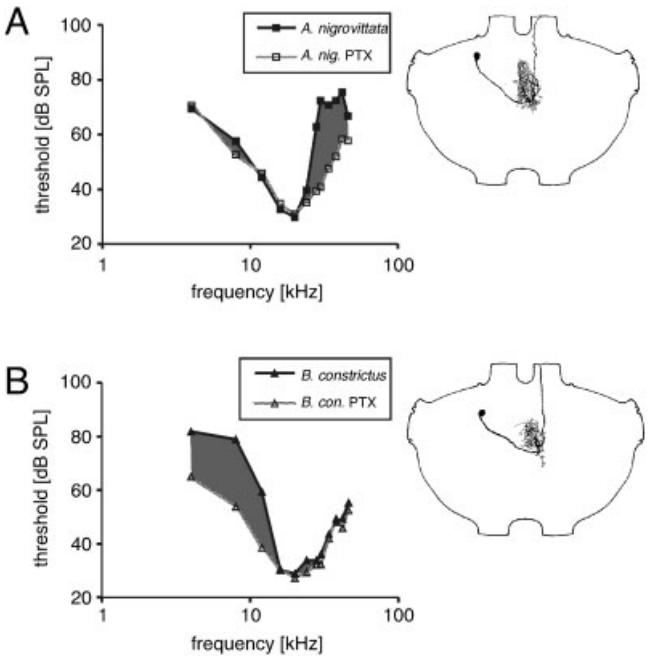

Fig. 4. Threshold curves of the AN1 interneurons of *Ancistrura nigrovittata* (**A**; n = 10) and *Barbitistes constrictus* (**B**; n = 4), two Phaneropterid species, before (solid line and closed symbols) and following application of picrotoxin (ptx; grey line and open symbols). The shaded area shows the threshold drop evoked by ptx. **Right:** Whole mount view of a member of the respective neuron is shown. Modified after Stumpner (1998, 2002).

pared to a pattern with a single frequency as a carrier, a stimulus of increasing bandwidth allowed increasingly higher fidelity in encoding the stimulus envelope. Thus, a set of differently tuned sensory neurons may provide several independent frequency channels from which information about the pattern can be extracted (c.f., the comodulation masking release, Klump, 1996; Moore, 1992). It is this independence that increases the reliability of responses in such a system as compared to a system with equally tuned sensory neurons (Ronacher and Krahe, 2000; Shadlen and Newsome, 1998).

Conclusions

Frequency processing in certain insect species has been demonstrated to directly contribute to specificity of behavioral responses. Flying crickets decide mainly on the basis of carrier frequency whether to turn to or away from a sound source. Certain bushcrickets have been shown to accept only signals of a certain range of carrier frequencies as coming from conspecifics. Some grasshoppers and bushcrickets obviously even use carrier frequency for sex discrimination. In most of these cases, the hearing organ seems well adapted for these tasks and interneurons in the thoracic nervous system show frequency processing like frequency-specific inhibition, which fits to the behaviors observed. There is reason to believe that cicadas have potentially the most complex frequency processing, but they are among the least investigated.

In most species, additional important information can be extracted from temporal patterns, which actu-

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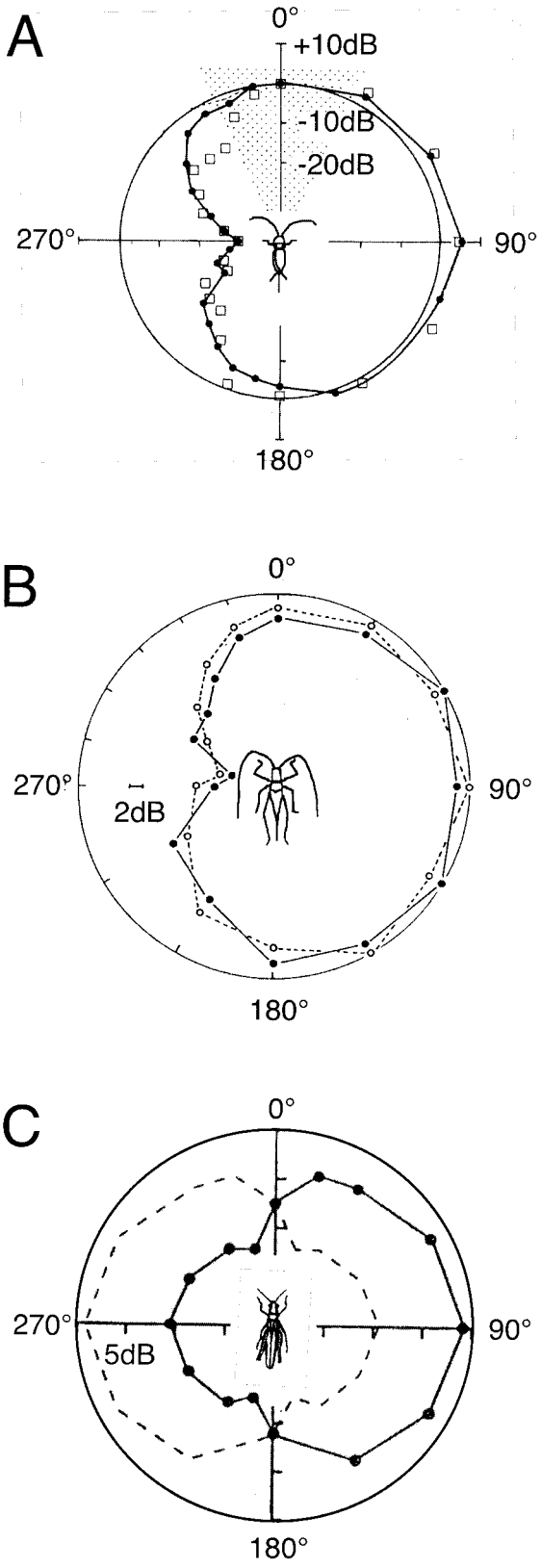

ally may be the major determinant of behavior. Moreover, the ability of the hearing organs to discriminate frequencies does not necessarily imply that a species makes use of this aspect of hearing; intensity range fractionation, or distance estimation or improved signal-to-noise ratio may be the prime tasks as well. Consequently, frequency specific inhibitions, which were found in most groups (see Table 1), may contribute to behaviors unrelated to frequency discrimination. In order to understand the principles of frequency processing in different groups, more data are needed concerning how behavior depends on frequency and how interneurons (even on the thoracic level) contribute to frequency-specific responses. Especially, little data are available on brain interneurons. Those neurons that we know of, mainly from crickets, indicate categorical responses to low or high frequencies (Brodfuehrer and Hoy, 1990; Schildberger, 1984).

DIRECTIONAL HEARING

Directionality at Periphery and in Behavior

Central processing of directional information requires binaural comparison of amplitude (interaural intensity differences) and arrival time or phase (interaural time differences). Such differences are due to the diffraction caused by the animal's body and interaural delays of arrival time of the sound wave, respectively. The amount of diffraction is determined by the proportions of body size and wavelength, while the difference in arrival time depends on the distance between the ears. Compared to larger animals, which can exploit these directionality cues more easily, insects face the difficulty that their body size is often small compared to the wavelength of the conspecific or a predator's sound signal. Furthermore, the distance between both ears is usually a few millimeters only, which causes differences in time of arrival in the range of a few microseconds. Such minute time differences are difficult to process reliably in a small nervous system. The latency differences resulting from different times of arrival are so small that they probably cannot be resolved by the insects (Krahe and Ronacher, 1993). Despite these physical constraints, many insects are able to perform precise localization behavior even at wavelengths that are considerably larger than their own body size.

Already the tympanal organs themselves exhibit a pronounced directional characteristic which is illustrated in Figure 5, due to a pressure gradient receiver (Michelson, 1994). Crickets, bushcrickets, and grasshoppers are alike insofar as the maximum sensitivity

Fig. 5. Directional sensitivity of the tympanal organs or the auditory nerve, respectively, in three Orthopteran groups. **A:** Cricket, *Gryllus campestris*. The connected closed circles are derived from laser vibrometer measurements at 5 kHz, the open squares indicate the response of the tympanal nerve at the same frequency, and the shaded area is the region within which crickets cannot consistently turn towards the sound source (±25°) (modified after Larsen et al., 1989). **B:** Bushcricket, *Leptophyes punctatissima*. The curves were measured behaviorally (solid line and closed symbols) and neurophysiologically (broken line and open symbols) at 40 kHz (modified after Rheinlaender et al., 1986). **C:** Grasshopper, *Chorthippus biguttulus*. This mean curve is derived from measurements of the tympanal nerve of four animals using the spectrum of the conspecific signal (broadband noise, modified after von Helversen, 1997).

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of the ear occurs to ipsilateral sound while the response is clearly reduced if the sound source is located contralaterally (Fig. 5; Boyd and Lewis, 1983). However, differences exist in the frontal auditory field where crickets exhibit a rather flat directional sensitivity (Fig. 5A) while in grasshoppers there is a steep drop in sensitivity as the sound source crosses the midline (Fig. 5C; Larsen et al., 1989; von Helversen and Rheinlaender, 1988). The directional characteristics of bushcrickets form an intermediate type of curve in the frontal area (Fig. 5B; Rheinlaender et al., 1986). Since the directionality of the tympana is less pronounced in the frontal auditory field of crickets, stimulus angles of ±25° are necessary for the animals to exhibit a reliable turning response (Fig. 5A, shaded area; Rheinlaender and Blätgen, 1982).

Differences also exist in the capacity for angular resolution that become obvious in the behavioral performance that reflects the output of central processing mechanisms. In Figure 6, the relationship between the turning angle and the target angle is shown. In crickets and bushcrickets, the turning angles increase with increasing angle between the animals' longitudinal axis and the sound source (Fig. 6A: Oldfield, 1980; Schmitz et al., 1982; Stabel et al., 1989; Fig. 6B: Hardt, 1988; Rheinlaender and Römer, 1990).

Male grasshoppers of the species *Chorthippus biguttulus* respond to a conspecific female song with a turn towards the louder side. Rheinlaender (1984) and von Helversen (1997) have shown that for a wide range of stimulation angles there is no correlation between the target angle and the turning angle (Fig. 6C). Hence, the directional response rather corresponds to a lateralization of the sound source, i.e., the animals evaluate only the sign of the target angle. Nevertheless, this performance occurs with high precision, since target angles of more than 10° from the midline are already sufficient to elicit error-free lateralization behavior (von Helversen, 1997). In terms of physical cues, this precision corresponds to interaural intensity differences of 1.6 dB or interaural time differences of 1.5 ms (von Helversen and Rheinlaender, 1988) and is derived from the directional characteristics of the tympanal vibrations. While humans and other small mammals resolve much smaller time differences, the intensity difference limens of grasshoppers are not inferior to those of vertebrates (Krahe and Ronacher, 1993; Stumpner and Ronacher, 1994). In the next sections, we will discuss to what extent known central mechanisms are causal for the directionality observed in the behavioral performance.

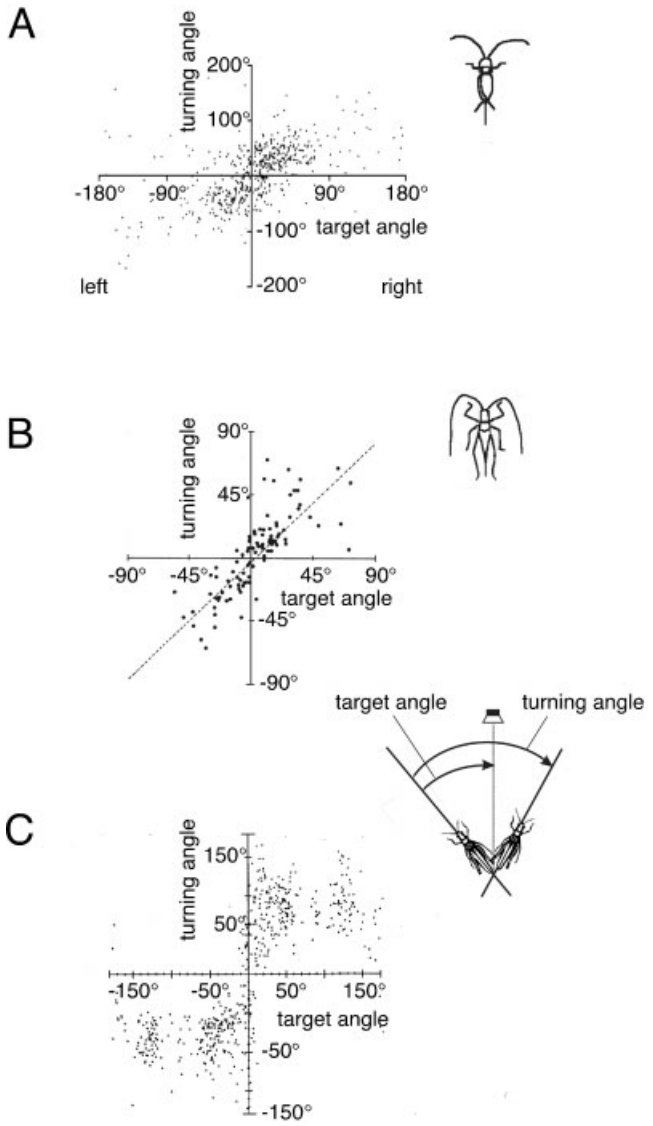

Fig. 6. Relationship between the target angle and the turning angle. **A:** Cricket, *Teleogryllus oceanicus*. Female response when the calling song is presented under closed loop conditions (the data for three different intensities are pooled: 69, 74, and 78 dB, carrier frequency: 4.5 kHz, modified after Oldfield, 1980). **B:** Bushcricket *Tettigonia cantans*, Female orientation to the calling song, Accumulated data of six females that were tested under closed loop conditions are represented (modified after Rheinlaender and Römer, 1990). **C:** Grasshopper, *Chorthippus biguttulus*. Male response when the female song is presented under open loop conditions, e.g., the female song was shortened to 400 ms. Data for several males are pooled. Carrier frequency: broadband noise (modified after von Helversen, 1997). Note the different scales in A–C. In contrast to grasshoppers, a linear relationship between stimulus angle and turning angle is obvious in crickets and bushcrickets. While the latter were tested under closed loop conditions, grasshoppers had no opportunity to correct their turning angle due to open loop conditions.

Serial or Parallel Processing of Directional and Pattern Information

For correct behavioral performance, sound localization as well as signal recognition must be accomplished jointly. Present behavioral evidence suggests fundamental differences between crickets and grasshoppers in the central processing of temporal pattern and directional information.

For crickets, serial processing of pattern and directional information is most likely. Intracellular recordings from a first-order ascending interneuron (AN1) during phonotactic walking revealed that crickets turn to the side on which the neuron is more strongly excited. Consequently, if the AN1-cell ipsilateral to the sound source is hyperpolarized, then the animals turn away from the loudspeaker (Schildberger and Hörner, 1988). Stabel et al. (1989) performed another crucial experiment in which an attractive signal was pre-

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sented from a loudspeaker situated above the animal, thus yielding no directional cues, while simultaneously an unpatterned tone was given from one side. Surprisingly, in this situation the crickets showed negative phonotaxis, directed away from the pure tone, apparently inverting the directional cues that arose from intensity differences. This paradox was resolved by the observation that AN1 showed different copying fidelities in this experimental situation. Hence, the crickets turned towards that side at which the pattern was preserved best (Stabel et al., 1989). Furthermore, Pollack (1986) described that crickets are able to discriminate between two effective song patterns of different attractiveness played simultaneously from either side. This view was confirmed by neurophysiological experiments on bilateral local interneurons (ON1), which represented selectively the pattern played from their side (Pollack, 1986, 1988). The conclusions from these sets of experiments were most clearly summarized by von Helversen and von Helversen (1995) who proposed that the crickets follow the rule "turn towards that side on which the song's temporal pattern is represented more clearly." This corresponds to serial processing of, first, pattern information and then directional information, and implies that these two aspects are not represented in separate pathways (Fig. 7A). For bushcrickets, Schul et al. (1998) also proposed serial processing on the basis of selective phonotaxis. In grasshoppers, however, behavioral experiments revealed a functional separation of recognition and localization. In contrast to crickets, information about the temporal pattern is obtained by pooling the inputs from both ears centrally and, hence, pattern and sound direction must be processed in parallel pathways (Fig. 7B; von Helversen and von Helversen, 1983, 1984, 1995). Lesion experiments demonstrated that this separation into parallel channels occurs quite early in the auditory pathway (Ronacher et al., 1986). This idea was supported by neurophysiological investigations by Stumpner and Ronacher (1994) who were able to show that thoracic auditory interneurons that encode information about sound direction are poor in encoding temporal features and vice versa. A separation into several parallel channels dedicated to directional and even different temporal cues of a sound signal is well known for the auditory system of vertebrates (Covey and Cassaday, 1991; Takahashi et al., 1984; Viete et al., 1997; for review see Oertel, 1999).

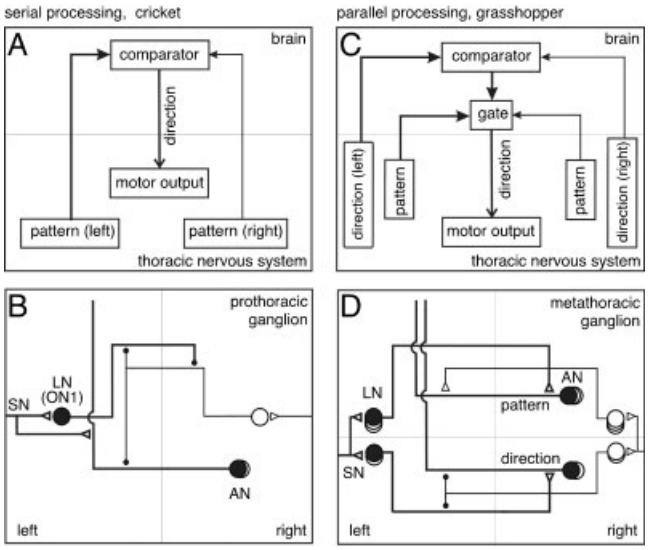

Fig. 7. Two different neuronal networks processing pattern and directional information. **A,B:** Serial processing in crickets. **C,D:** Parallel processing in grasshoppers. A,C: Block diagram of information processing ascending from the thorax to the brain. A: A comparator receives input from two pattern recognizers, one from each hemisphere. The strength of both inputs is compared to derive directional information. C: Two parallel pathways for pattern and direction ascend to the brain, where a comparator makes a left/right decision if the recognition of pattern is positive (gate). B,D: Schematic networks in the prothoracic or the metathoracic ganglion, respectively. The black somata and thick black axons indicate elements that receive excitation from the left side. For reasons of clarity, the ascending neurons are shown for one hemisphere only. Open triangles indicate excitatory, filled circles inhibitory synapses. B: The ascending neuron (AN) receives excitatory input from left side receptors (pattern) and inhibitory synapses from the right ON1 (direction). The directionality of ON1 is enhanced by reciprocal inhibition. D: Ascending neurons that code for direction are inhibited from the side contralateral to the sound (right), while those neurons that code for the temporal pattern sum up the inputs from both sides (see also C). (SN) sensory neuron, (ON1) omega neuron, (LN) local interneurons, (AN) ascending interneurons. Compare also with Table 1.

Central Mechanisms

The previous sections revealed rather different processing strategies of acoustic information both in terms of angular resolution as well as a separation of pattern and directional information. Hence, several questions arise: (1) How is pattern and directional information represented in the auditory pathway of the respective insects ? (2) Since directional hearing involves reciprocal inhibition for contrast enhancement, one may expect detrimental effects on information that is still available at the level of sensory neurons. And (3), at which levels of processing (local or ascending interneurons) do such inhibitions occur and what are their effects on the different abilities for angular discrimination? In Figure 7, a sketch of the different processing steps for direction and pattern in the brain (Fig. 7A,C) as well as the main synaptic connections in the thoracic auditory pathways (Fig. 7B,D) is shown for crickets and grasshoppers, respectively. In terms of the network, some basic aspects of information flow within the CNS are quite similar, although structural differences exist between crickets, bushcrickets, and grasshoppers in the peripheral and central nervous system (Fig. 7). Sensory neurons, which copy the amplitude modulations of the incoming acoustic signal, project ipsilaterally onto local interneurons, T-fibers, or, at least in Ensifera, also onto ascending interneurons. The latter transmit information to the brain where the final processing of acoustic information and a decision about motor output is performed (Fig. 7A,C; Bauer and Helversen, 1987; Ronacher et al., 1986). It is important to note that for encoding directional information in the brain, a comparison of the output from the ipsi- and contralateral ascending neurons is required. In crickets, the simplest version of neuronal elements and synaptic connections that process auditory information consists of only 3 bilateral pairs of interneurons (ON1, AN1, AN2, Fig. 7B), all three of which receive direct excitation from sensory neurons (Hennig, 1988; Pol-

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lack, 1994). Within the network, direction dependent inhibition is mediated by a central pair of local interneurons (ON1) that also exhibit reciprocal inhibition (Fig. 7B). Hence, pattern as well as directional information converges onto the same ascending auditory interneurons (AN1, AN2). The same basic circuitry also seems to exist in the thoracic auditory pathway of bushcrickets, although in this group more neuronal elements, like T-fibers, appear to be important and certain functional differences between potentially homologous interneurons may exist (e.g., in T-fibers: Atkins and Pollack, 1987; Faure and Hoy, 2000; Schul, 1997; Wohlers and Huber, 1982).

In grasshoppers, the ascending interneurons are functionally separated in elements coding for the sound pattern and those carrying directional information (Fig. 7D, Stumpner and Ronacher, 1994). Most local interneurons copy the temporal structure of a stimulus in their spiking pattern, but also account for the directional characteristics of ascending auditory interneurons by mediating contralateral inhibition. Presently, only two ascending interneurons AN1 and AN2 are suggested as candidates to encode directional cues (Rehbein, 1976; Rheinlaender and Mörchen, 1979; Römer and Rheinlaender, 1983; Römer et al., 1988; Stumpner and Ronacher, 1991, 1994). Both neurons are inhibited when the ear contralateral to the ascending axon is stimulated. However, it is not known which neurons mediate the inhibition (Fig. 7D). On the other hand, neurons coding for the song pattern sum ipsi- and contralateral inputs (Fig. 7D): local interneurons transfer excitation or inhibition (not shown) onto ascending interneurons, which therefore often exhibit complex patterns of EPSPs and IPSPs as well as optimum type intensity response curves (Table 1; Marquart, 1985a,b; Römer and Marquart, 1984; Stumpner and Ronacher, 1991).

An assessment of the effects of synaptic integration on the processing of directional information first requires a consideration of the neuronal code that is used. At the level of sensory neurons, a comparison of the left and right ear may exploit two types of information, that is, spike count and latency, both of which reflect intensity differences between the ears. In several neurophysiological experiments with AN1 in grasshoppers, it has been shown that both spike rate and latency differences could serve as directional cues (Rheinlaender and Mörchen, 1979; Römer and Rheinlaender, 1983). Römer and Rheinlaender (1983) used a procedure in which the neuron was stimulated from both sides independently. By increasing the stimulation from the inhibitory side, the excitatory response was cancelled out. Since the response latencies of both sides were not varied in this procedure, the differences in spike count alone served to determine directionality. In another experimental approach, the temporal occurrence of single excitatory and inhibitory potentials was varied without changing their intensity (Rheinlaender, 1984). If the excitatory input was delayed compared to the inhibitory input, the response of AN1 was suppressed, while in the reverse situation the excitation prevailed. In this case, only the temporal sequence of EPSPs and IPSPs was decisive to establish directionality. Thus, directional information may be represented by both a temporal as well as a rate code.

Enhancing Directionality by Inhibitory Processes

In the following section, we will focus on the effects of direction-dependent inhibitions that occur at the level of local and ascending interneurons (Fig. 7B,D) and their consequences on the ability for angular discrimination that are known from behavior. In the simplest case, contralateral inhibition may sharpen directional cues by mutual inhibition as, for instance, in the local ON1 interneurons of the cricket (Fig. 7B; Selverston et al., 1985; Wiese and Eilts, 1985). The cell ipsilateral to the sound source receives stronger excitatory input from sensory neurons than its contralateral counterpart. The inhibitory output provided by the ipsilateral cell will then reduce the spike count as well as increase the latency of the contralateral cell and thus enhance the directionality by affecting both coding principles for direction (see above).

In crickets, the reciprocal inhibition between the ON1s (Figs. 7B and 8A) was estimated to reduce the spike count by about 60% (Kleindienst et al., 1981), but complete inhibition may also be observed (see Fig. 8A). This enhanced binaural contrast suggests a function in improving the directional sensitivity of postsynaptic cells. Indeed, a direction-dependent reduction of spike count in the AN1 is presumed to be caused by the activity of the ON1 (Fig. 8B; Horseman and Huber, 1994; Stabel et al., 1989). The inhibitory input of ON1 follows the excitation of AN1 with a certain delay (Faulkes and Pollack, 2000). The precise timing of this inhibition from ON1 seems neither critical for the contrast enhancement of spike counts in AN1 (rate code), nor did the delayed inhibition amplify interaural time differences (temporal code). Therefore, a possible function of the delay in preserving existing interaural time differences was suggested (Faulkes and Pollack, 2000). Further evidence for the inhibitory effects of ON1 onto AN1 comes from experiments in which the activity of the ON1 ipsilateral to a sound source was decreased or eliminated and, therefore, the inhibitory input to the contralaterally ascending AN1 was removed. The ratio of spike counts between the two AN1 would then shift towards the contralateral one because the inhibitory input on the ipsilateral ascending AN1 is still effective. As supposed, this causes systematic errors in walking direction during positive phonotaxis (Atkins et al., 1984; Schildberger and Hörner, 1988). It is interesting to note that at the level of the local interneurons in crickets, the directionality cues from the periphery appear much enhanced (see Figs. 5A and 8A), whereas at the level of ascending interneurons (Fig. 8B) as well as the behavior (Fig. 6A) this is much less apparent.

The ON1 of crickets and bushcrickets (here often just called "omega" since in contrast to crickets no ON2 is known) bears great resemblance not only in morphology, but also in the reciprocal inhibition that enhances directional sensitivity (Fig. 8A,C). ON1 of both groups selectively encodes the temporal structure of a high-intensity signal when a low-intensity stimulus is presented simultaneously even though the low-intensity stimulus is clearly encoded when presented alone (Pollack, 1986, 1988; Römer and Krusch, 2000). The phenomenon of "selective attention" in the ON1 is suggested to be caused by inhibitory mechanism based on

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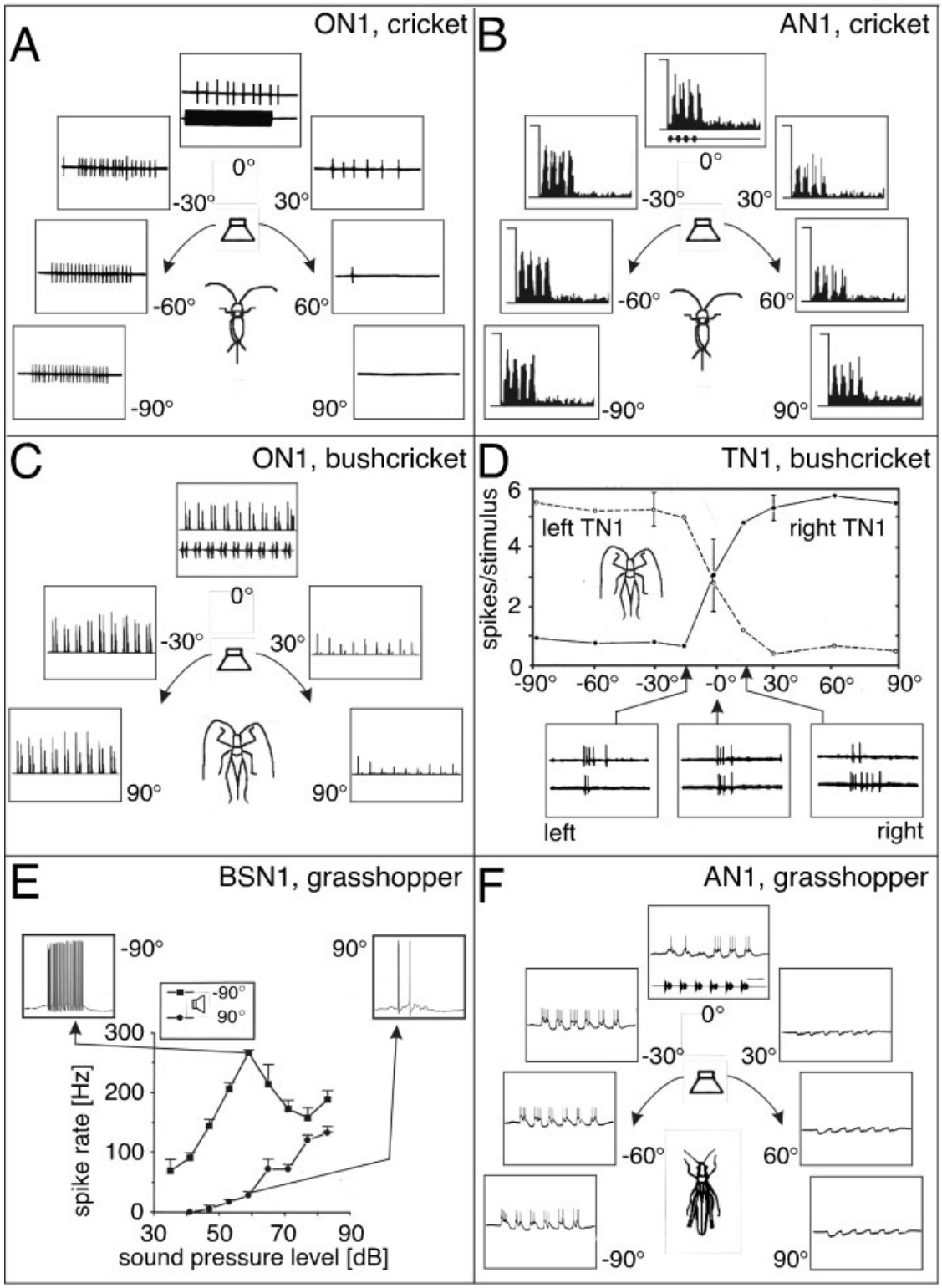

Fig. 8. Directional characteristics of local and ascending thoracic auditory interneurons at different stimulus angles are illustrated with sample recordings. A,B: Cricket, *Gryllus bimaculatus*. **A:** The extracellularly recorded ON1 in response to an unmodulated 4.5 kHz sine of 120 ms is shown (modified after Wiese and Eilts, 1985). **B:** PSTHs of an AN1 in response to an artificial calling song (modified from Stabel et al., 1989). C, D: Bushcricket, *Tettigonia viridissima*. **C:** The PSTHs indicate the response of an ON1 to a double pulse pattern (modified after Römer and Krusch, 2000). **D:** Averaged directional response of a pair of T-shaped interneurons (TN1) to different stimulus angles (modified after Rheinlaender and Römer, 1990). Spike recording are shown for −15°, 0°, and 15°. E, F: Grasshopper, *Locusta migratoria*. **E:** Averaged intensity response curve of a BSN1 for ipsi- and contralateral stimulation with 100 ms white noise pulses. Sample recordings at 59 dB from the left and the right side are shown as insets (modified after Franz and Ronacher, 2002). **F:** Intracellular recording of an AN1 in response to an artificial stridulation signal (modified after Rheinlaender, 1984).

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a calcium-dependent potassium conductance (Sobel and Tank, 1994). The directional characteristics of ascending auditory interneurons in bushcrickets are not known in detail, but contralateral inhibition in AN1 has been described (Stumpner, 1997). However, in bushcrickets the directional dependence of a T-fibre with ascending axon to the brain is much more pronounced than that of the AN1 in the cricket (Fig. 8B,D; e.g., Rheinlaender and Römer, 1980; Rheinlaender et al., 1986). By this pattern of activity, two acoustic hemispheres result, an observation that does not corroborate the angular discrimination ability observed in the behavior (Fig. 6B), but rather corresponds to the lateralization behavior known from grasshoppers (Fig. 6C, see, however, Rheinlaender and Römer, 1980). In grasshoppers, there is a neuronal correlate for the lateralization behavior by the previously mentioned ascending interneurons, AN1 and AN2. The directional characteristic of AN1 is divided in two hemispheres exhibiting excitation or inhibition, respectively (Fig. 8F, Rheinlaender, 1984). One of the presynaptic elements to AN1 is the local interneuron BSN1 that mediates excitation from the ipsilateral side (see Fig. 7D; Marquart, 1985b). At medium sound intensities, the directional sensitivity of BSN1 is not unlike that of the ON1s in crickets and bushcrickets (Fig. 8A,C,E) and hence lacks the strict "separation" into two hemispheres that is observed at the postsynaptic level (Fig. 8F).

The processing of pattern and directional information in parallel pathways as shown for grasshoppers causes a gain in precision for directional sensitivity and a loss of information about the temporal structure of the pattern in one pathway, and the reverse in the other (Stumpner and Ronacher, 1994). Thus, the copying fidelity for the temporal structure of a sound stimulus by the AN1 is poor even on the side where sound elicits an excitatory response. On the other hand, AN1 is very sensitive for the sound direction, especially in the frontal auditory field, which correlates with the lateralization in behavior. Also, the serial processing of crickets somehow reflects their ability for angular resolution. In crickets, AN1 is the most important element carrying information about conspecific song patterns and sound direction into the brain. It is, therefore, not surprising that neuronal cues (spike count and latency) do not unequivocally code for sound direction when stimulus angles are small.

Conclusion

Because of their small size and physical constraints, insects like crickets, bushcrickets, or grasshoppers, face problems in localizing a sound source. Although the tympanal organs of all three groups are highly selective for sound direction, differences in their directional characteristics occur already at the very periphery. Differences are also obvious in the behavioral performance of those animals: while crickets and bushcrickets exhibit a capacity for an angular resolution, the directional response of grasshoppers rather corresponds to a lateralization that is highly precise especially in the frontal auditory field.

Crickets and bushcrickets process pattern and directional information serially, whereas grasshoppers exhibit parallel processing. Consequently, in the cricket nervous system, information about the temporal structure of a stimulus and the sound direction converge onto the same interneurons. In grasshoppers, we find a functional separation of neurons processing either temporal pattern or directional information. Contralateral inhibition operates in both systems as an effective mechanism to sharpen the directionality of auditory interneurons. However, in the auditory pathway of crickets, this gain is opposed by a loss in the fidelity for pattern processing.

Possibly these different processing strategies indicate limitations and trade-offs of these small nervous systems. Ideally, one may expect that both pattern and directional information are processed in different channels in order to obtain the highest possible precision as observed in many vertebrates. Grasshoppers may increase their precision of lateralization for directional hearing by parallel processing at the cost of angular resolution. Crickets and bushcrickets may retain the capacity for angular resolution from the periphery at the cost of direction-dependent copying fidelity for acoustic patterns.

TEMPORAL PROCESSING

Signal Analysis and Pattern Recognition

Due to the limited capacity for spectral analysis in the auditory pathway of most insects (see FREQUENCY PROCESSING and Mason and Faure, pages 338–350, this issue), the information that is most relevant for the recognition of a conspecific song has to be extracted from the envelope of the acoustic signal. Hence, three important questions arise: (1) what kind of signal analysis is employed in the central nervous system, (2) what is the temporal resolution within the auditory pathway, and (3) what is the time window over which the analysis is performed and information is integrated? Once the answers to these questions are found by means of behavioral experiments, one may ask which neuronal mechanisms are actually involved in pattern processing. Here we would like to focus on the first two questions and then review how information about the signal envelope is represented in the activity of interneurons in the auditory pathway of two-model systems, that is "the" cricket and "the" grasshopper.

Processing of a signal envelope does not necessarily imply that signal analysis is performed in the temporal domain, since there are three basically different approaches by which information can be extracted from an envelope: (1) processing of the amplitude spectrum obtained by a Fourier transformation (FFT; Fig. 9), (2) processing by auto- or cross-correlation (Fig. 10), and (3) processing in the time domain (Fig. 11; see also von Helversen and von Helversen, 1998).

1. The mathematical concept and basis for the Fourier analysis of a "temporal" signal is the linear summation of frequencies that allows unequivocal reconstruction of the original signal. Therefore, for each frequency an amplitude as well as a phase is determined, the values of which give rise to the respective spectra (see Fig. 9A,B). In this example (Fig. 9A,B) of two signals with the same period of 100 ms but different duty cycles, the amplitude spectra are identical, while the phase spectra differ. In order to reconstruct these two patterns unambiguously from

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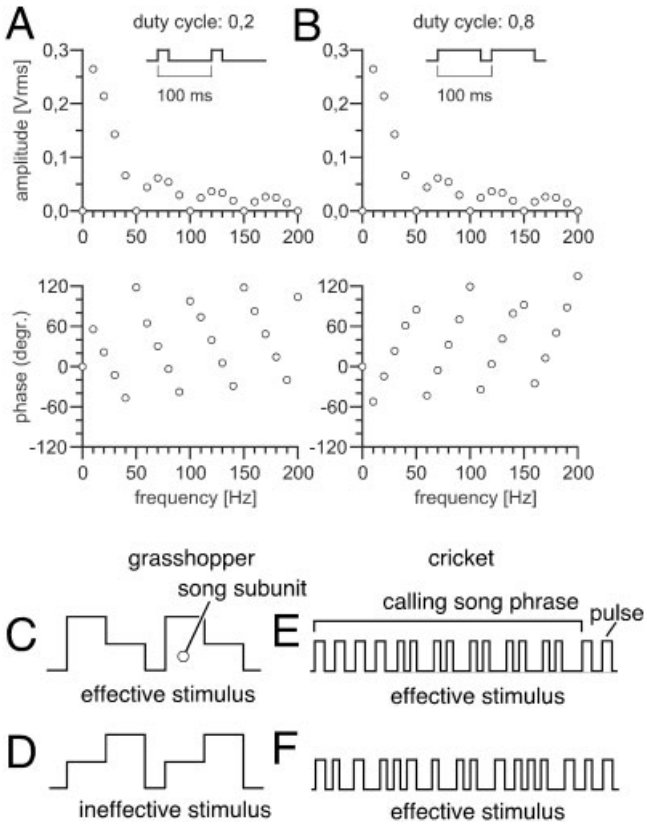

Fig. 9. Signal analysis by Fourier-transformation and experimental separation of amplitude and phase. **A, B:** Amplitude and phase spectra of two signals with the same period (100 ms), but different duty cycles are compared. While the amplitude spectra of both signals are the same, the phase spectra differ. Note that the amplitude spectra for the same period are only identical if the patterns are symmetrical in terms of pulse and pause durations as in A and B, but different if other duty cycle values are employed. The peak at 10 Hz, however, is always present for this stimulus period. For FFT computation, the mean amplitude was subtracted from both patterns and hence the DC-component (i.e., frequency of zero Hz) is zero for both spectra. **C, D:** Two signals that show the same amplitude spectrum, but different phase spectra. Note that the signal in D is the same as in C but played backwards (modified after von Helversen and von Helversen, 1998). **E:** One phrase of the regular calling song of a cricket (*Teleogryllus oceanicus*) is shown. **F:** The pulse periods are the same as in E, but the temporal order and thus the phase of the pattern is changed (shuffled song).

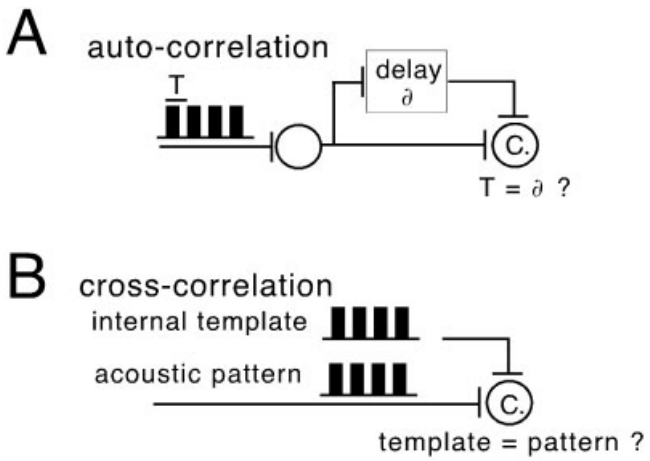

Fig. 10. Signal analysis by correlation. **A:** Auto-correlation: the incoming acoustic signal is delayed within the auditory pathway and then converges onto the same neuron (C) as the undelayed signal. The "C."-neuron acts as a coincidence detector and responds best if the pulse period of the signal has the same magnitude as the internal delay. **B:** Cross-correlation: the incoming signal is compared with an internal template. The coincidence-detector "C." will respond best if the pattern shows the same temporal structure as the internal template.

sine waves, the same set of frequencies at identical amplitudes is required, but the phase of each frequency would have to be different. Frequency analysis based on Fourier transformation usually refers to a spectral analysis by which only the amplitude spectrum is evaluated and the phase spectrum neglected. Then, the two signals shown in Figure 9A,B appear identical. On the other hand, if both the amplitude as well as the phase spectrum are evaluated during signal analysis, then this is fully equivalent to processing of the signal envelope in the time domain (as in Fig. 11). Hence, experiments in which the phase spectrum of the signal is changed, but the amplitude spectrum is kept constant allow for deciding whether a frequency analysis of the signal envelope is performed. Indeed, in a series of phonotactic experiments with *Teleogryllus oceanicus* females, Pollack and Hoy (1979) presented stimuli that contained the pulse periods of the conspecific calling song (Fig. 9E), but in a rearranged temporal sequence that followed a random pattern ("shuffled song," Fig. 9F). Thus, spectral amplitude information in terms of "natural" periods was retained, but the phase information of the calling song was dramatically changed. Surprisingly, crickets responded to such a random pattern of pulse periods almost as well as to the natural calling song (for similar results, see also Hennig and Weber, 1997). Although this finding may be interpreted as the result of a frequency analysis of the song envelope in the cricket brain, no evidence for this type of analysis was obtained in the sibling species, *T. commodus* (Hennig and Weber, 1997). For grasshoppers, von Helversen and von Helversen (1983, 1998) precluded a frequency analysis of the signal envelope by a very simple experiment in which an attractive signal (Fig. 9C) was played backward (Fig. 9D) and then became unattractive. Obviously, the amplitude spectra of the patterns are identical (Fig. 9C,D), while the phase spectra differ. On a larger time scale, phase information was also shown to be important in another grasshopper (*Chorthippus dorsatus*; Stumpner and von Helversen, 1992). Hence, present evidence from behavioral experiments does not support the view of a frequency analysis of the signal envelope in the cricket or the grasshopper, with the notable exception of *T. oceanicus* (see, however, below).

2. Auto- and cross-correlation analysis are widely used tools for signal analysis and detection in technical systems. Applied to processing within the auditory pathway of insects, an auto-correlation is assumed to compare the original signal with a delayed version by means of a coincidence detector that responds best if the pulse period of the signal has the same magnitude

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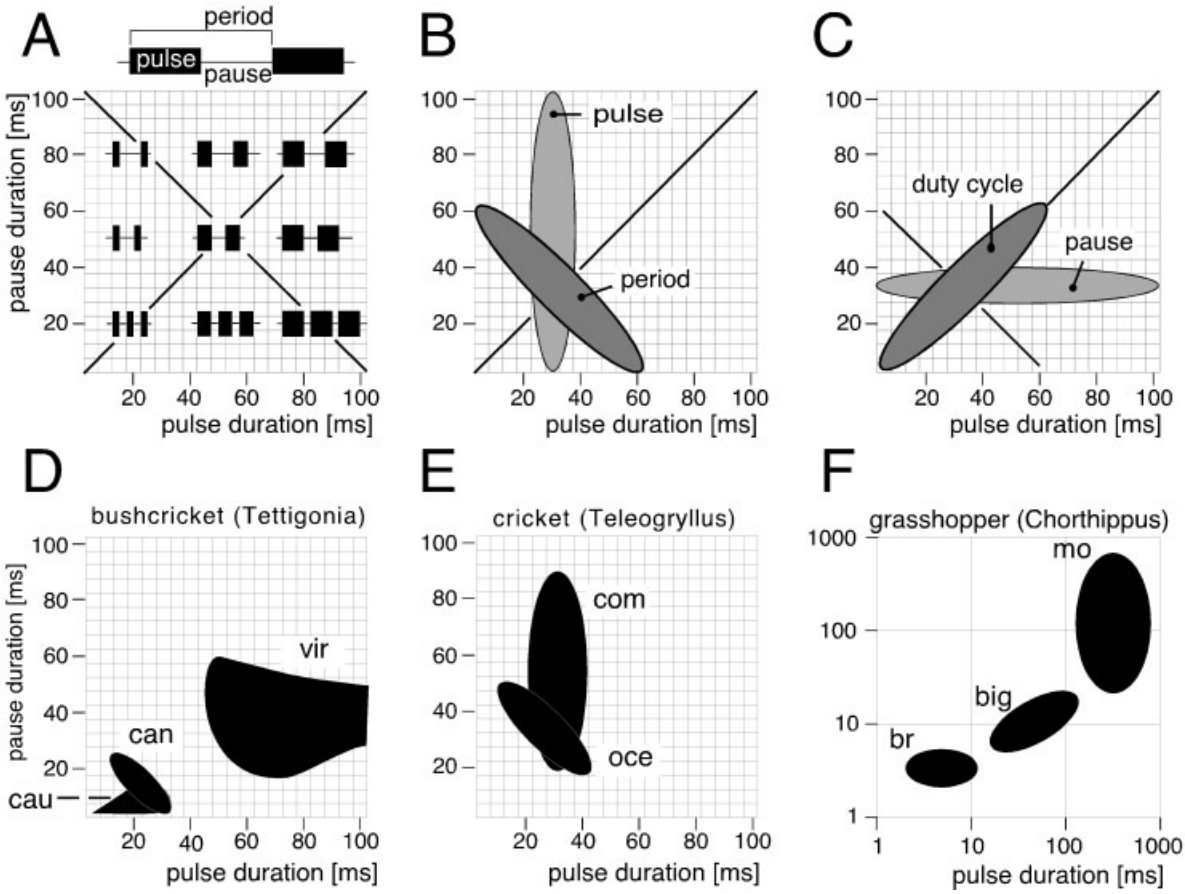

Fig. 11. Signal analysis in the time domain and measured response arrays. **A:** Periodical patterns that are built from pulses and pauses can be combined to form patterns with given duty-cycles and periods. In A, selected pulse patterns indicate the respective combinations of pulse and pause durations within such an array. Lines connect patterns that show the same period irrespective of the duty cycle (to lower right) and patterns with the same duty cycle but different periods (to upper right). **B, C:** Expected response arrays, if a receiver computes (B) the period or the pulse duration, or (C) the pause duration or a particular duty cycle. Note that the distinct receiver response arrays in B would return virtually the same results, if only patterns with the same duty cycle of 50% were used. Examples for B and C can be seen in D–F, which show response arrays from sibling and sympatric species in different Orthopteran groups: **D:** Bushcricket, *Tettigonia* (*Tett. cantans* (can), *Tett.caudata* (cau), *Tett. virdissima* (vir)). Carrier: broad band spectrum (redrawn from Schul, 1998). **E:** Crickets, *Teleogryllus* (*T. oceanicus* (oce), *T. commodus* (com)), Carrier: conspecific carrier frequency. (redrawn from Hennig, 2001). **F:** Grasshoppers, *Chorthippus* (*Ch. brunneus* (br), *Ch. biguttulus* (big), *Ch. mollis* (mo)). Carrier: white noise. Note the logarithmic scale on both axes (redrawn from von Helversen and von Helversen, 1994).

as the internal delay (Fig. 10A; see Reiss, 1964; Weber and Thorson, 1989). Due to its simplicity, in terms of known neuronal mechanisms such as delays and coincidence detectors, and the precise predictions about the filter characteristics for temporal patterns (see Weber and Thorson, 1989), this concept appears very attractive. On the other hand, a major objection concerns the rather long delays of 30–60 ms that are required for operation and that seem unrealistic for a small insect brain. However, the wide range of response latencies in auditory brain interneurons of the locust reported by Römer and Seikowski (1985) would easily accommodate delays of that magnitude. Nevertheless, to date no evidence is available to support this type of auto-correlation for pattern processing in insects. For a cross-correlation, an incoming signal is compared to an internal template (Fig. 10B). Presently, there is no evidence to support a correlation analysis of either version in insects. For crickets, it is the positive response to a "shuffled pattern" (Fig. 9F, Hennig and Weber, 1997; Pollack and Hoy, 1979) that is difficult to explain by a correlation analysis (for a summary of further arguments, see Weber and Thorson, 1989). For grasshoppers, von Helversen and von Helversen (1998) rejected the concept of cross-correlation on the basis of behavioral tests with numerous patterns of varying correlation coefficients with a presumed internal template derived from the song pattern. Nevertheless, cross-correlation is known, for instance, from bat echolocation (Simmons et al., 1990).

3. Processing in the time domain refers to the measurement of temporal features of a periodical signal, that is periods, durations, pauses, and duty-cycles (Fig. 11A–C). It is important to realize that in order to determine which type of temporal analysis is actually performed, a range of different combinations of pulse and pause durations have to be tested as illustrated in Figure 11. Numerous behavioral stud-

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ies have examined the characteristics of the recognition system with periodical stimuli in which the period of the stimulus was changed but the duty cycle kept at 50% in order to equalize the acoustic energy between stimuli. The test patterns then fall on a diagonal line, if plotted in an array of pulse and pause durations (Fig. 11A). However, such tests do not allow distinguishing between a range of temporal filters as shown in Figure 11 and indicated by the diagonal line that connects patterns of equal duty cycle of 50% (Fig. 11). Expected response arrays are sketched in Figure 11B,C, if period or pulse duration (Fig. 11B), pause duration, or duty cycle (Fig. 11C) is processed. To date, only a few studies present more elaborate test series in which not only the period of the stimulus was varied, but also other temporal parameters of the pattern (Fig. 11D–F). These studies revealed a plethora of response arrays that arose from temporal processing during which pulse durations (grasshoppers, crickets), pauses (grasshoppers, bushcrickets), periods (bushcrickets, crickets), or duty cycles (bushcrickets) of the signal were measured (Fig. 11D–F). Interestingly, the period response arrays in Figure 11D,E do not cover the whole range of possible duty cycles, but are reduced either at low (Fig. 11D) or high duty cycles (Fig. 11E). In view of the amplitude and phase spectra of Figure 9A,B these response arrays also provide evidence against a frequency analysis of the signal envelope, even for the cricket *T. oceanicus* that responds to the shuffled song pattern. From those experiments in which the response arrays were determined in more detail, two remarkable points emerged: first, rather different response arrays became evident that would not have been observed (or even misinterpreted) by keeping the duty cycle of the stimulus constant. Second, even in closely related species that likely share homologous neuronal circuits for pattern analysis, phenotypically very different response arrays emerged that still pose a major challenge in terms of evolutionary transformation of related neuronal mechanisms.

In summary, present behavioral evidence suggests that for intraspecific communication, insects process the acoustic signal envelope in the temporal domain rather than by a Fourier transformation or a correlation analysis. The question then arises whether and how these different features of the signal are extracted, encoded, and represented by interneurons at lower and higher levels in the central nervous systems of insects. An important question in this respect concerns the limits of temporal resolution that forms a prerequisite for the analysis and distinction of pattern envelopes within the auditory pathway.

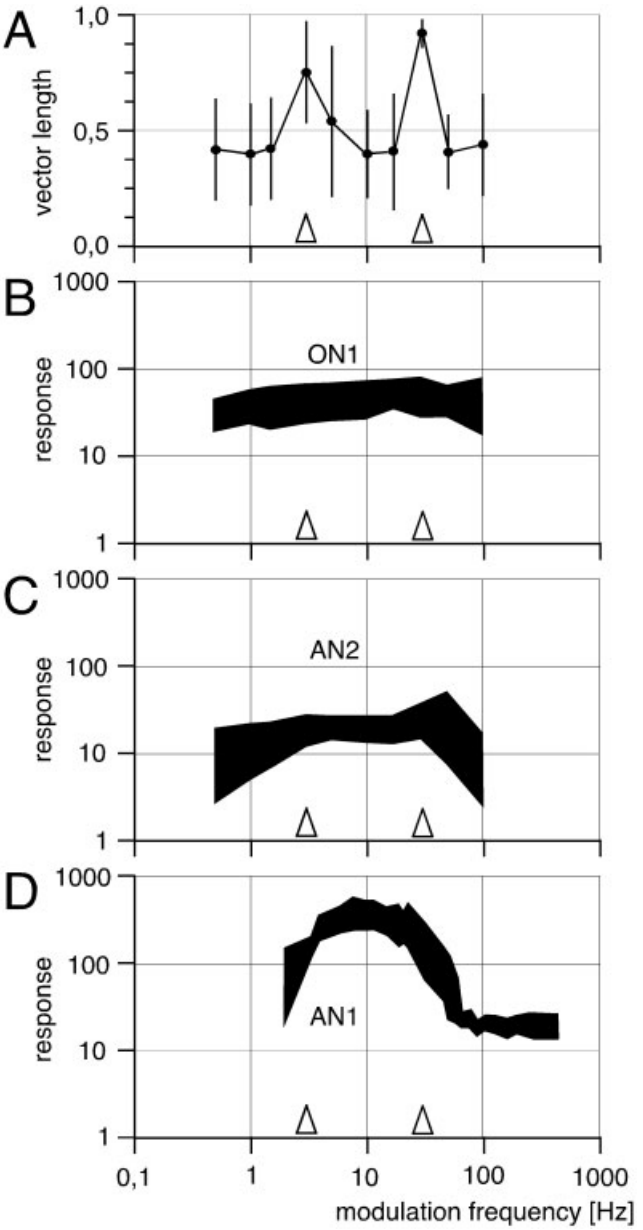

Fig. 12. Temporal modulation transfer function (tMTF) of thoracic interneurons in crickets measured with a sinusoidally amplitude modulated sine. **A:** Behavioral response of *Gryllus bimaculatus* showing enhanced phonotactic responses at 3 Hz (chirp frequency) and 30 Hz (pulse frequency). tMTFs of thoracic interneurons (**B**) ON1, (**C**) AN2, and (**D**) AN1 reveal no particular tuning neither to the lower chirp frequency nor the higher pulse rate within a chirp. Obviously, these neurons transmit the pulse pattern with equal fidelity over a wide range of pulse periods. Note that the ordinate in B–D represents scaled responses derived from a synchronization measure of spiking response. Ranges from 5–8 specimens of each interneuron are indicated. A–C redrawn from Wendler, 1990; D, *T. oceanicus*, Hennig, unpublished data.

Temporal Resolution and Synaptic Integration of Excitation and Inhibition Within the Thoracic Auditory Pathway in Crickets and Grasshoppers

Temporal resolution in the auditory pathway refers to the capacity to detect amplitude fluctuations in the signal envelope. In vertebrates, two paradigms are frequently used to determine the limits of temporal resolution, that is the temporal modulation transfer function (tMTF) and gap-detection (Michelsen, 1985). Both of those can be performed at the behavioral as well as the neurophysiological level (for a summary, see Prinz and Ronacher, 2002). An example for a behaviorally determined transfer function in crickets (*Gryllus bi-*

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maculatus) is shown in Figure 12A (Wendler, 1990). In this case, two peaks indicating preferred amplitude modulation frequencies emerge that correspond to the longer chirp period (at 3 Hz) and the shorter pulse period (at 30 Hz) of the calling song of this species (Fig. 12A). The data from thoracic interneurons (ON1, AN2, AN1) of crickets reveal that amplitude fluctuations are transmitted with high fidelity over a wide frequency range that encompasses the behaviorally relevant patterns (Fig. 12) (Wendler, 1990; for similar measures of AN1 and AN2, see also Tschuluuni, 1999). Hence, conspecific parameter values are not emphasized by these neurons.

In grasshoppers, a transfer function measured behaviorally (von Helversen and von Helversen, 1998) as well as in a modified gap-detection paradigm (see Fig. 13C) arrive at the same limit for temporal resolution of about 1–2 ms (behavior: von Helversen, 1979; von Helversen and von Helversen, 1997; CNS/AN4: Franz and Ronacher, 2002; Lang, 1996; Ronacher and Stumpner, 1988; Stumpner and Ronacher, 1994). At the thoracic level of processing, it is the synaptic integration in interneuron AN4 at which the limits of temporal resolution can be observed to arise from the different timing as well as time constants of inhibitory and excitatory input (Fig. 13).

A recent study addressing the capacities for information transfer at the peripheral level, i.e., receptors, in grasshoppers by using reverse reconstruction algorithms (Rieke et al., 1997) also suggests that most information is transmitted on a 2.5- to 5-ms time scale, which is a bit lower than the 1–2-ms gap detection threshold measured previously (Machens et al., 2001). An elaborate investigation of the temporal modulation transfer function (tMTF) that can be directly compared to psychophysical studies in vertebrates by using sinusoidal amplitude modulated (SAM) carriers performed on the auditory receptors of grasshoppers also confirms these results (Prinz and Ronacher, 2002).

These different conceptual approaches may help to reveal which features of a stimulus are transmitted or encoded in receptor firing and also produce common measures for the capacity of information transmission and temporal resolution at the receptor level. One should realize that between the so-called minimal integration time as derived from a tMTF and the minimal gap that is detected in a signal, there are still small but consistent discrepancies in insects as well as vertebrates (as summarized by Prinz and Ronacher, 2002). Presently, there is a need to apply these different methods to interneurons in the auditory pathway, first, in order to reconcile the known short time constants observed and, second, to elucidate the synaptic input patterns that may give rise to the limits of temporal resolution. Tentatively, the known patterns of synaptic input in the thoracic auditory pathway of insects that affect temporal resolution may be summarized under 3 headers: (1) excitation, (2) inhibition followed by excitation, and (3) excitation and simultaneous inhibition. (1) For excitation, it is mainly the different time constants of excitatory potentials that delimit temporal resolution. Numerous examples are known from "noctuid moths" (Boyan and Fullard, 1986; 1988; Boyan et al., 1990; Boyan and Miller, 1991) in which also rather short EPSPs are known to preserve the information

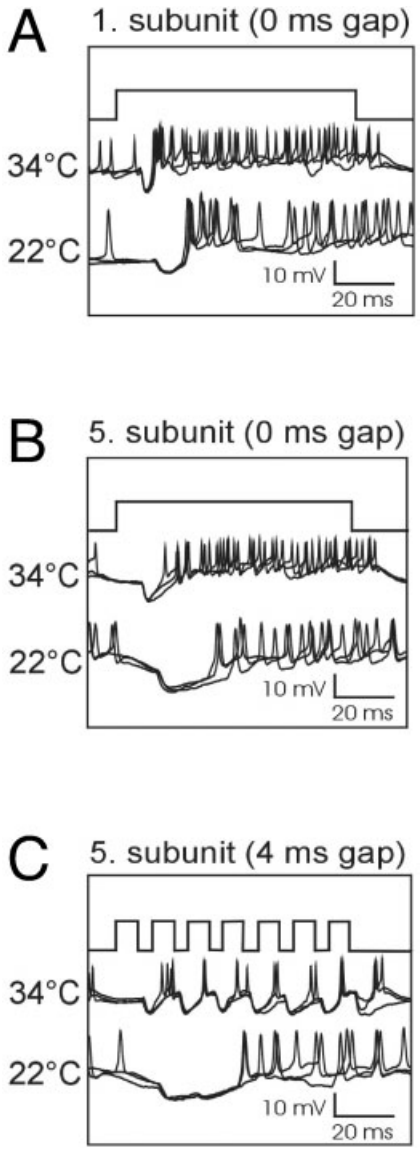

Fig. 13. Interplay of excitation, inhibition, different time constants, and adaptation, and their effects on temporal resolution and filtering in an ascending interneuron of the grasshopper (AN4; modified from Franz and Ronacher, 2002). **A:** Responses to a sound pulse (termed subunit) in which the time constants of excitation and inhibition changed due to different temperatures. **B:** Same as in A but after 400 ms of ongoing stimulation with a periodical pattern. **C:** Same as in B but with a subunit interrupted by gaps of 4-ms duration.

from a "fast" periphery (Michelsen et al., 1985; Surlykke et al., 1988). Integration of purely excitatory input is also commonly observed in grasshoppers (AN6; Stumpner, 1988), yet not in the "bottleneck" interneurons of the cricket auditory pathway (i.e., AN1, AN2, ON1; see Fig. 7; Horseman and Huber, 1994; Wohlers and Huber, 1982). Further improvement of temporal resolution by purely excitatory inputs may also be achieved by parallel input of many receptor fibers onto an auditory interneuron (Michelsen, 1985; Ronacher and Römer, 1985). (2) Inhibition followed by excitation is known for a range of auditory interneurons in grass-

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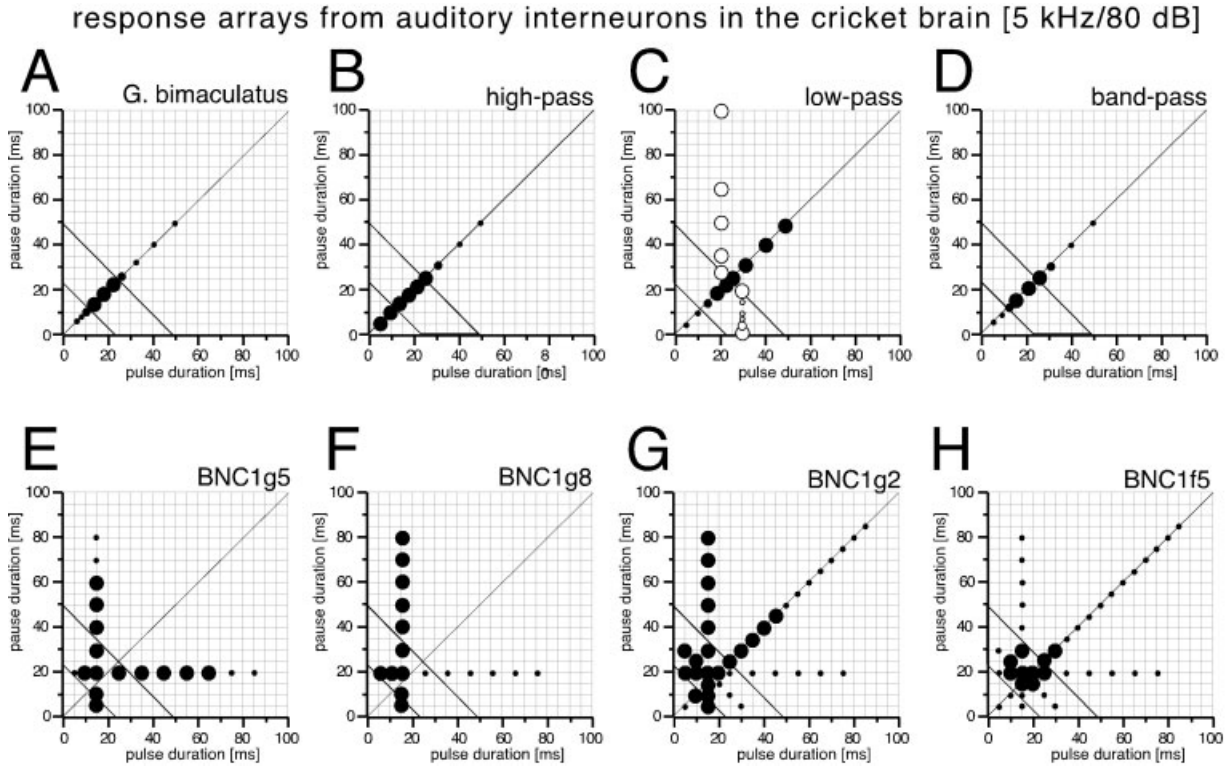

Fig. 14. Response arrays of auditory brain interneurons in the cricket *Gryllus bimaculatus*. **A–D:** The test patterns possessed the same duty cycle of 50% (diagonal line to upper right). Large dots: good response; medium-sized dots: intermediate response; small dots: weak or no response (black dots: redrawn from Schildberger, 1984; open dots in C: redrawn from Schildberger, 1985). A: Response array measured by a behavioral assay on a locomotor compensator. Lines from upper left to lower right mark the periods between which best responses were observed. B–D: Response array of interneurons known as (B) high-pass, (C) low-pass, and (D) band-pass filters. **E–H:** Response arrays of 4 brain interneurons measured along various axes within the array (calculated from Tschuluuni, 1999). Large dots: stronger response; small dots: weaker response. Response curves shown in Tschuluuni (1999) were transected at the 50% level. Note that the responses shown in E–H were recorded from identified high-frequency interneurons that were stimulated with low carrier frequencies. The strength of the responses plotted in E–H reflects synaptic input from low-frequency interneurons and may serve as a measure for their response properties.

hoppers (Römer et al., 1981; Römer and Marquart, 1984; Stumpner and Ronacher, 1994), most prominently for the interneuron AN4 that, due to this particular pattern of synaptic input, exhibits high sensitivity for small gaps in the song pattern (Fig. 13; Franz and Ronacher, 2002; Ronacher and Stumpner, 1988). This type of synaptic input is also known from auditory interneurons in cicadas (Münch, 1999) as well as interneurons in the olfactory pathway in moths (Christensen and Hildebrand, 1997). (3) Simultaneous excitation and inhibition is a common pattern to reduce the spike count and described for a number of auditory interneurons from various insect groups (Kalmring, 1975; Rheinlaender, 1975; Römer et al., 1981; Römer and Dronse, 1982; Römer and Krusch, 2000; Römer and Marquardt, 1984; Römer and Seikowski, 1985; Stumpner and Ronacher, 1991; Schul, 1997; Stumpner, 1999a). As yet, the type of delayed inhibition that accounts for period filtering in mammals (Grothe, 1994) is, to our knowledge, not described for the auditory pathway of insects (see however Faulkes and Pollack, 2000; Wiese and Eilts, 1985).

Generally, the precise effects of these different patterns of synaptic input on the limits of temporal resolution are less well understood, which is also due to the mostly unknown tMTFs within the respective auditory pathways. Although there clearly is some processing of temporal information at the thoracic level in grasshoppers as well as crickets (also note the views of serial or parallel processing of directional and pattern information in the previous section on directional hearing), there is no evidence for strongly enhanced responses of auditory interneurons to conspecific periodic signals at the thoracic level.

Response Arrays and Properties of Auditory Interneurons in the Brain of Crickets and Grasshoppers

The thoracic auditory pathways of crickets and grasshoppers transmit information about their acoustic environment with levels of complexity that are probably related to different evolutionary design, but the final analysis is performed in the brain (OSG). The prevalent concept of the past 2 decades of how information about the conspecific song pattern is extracted in a cricket brain is based on the finding of auditory interneurons that respond selectively to particular pulse periods (Schildberger, 1984). Then, the behavior-

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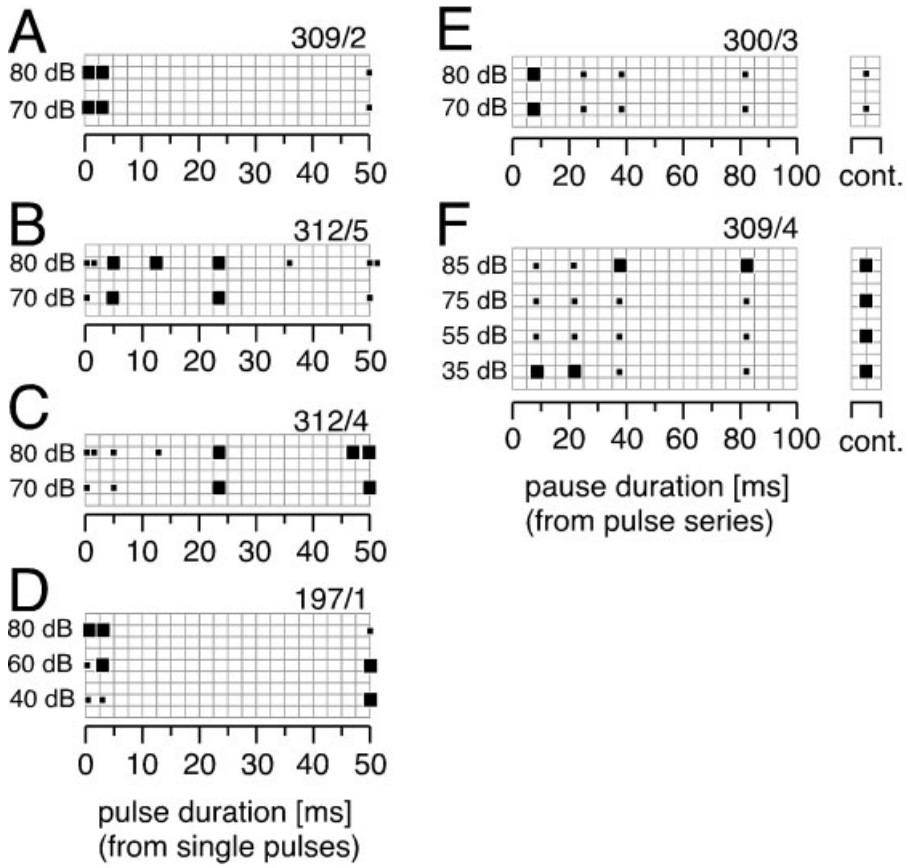

Fig. 15. Response types and arrays from unidentified auditory interneurons in the locust brain (modified from Adam, 1969). **A–D:** Responses of 4 interneurons to single stimuli of various duration at different intensities. Large squares: good response; small squares: weak response; 50% level was used for separation. Interneurons exhibit different selectivities for shorter pulse durations (A), medium pulse durations (B), and longer pulse durations (C). Interneuron in D responds stronger to short pulse durations at higher intensities, but to longer pulse durations at lower intensities. **E,F:** Responses of 2 interneurons stimulated with a pulse train of constant pulse duration (E: 16 ms, F: 17 ms), but varied pause duration at different intensities. Responses to a continuous, long pulse are shown to the right. The interneuron in E responds best to a pulse series with short pause durations, but fails to respond to a continuous tone. The interneuron in F responds strongly to continuous tones over a wide intensity range, but is inhibited by a periodical pattern at intermediate intensities. At low intensities, only patterns that possess shorter pauses (and thus periods) elicit at stronger response, while at higher intensities only patterns with longer pauses (and thus periods) drive the cell.

ally determined filter curve of *Gryllus bimaculatus* (Fig. 14A) can be understood as the result of a high-pass filter and a low-pass filter that converge onto a neuron that acts as logical "AND" and, therefore, shows band-pass characteristics (Fig. 14B–D; Schildberger, 1984). Bearing in mind, however, the remarkable diversity of response arrays known from behavioral investigations even in rather closely related species (Fig. 11D–F), the response characteristics known for behavior and interneurons of *G. bimaculatus* do not fully describe and thus do not allow an unequivocal view of the temporal filter processes. In the light of these limitations, recent data on identified auditory interneurons that reflect synaptic input patterns of low-frequency cells are important, since response arrays as in Figure 14E–H can be constructed (from Tschuluuni, 1999). While there are interneurons that appear to respond to a wide range of different combinations of pulse durations and pauses (Fig. 14E), other interneurons are more restricted (Fig. 14F–H). Notably, had the responses of these cells only been determined by periodical patterns with a duty cycle of 50% (see Fig. 14B–D), the response characteristics of interneurons in Figure 14G and H could also be classified as low- and bandpass filters, respectively. See, however, also the similar observation for a low-pass interneuron by Schildberger (1985; open circles in Fig. 14C). From these observations, however, one should not conclude that the concept of high-, low-, and bandpass neurons that form a filter for a small range of periods across a wide range of different duty cycles is invalid. First of all, corresponding response arrays are known (Fig. 11D,E) and, second, such filter characteristics were also described for vertebrate auditory pathways (frogs: Rose et al., 1985). Nevertheless, the response arrays of interneurons shown in Figure 14F,G could give rise to response characteristics known for other crickets (see *T. commodus* in Fig. 11D) that are difficult to deduce from filters for periods alone. Beyond this, with the assumption that a period filter composed from low- and high-pass characteristics represents an evolutionary ancestral design, it still remains a major challenge to convert known response arrays for period (Fig. 11D,E) to pause, duty cycle, or duration filters by changing the response characteristics of low- and high-pass filters, respectively (compare Fig. 11A,B and 14B,C; Schul, 1998).

In the cricket as well as the grasshopper, it remains unknown to date by which type of synaptic integration the filter and response arrays arise that can be observed experimentally (Adam, 1969; Schildberger, 1984; Tschuluuni, 1999). However, the response properties and arrays of auditory interneurons in the locust brain obtained by extracellular recordings from stone age suggest that the timing as well as time constants of excitatory and inhibitory input form the basis for pulse (Fig. 15A–D) or pause selectivity (Fig. 15E,F) or both (Fig. 16). Notably, some of these interneurons showed complex intensity dependence in their responses (Fig. 15D,F), which point to different thresholds for excita-

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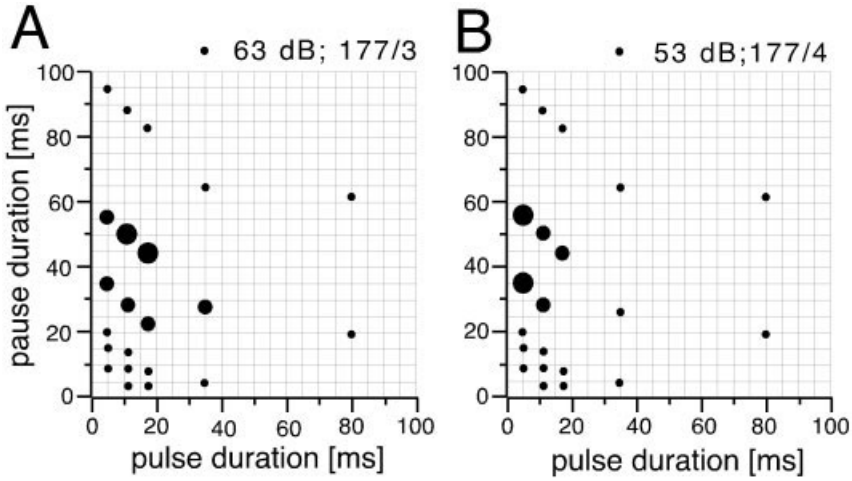

Fig. 16. Response arrays from 2 unidentified auditory interneurons in the locust brain measured along lines of the same period (modified from Adam, 1969). Large dots: strong response; medium-sized dots: intermediate response; small dots: weak or no response (compare Fig. 14). **A,B:** Both interneurons respond best to periodical patterns that exhibit pulse duration smaller than 30–40 ms and pause durations that range from 20 to 70 ms. Note that both interneurons were recorded in the same animal, the intensities in A and B differ, and interneuron 177/3 from A hardly responded at the intensity of 53 dB used for the neuron in B.

tion and inhibition. These patterns of synaptic integration that may account for the temporal filter properties of given brain interneurons would likely also produce intensity response curves that show an optimal intensity range as it is known from the behavior (von Helversen and von Helversen, 1997) as well as from numerous interneurons in "the" grasshopper (see Fig. 8E; Marquart, 1985b; Römer and Seikowski, 1985; Stumpner and Ronacher, 1991). Thus, the synaptic integration of excitation and inhibition not only deserves attention in terms of timing (Fig. 13) but also in terms of the respective thresholds, especially if the amplitude modulation of a pattern is important (see Fig. 9C,D). Adam (1969) did not only show and emphasize different time courses and patterns of excitation and inhibition in some of his recordings and noted their possible significance for selective responses to durations and pauses, but also observed response patterns that are reminiscent of the types described in the Nucleus cochlearis of vertebrates [see also Coro and Alonso (1989) for this kind of classification of responses of auditory interneurons in noctuid moth] by which temporal selectivity arises already in early stages of auditory processing. Even auditory interneurons with rebound phenomena were described (Adam, 1969) that today account for various types of selectivity towards periodical stimuli (duration in bats; Covey and Casseday, 1999; period in vertebrates: fish, Crawford, 1997; mammals, birds: see Langner, 1992).

At present there are clear deficits in our knowledge about the response types and arrays of auditory interneurons in insect brains. Some older (Adam, 1969) as well as recent (Tschuluuni, 1999) data extend our knowledge about the response patterns of individual brain interneurons. With respect to the neuronal mechanisms that can account for the described response arrays, Schul and Bush (2001) recently proposed a resonant mechanism for the period filter of *Tettigonia cantans* (see Fig. 11D) on the basis of behavioral experiments. This concept extends the present list of mechanisms for processing of temporal information in the auditory pathway of insects. Interestingly then, oscillatory responses from auditory interneurons in crickets were recently found (Fig. 17). While the neuronal

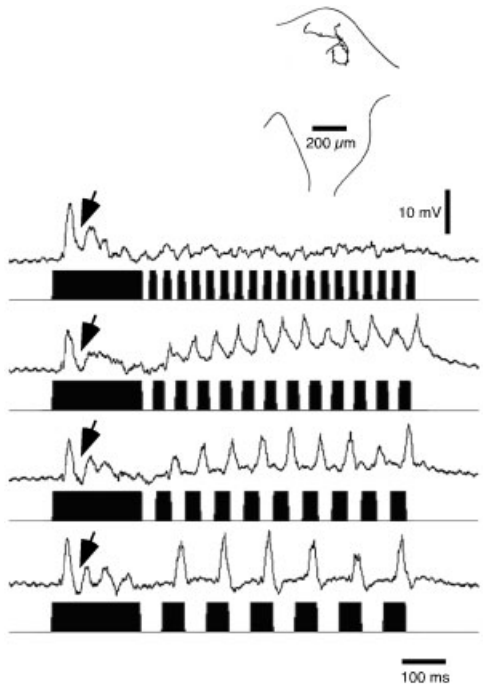

Fig. 17. Recording from an auditory interneuron in the brain of the cricket *T. oceanicus* (Hennig, unpublished observations). Stimuli consisted of a 200-ms pulse followed by a periodic pulse train with a duty cycle of 50% and varied pulse periods (carrier frequency: 4.5 kHz, 80 dB SPL). The response consists of graded potentials that occur periodically already during the first long, unmodulated tone burst (see arrows) and summate to an increased response level, if the period of the pulse train is similar to the period of the initial oscillations (second trace from top).

mechanism underlying such reverberations (arrows in Fig. 17) remains elusive at present and could be the result of a membrane property of that particular cell or a network property, it is exactly this kind of phenomena that is held responsible for a variety of stimulus encoding and filtering properties in rather different modalities as well as evolutionarily unrelated nervous systems, e.g., vertebrate auditory, vertebrate visual, vertebrate hippocampus, and locust olfaction.

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CONCLUSION

The present review constitutes an attempt to summarize the concepts and neuronal mechanisms of information processing in the auditory pathway of insects. We have referred to how auditory information is processed in the vertebrate auditory pathway wherever appropriate. A range of similar mechanisms is common to both groups, starting with the role of inhibitions at various levels of processing, that is, frequency, directional information, and temporal processing, and continuing to the level of design principles such as the parallel processing of otherwise conflicting types of information; grasshoppers (amplitude and time, i.e., barn owl), electric fish (amplitude and phase). For insects, a summary of the known and not so known mechanisms is given in Table 1 that refers to the single interneurons in the auditory pathway and indicates the references.

In contrast to vertebrates, almost everything of the processing of auditory information in an insect auditory pathway has to do with time. With respect to temporal resolution, it is remarkable that a small grasshopper with a rather limited set of auditory interneurons rivals many vertebrates in its capacity to detect small gaps in a signal envelope (Stumpner and Ronacher, 1994). Interestingly, this capacity did most likely not evolve in the context of acoustic communication but rather of predator detection, since it is a capacity that occurs also in grasshoppers that do not show much in terms of acoustic communication (i.e., the locust). Hence, there is a general design principle of the auditory processing in grasshoppers that probably also accounts for the separation of directional and pattern information that is not observed in such a clarity in other Orthopteran species. The reasons for these differences can only be understood in terms of their evolution (Schul, 1998; Stumpner and von Helversen, 2001; von Helversen and von Helversen, 1995).

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