Chapter 8
Central Neural Processing of Sound Signals in Insects

Berthold Hedwig and Andreas Stumpner

Abstract The sense of hearing contributes importantly to an animal's fitness. It allows detection of predators and prey and communication with conspecifics even in the dark and over large distances. Hearing organs evolved in about 20 groups of insects. Hearing is used by moths and other insects for avoiding predatory bats; by cicada, crickets/bushcrickets, moths, and grasshoppers for intraspecific communication; and by parasitic flies to locate singing hosts. Despite the variety of these insect groups, the neural processing of sound signals faces very similar fundamental challenges related to signal detection, directional processing, frequency discrimination, pattern recognition, and coping with self-generated noise. Solutions to these problems are implemented by specific network, cellular, and synaptic properties of neural circuits. Owing to their rather simple organization, insect auditory pathways can be explored and analyzed at the level of identified neurons to reveal fundamental mechanisms of auditory processing.

Keywords Auditory pathway • Corollary discharge • Feature detection • Interneurons • Neuropil • Pattern recognition • Reciprocal inhibition • Tonotopic organization

B. Hedwig (✉)
Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom
e-mail: bh202@cam.ac.uk

A. Stumpner
Georg-August-Universität Göttingen, JFB-Institut für Zoologie und Anthropologie, Schwann-Schleiden-Forschungszentrum, 37077 Göttingen, Germany
e-mail: astumpn@gwdg.de

8.1   Introduction

The sense of hearing contributes importantly to an animal's fitness. It allows detection of predators and prey and communication with conspecifics even in the dark and over large distances. It is therefore not surprising that, driven by natural and sexual selection, tympanal hearing organs evolved in about 20 groups of insects (Yager 1999; Strauß and Lakes-Harlan 2014; see Greenfield, Chapter 2). Hearing is used by moths and other insects for avoiding predatory bats; by cicada, crickets/bushcrickets, moths, and grasshoppers for intraspecific communication; and by parasitic flies to locate singing hosts. Despite the variety of these insect groups, the neural processing of sound signals faces very similar fundamental challenges related to signal detection, directional processing, frequency discrimination, pattern recognition, and coping with self-generated noise (Pollack 1998; Stumpner and von Helversen 2001; Hennig et al. 2004; Hedwig and Pollack 2008).

The challenges of auditory processing are similar not only across different groups of insects but also between insects and hearing vertebrates. What are the neural principles and mechanisms underlying auditory processing? Acoustic signals are first coded by a population of sensory afferent neurons that carry their spike activity to the central nervous system (CNS). Central neural mechanisms refine the functional properties of the auditory pathway through specific network, cellular, and synaptic mechanisms. As an advantage due to their rather simple organization, the auditory pathways in insects can be explored and analyzed at the level of identified neurons. Here the focus is on the processing of intraspecific communication signals for mate attraction; a review of auditory predator avoidance is given in Chapter 4 by Pollack (2015).

8.2   Overview of Central Auditory Pathways

Despite the variety in insect appearance and body structure, the "Bauplan" and organization of the CNS are highly conserved. The CNS comprises a series of segmental ganglia linked by longitudinal fiber tracts. Within the ganglia, specific regions of neuropils concerned with processing of specific types of sensory information can be recognized across insects. In some cases, individually identified nerve cells are homologous between segmental ganglia or even across insect groups (Boyan 1993). Developmental and evolutionary evidence (Yager 1999; Strauß and Lakes-Harlan 2014) indicate that hearing organs derived from chordotonal organs, which are mechanosensory structures found in many regions of the body in insects. Chordotonal-derived ears have evolved in the legs of crickets and bushcrickets, the lateral body wall of grasshoppers, the prosternum (chest) of parasitoid flies, a variety of locations in moths, and elsewhere in other insects (Fullard and Yack

1993; Fig. 8.1A). Owing to the preestablished afferent projection patterns of the nonauditory precursor organs within the CNS, afferent projections of auditory neurons, which may originate at very different locations, reveal a set of common features (Fig. 8.1B). Like many chordotonal afferents, the axonal projections within the CNS do not cross the midline and stay strictly ipsilateral with respect to the auditory organ. In the body segment that carries the auditory organ, afferent projections are restricted to the corresponding ganglion (e.g., in crickets, bushcrickets) or extend over several segments (e.g., in grasshoppers, mantis, cicada, moths, flies). Like other mechanosensory afferents, auditory afferents terminate in neuropils known as the ventral association centers of the thoracic ganglia (Fig. 8.1C), where they may form a specific "auditory neuropil." This neuropil is prominent in species with well-developed auditory pathways and may be tonotopically arranged in species with elaborate frequency processing (Römer et al. 1988; see Sect. 8.5).

The number of auditory afferents varies greatly among species; some moths employ only a single afferent and cicada, which have the most complex communication signals, use more than thousand (Yack 2004). At the thoracic level, activity is distributed to and processed by several classes of "auditory neurons"; see Boyan (1984) for a critical discussion of the term. Local neurons are contained entirely within a single segmental ganglion, ascending and descending neurons project to more anterior and more posterior ganglia, respectively, and so-called T-shaped neurons have both ascending and descending projections (Fig. 8.2). Many local neurons exhibit a bilateral functional differentiation, receiving input from afferents on one side of the ganglion and providing output via axonal projections to the contralateral neuropil, allowing for first-order binaural processing (see Sect. 8.4) in which also nonspiking interneurons may be involved (Stiedl et al. 1997). The dendrites of ascending interneurons may not be restricted to the auditory neuropil as they may receive inputs from other sensory pathways, for example, vibration. The axon can have projections on the contralateral side of the ganglion for local bilateral processing or forward activity directly toward auditory circuits in the brain. In Ensifera (i.e., crickets/bushcrickets) in which the auditory neuropil is located in the prothoracic ganglion, descending and T-shaped neurons carry auditory activity also toward the posterior thoracic ganglia, where it may be integrated into local motor circuits.

The number of ascending interneurons varies across taxa, revealing that different neuronal circuits evolved for auditory processing; there are only two in crickets (Wohlers and Huber 1982) and at least 4–5 in bushcrickets (Stumpner and Nowotny 2014), 15–20 in grasshoppers (Römer and Marquart 1984; Stumpner and Ronacher 1991), 6 in moths (Boyan and Fullard 1986), 3 in flies (Stumpner and Lakes-Harlan 1996), and 15 in cicadas (Fonseca and Correia 2007; Fonseca 2014), respectively. In some species, response properties of identified ascending neurons have been correlated with different aspects of auditory processing, including intensity tuning (see Sects. 8.3 and 8.5), directional tuning (see Sect. 8.4), and frequency tuning (see Sect. 8.5), indicating that already at the thoracic level, activity across the population of afferents is not just summed but also specifically processed before it is forwarded to the brain. The characteristic projection patterns of the ascending neurons
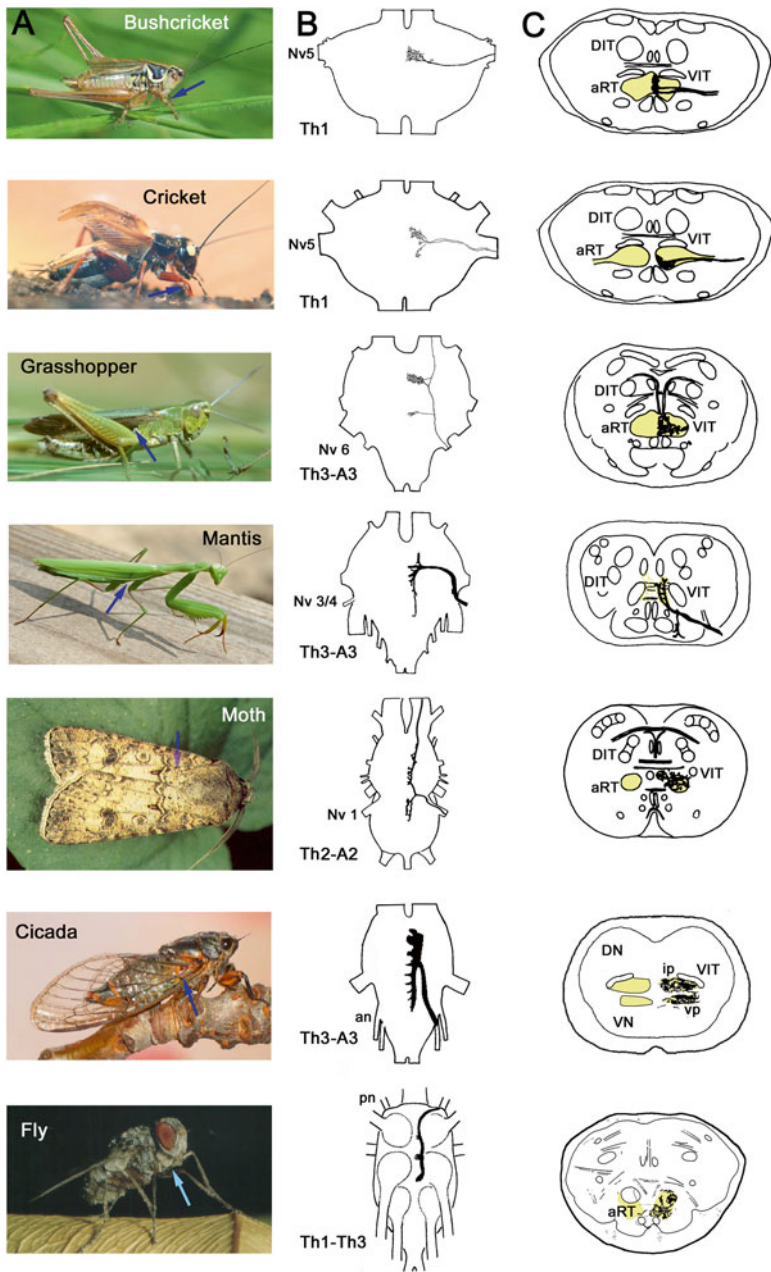
Fig. 8.1 Central auditory pathways. (**A**) Examples of insect taxa with tympanal hearing organs; position of organs indicated by *arrow*. (**B**) The central projection pattern of auditory afferents within the thoracic ganglia. (**C**) Details of the afferent axonal arborizations and auditory neuropils (marked in *yellow*) in the corresponding ganglia as indicated by transverse sections. [Image of mantis courtesy of C. Galand (www.entomart.be), image of moth courtesy of A. Surlykke, image of fly courtesy of K. G. Heller, all other images by the authors. Bushcricket afferent from Römer et al. (1988), cricket afferent after Eibl and Huber (1979), grasshopper afferent from Hedwig (1988), mantis afferent and section after Yager and Hoy (1987), moth afferent and section modified from Boyan et al. (1990), cicada afferent and section after Wohlers et al. (1979), fly afferent and
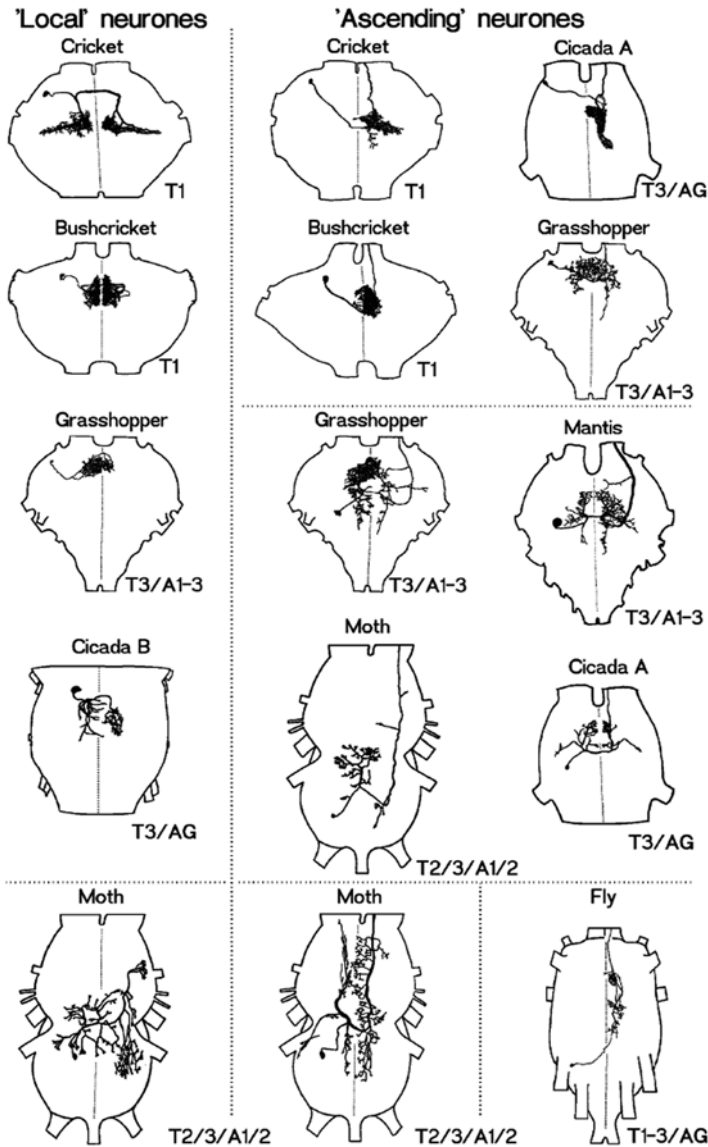
Fig. 8.2 Neuron types. Thoracic local and ascending auditory interneurons in different insects. Note the structural similarity between neurons within one class [From Stumpner and von Helversen (2001) with permission]

Fig. 8.1 (continued) section from Lakes-Harlan et al. (1999) and Stumpner et al. (2007), sections of bushcricket, cricket, and grasshopper modified from Boyan (1993).] an, auditory nerve; pn, prosternal nerve; DIT, dorsal intermediate tract; VIT, ventral intermediate tract; aRT, anterior ring tract; DN, dorsal neuropil; VN, ventral neuropil; vp and ip, ventral and intermediate projections of the sensory neurons, respectively

(see Sect. 8.6), together with behavioral evidence obtained after local temperature changes of the CNS (Bauer and von Helversen 1987) and after connective-lesion experiments (Pollack and Hoy 1981; Nolen and Hoy 1984; Dawson and Fullard 1995), indicate that the brain controls acoustically mediated behavior.

8.3 Intensity Coding

8.3.1 Overview

Intensity coding is important for judging the distance of a sound source, for directional decisions and may allow differentiating between individual conspecifics when independent (e.g., spectral) information about distance is available. It is based on the activity level provided by the auditory afferents in response to a sound stimulus of a given intensity (Fig. 8.3A, B).

Auditory afferents typically have a working range of 15–25 dB or occasionally up to 40 dB (Fig. 8.3B, C) between threshold and saturation (Mason and Faure 2004). They may also show nonmonotonic intensity response functions with decreasing spike rates at high intensities (e.g., in moths; Coro and Perez 1993; Fullard et al. 1998), which may be caused by mechanical properties of the ear. Within a population of afferents, individual cells often differ in sensitivity, so that their individual dynamic ranges begin at different threshold sound levels. This so-called range fractionation increases the overall dynamic range of the system (Rheinlaender 1975; Oshinsky and Hoy 2002).

The intensity dependence of auditory afferent responses translates stimulus amplitude into specific activity levels of first-order thoracic interneurons. Inhibitory neurons in the auditory pathway, with receptor-like phaso-tonic response patterns, are the basis for subsequent processing via reciprocal or lateral inhibition to sharpen directional and frequency-specific responses. In many interneurons, this leads to nonmonotonic intensity response functions (see Sect. 8.5).

Spike rate as well as response latency of sensory neurons and interneurons depends on sound intensity, with latency decreasing and spike rate increasing with intensity (e.g., Yager and Hoy 1989; Imaizumi and Pollack 2001).

Fig. 8.3 (continued) of the cricket *T. oceanicus* (4.5 kHz, 500 ms). The three curves are based on recordings at three different intensities. The inset below shows the stimulus and raster plots of five exemplary responses. (**F**) Intensity response functions of neurons in different insects, all responding (phaso-)tonically to white noise stimuli or stimuli at their preferred frequency. Note, the *x*-axis does not give absolute values; curves separated for clarity. Flies: *Homotrixa alleni* and *Therobia leonidei*; mantis: *Mantis religiosa*; cicada: *Tettigetta josei*; cricket: *Gryllus bimaculatus*; grasshopper: *Chorthippus biguttulus*; bushcricket: *Neoconocephalus ensiger* [(**A**) from Boyan and Fullard (1986); (**B**) modified after Boyan and Fullard (1988); (**C**) modified after Tougaard (1998); (**D**) modified after Surlykke et al. (1988) and Sabourin et al. (2008); (**E**) modified after Benda and Hennig (2008); (**F**) modified after Schildberger (1984), Yager and Hoy (1989), Stumpner and Ronacher (1991), Stumpner and Lakes-Harlan (1996), Münch (1999), Faure and Hoy (2000), and Stumpner et al. (2007); with permission]
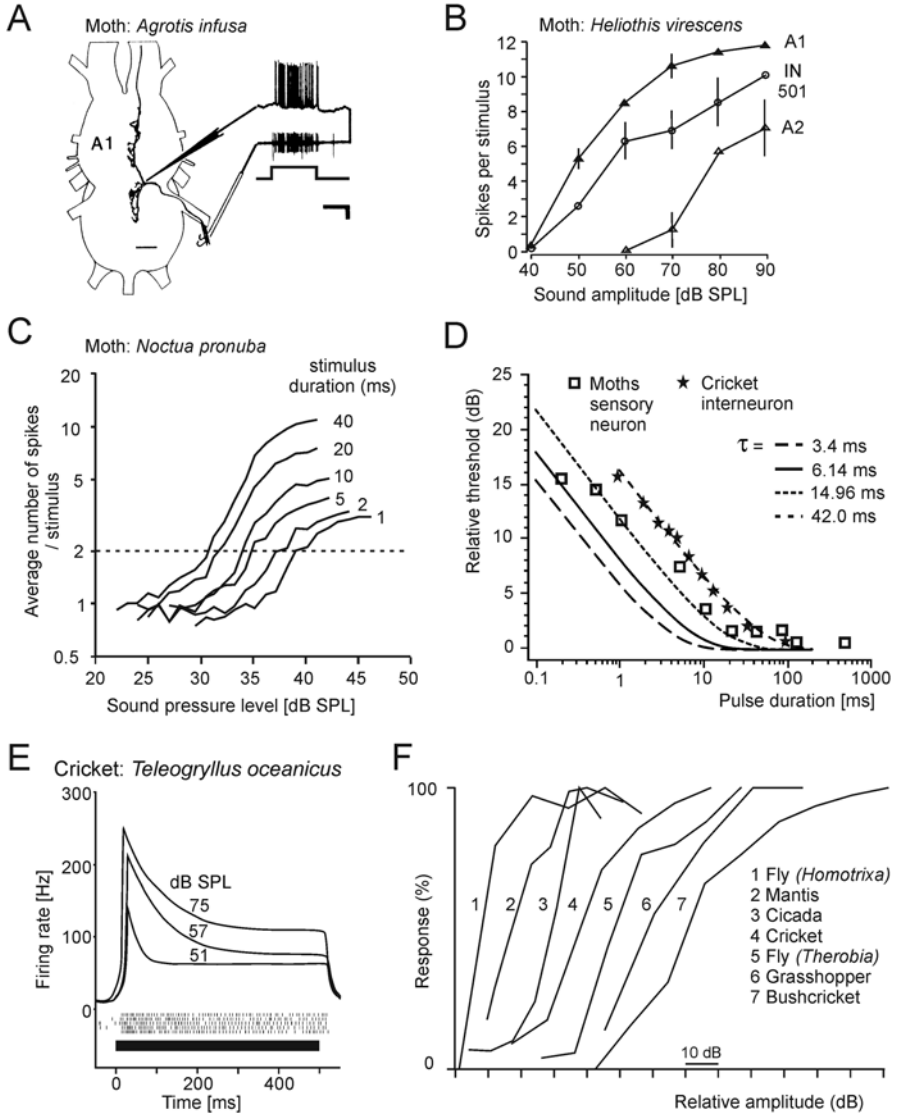
Fig. 8.3 Intensity functions. "Simple" responses and integration properties of primary sensory neurons and interneurons. (**A**) Extracellular and intracellular recording from an auditory sensory neuron (A1) in the moth *Agrotis infusa*. (**B**) Mean spiking response (±SD) of both auditory sensory neurons (A1, A2) and a tonically responding interneuron (IN 501) to 10-ms stimuli (16 kHz) of increasing sound amplitude. (**C**) Intensity response function of the A1 sensory neuron of the moth *Noctua pronuba* to stimuli of different durations. The stippled line indicates a threshold at two spikes per stimulus for calculation of data as in (**D**). (**D**) Dependence of threshold on pulse duration in sensory neurons and interneurons and graphs for various integration time constants [τ; $f(t) = -10 \log (1 - e^{-t/\tau})$] for two example insect neurons with $\tau = 14.96$ ms and 42.0 ms; data points from moth: *Agrotis segetum* sensory neuron ($n=9$) and cricket: *Teleogryllus oceanicus* ON1 interneuron ($n=11$). (**E**) Spike frequency adaptation in a tonically responding interneuron (AN1)

8.3.2   Temporal Integration

Insect ears integrate energy in the temporal and in the spectral domain (Tougaard 1998; Gollisch et al. 2002). As a consequence, the threshold of auditory primary sensory neurons depends on the intensity and duration of a stimulus. In a moth sensory neuron, the threshold decreases by up to 20 dB between 0.1-ms and about 30-ms pulse duration (Fig. 8.3C, D; Surlykke et al. 1988). In the simplest case, first-order local or ascending auditory interneurons show afferent-like responses with respect to stimulus integration times, and thresholds, like those of afferents, decrease with increasing stimulus duration (Fig. 8.3D) (Faure and Hoy 2000; Sabourin et al. 2008). The integration time constants of sensory neurons and interneurons range between 6 and 70 ms and clearly depend on carrier frequency, with a considerably shorter time constant at an ultrasonic compared to a sonic frequency. These values, however, are affected by additional factors such as the nonlinearity introduced through choosing a certain spiking response as threshold criterion. Using methods that avoid such nonlinearities, an energy detector in moths has been estimated to have a time constant shorter than 4 ms (Tougaard 1998).

Temporal integration also can be a means of protecting the animal from false alarms. Neural filtering against low-intensity background noise, for example, occurs at the level of single thoracic neurons in moths and crickets/bushcrickets. In an identified moth interneuron, the amplitudes and integration times of afferent-triggered excitatory postsynaptic potentials (EPSPs) are such as to cause only brief, subthreshold interneuron responses when the afferent fires below approximately 100 spikes/s, as occurs during spontaneous activity or when the insect is exposed to low-intensity ultrasound (Boyan and Fullard 1988; Fullard 1998). Only high-rate firing of the afferent, as elicited by the echolocation calls of hunting bats, can depolarize the interneuron to spiking threshold.

8.3.3   Adaptation

Responses of auditory primary sensory neurons generally copy the amplitude envelopes of pulsed sound stimuli, but they are phaso-tonic in nature. That is, for long-lasting stimuli, the initially high firing rate drops by 20–50 %, reaching a steady-state level only after about 100 ms (e.g., Fullard et al. 1998; Gollisch et al. 2002). This drop of activity to an unchanged stimulus is called adaptation and generally facilitates the detection of changes in stimulus level and helps to maintain a neuron's responsiveness. Although the rate and extent of adaptation vary according to neuron type, sound intensity, and in some cases carrier frequency, the overall effect is to emphasize pulse onsets and brief pulses in acoustic signals (Ronacher and Hennig 2004). Extremely phasic responses occur in some receptor neurons of the parasitoid fly *Ormia ochracea*, which produces only a single spike at stimulus onset regardless of stimulus duration or intensity (Oshinsky and Hoy 2002).
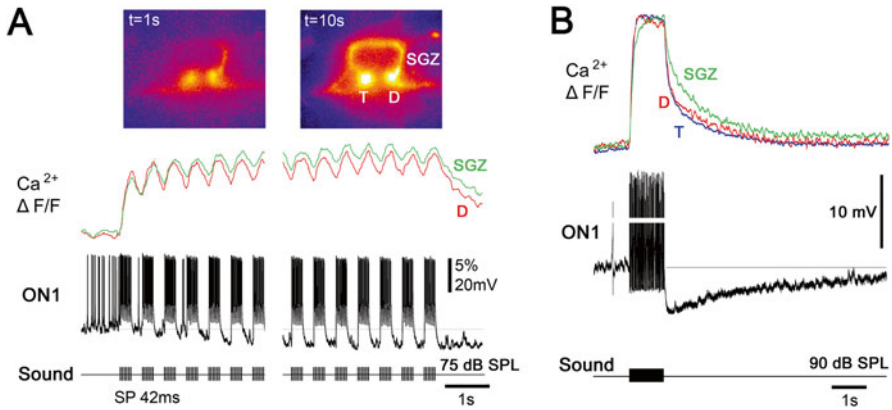
Fig. 8.4 Imaging calcium changes during signal processing. Changes in cytosolic calcium concentration as indicated by Oregon Green BAPTA-1 and intracellular recorded neuron activity during acoustic stimulation in a cricket ON1 neuron. (**A**) Repetitive stimulation with calling song causes an increase in the calcium indicator fluorescence signal that is modulated in the pattern of the sound stimulus and coupled to the spike activity. Over the course of acoustic stimulation, the membrane potential becomes more negative in line with the calcium increase; the initial background activity of the neuron is suppressed. (**B**) Calcium increase and neural activity during a 1-s acoustic stimulus. After the stimulus, the calcium signal gradually decreases in the different compartments of the neuron and the membrane potential recovers from hyperpolarisation. D, dendrites; T, axon terminals; SGZ, spike-generating zone; SP, syllable period [From Baden and Hedwig (2007) with permission]

As in receptor neurons, adaptation in tonic interneurons depends on intensity and can be fitted to linear first-order dynamics (Fig. 8.3E; Benda and Hennig 2008). Also like receptors, interneurons, in all taxa, may exhibit phaso-tonic firing patterns and saturating intensity response functions (Fig. 8.3B, F). The spike activity of these neurons copies the amplitude modulation of the stimulus (see Ronacher, Chapter 9) and forwards this activity for further processing toward the brain (see Sect. 8.6). In interneurons that integrate the inputs from many sensory neurons, the dynamic range may reach 60 dB or more (Rheinlaender 1975; Faure and Hoy 2000).

Intensity filtering provides a mechanism akin to selective attention. The cricket ON1 interneuron and thoracic interneurons in bushcrickets will respond to the louder sound only when two series of low- and high-intensity pulses are presented simultaneously (Pollack 1988; Römer and Krusch 2000). Continuous acoustic stimulation causes a gradual hyperpolarization of these interneurons, with the consequence that EPSPs triggered by low-amplitude stimuli, which are effective to elicit spiking when presented alone, remain subthreshold. The hyperpolarization of the membrane potential is coupled to an increase in the cytosolic calcium level (Sobel and Tank 1994; Baden and Hedwig 2007), which in turn is thought to activate an outward potassium current with a time constant of several seconds (Fig. 8.4A, B).

The response characteristics of interneurons depend on ambient temperature as insects are ectothermic organisms (Janiszewski and Otto 1989); robust auditory processing therefore needs to compensate for any changes in overall activity level.

8.4 Directional Processing

8.4.1 Background and Behavior

Directional processing of sounds is crucial for phonotactic orientation toward mates or prey and for predator escape responses. These behaviors pose different demands on auditory processing. During a phonotactic approach, sound intensity will increase, whereas during an escape it will decrease; also, there is only one correct direction in an auditory approach, whereas for an escape there are many, making escape responses generally less directional.

For the detection of sound direction, binaural animals rely on differences in responses of the two ears and may therefore exploit interaural time differences (ITDs) and/or interaural level differences (ILDs). These bilateral differences decline to zero as the angle of sound incidence approaches the animal's longitudinal axis. In insects, because of their small size, the bilateral time differences per se may be minute as sound takes only approximately 15 μs to travel between ears 5 mm apart. ILDs caused by sound diffraction depend on sound frequency and body size, which has a stronger effect on signals with short wavelength. As a result of sound diffraction at a cricket's body, ILDs for the calling song may be in the range of only 1–2 dB (Michelsen et al. 1994) and may not be detectable at all in parasitoid flies that localize the same signals (Robert et al. 1996). The biomechanical properties of the hearing apparatus, however, may transform and enhance the biophysical differences (Robert et al. 1996; Michelsen 1998), leading to significant bilateral differences in auditory afferent activity (see Windmill and Jackson, Chapter 6).

Different species show varying degrees of accuracy in orienting toward a sound source. Acoustically guided turning behavior of male grasshoppers is almost errorless when sound arrives from the side but becomes inaccurate in the frontal ±30° (von Helversen 1997). Bushcrickets require stimulus angles of 6–10° and 1-dB amplitude difference to turn significantly toward the more strongly stimulated side (Rheinlaender et al. 2006; Römer 2015). In contrast, parasitoid flies (Mason et al. 2001) and crickets (Schöneich and Hedwig 2010) demonstrate hyperacute directional sensitivity, especially in the frontal range of sound incidence where, in crickets, a bilateral intensity difference of only 0.4 dB is sufficient for precise orientation.

Three parameters of the bilateral afferent activity can be used to determine sound direction (Mason and Faure 2004). First, at the population level, a larger number of afferents will respond in the auditory organ driven by the louder sound (Madsen and Miller 1987; Oshinsky and Hoy 2002). Second, firing rates and spike counts of individual afferents will increase with increasing stimulus strength. Finally, response latency, which may be coded with extremely low temporal jitter (Oshinsky and Hoy 2002), decreases with increasing stimulus level. Spike rate and response latency are physiologically tightly coupled (Mörchen et al. 1978), but they can be dissociated under experimental conditions to reveal their individual impacts on the activity of directional interneurons (Rheinlaender and Mörchen 1979) and on

behavior (von Helversen and Rheinlaender 1988). In behavioral tests on acrid grasshoppers, bilateral differences in stimulus level of 1.0 dB, and 0.5-ms latency differences are sufficient to allow reliable orientation to the side of the louder or earlier sound.

Directional responses at the interneuron level arise from a combination of excitation by ipsilateral acoustic stimuli and inhibition by contralateral stimuli (Gerhardt and Huber 2002; Hedwig and Pollack 2008). This processing of afferent inputs at the level of the thoracic interneurons enhances bilateral auditory contrast. The underlying neural mechanism is based on reciprocal or recurrent inhibition and is best understood in a pair of mirror-symmetrical omega-shaped interneurons (ON1; Fig. 8.5A) in the cricket prothoracic ganglion (Wohlers and Huber 1982; Wiese and Eilts-Grimm 1985). Dendrites of ON1 are restricted to one side of the ganglion, and the axonal projections overlap with the dendritic arborization of the contralateral ON1 neuron. Each neuron receives excitatory input from the afferents ipsilateral to its dendrites and monosynaptically inhibits its contralateral partner (Fig. 8.5B, C; Selverston et al. 1985). Owing to their reciprocal inhibitory connections, the ON1 neuron that is activated with a shorter latency and stronger excitation will inhibit its contralateral partner, reducing excitation and thereby also diminishing any recurrent inhibition (Fig. 8.5C). With this mechanism in place, directionality at the interneuronal level is greatly enhanced in comparison to the afferent activity (Fig. 8.5D; Boyd and Lewis 1983; Larsen et al. 1989).

As the interneuron responses become side specific, they clearly separate the left and right auditory hemispheres except in the frontal region, where the difference in activity of the left and right neurons varies linearly with stimulus direction (Fig. 8.5E). This characteristic of direction-dependent responses due to reciprocal inhibition also occurs in the ON1 of bushcrickets (Römer and Krusch 2000; Molina and Stumpner 2005). A modeling approach to the function of the inhibitory circuitry, however, implies a less significant effect of contralateral inhibition (Horseman and Huber 1994).

Bush- and tree-dwelling insects need to orient in a complex three-dimensional habitat, where orientation in elevation, as well as in azimuth, is necessary. Bushcrickets employ active scanning movements with their body that in principle could provide information about the elevation of a sound source and may require comparison of sequentially acquired auditory activity. Processing of elevation cues has recently been explored at the peripheral and central level of neuronal responses (Kostarakos et al. 2007; Römer 2015; Lakes-Harlan and Scherberich 2015).

8.4.2   Integration of Directional Cues with Motor Responses

Little is understood at a cellular level about how directional auditory cues are integrated into motor activity. Within the CNS, two different routes may be employed. Afferent activity could be forwarded directly to motor networks, resulting in bilaterally different reflex-like motor responses as in negative phonotaxis of flying
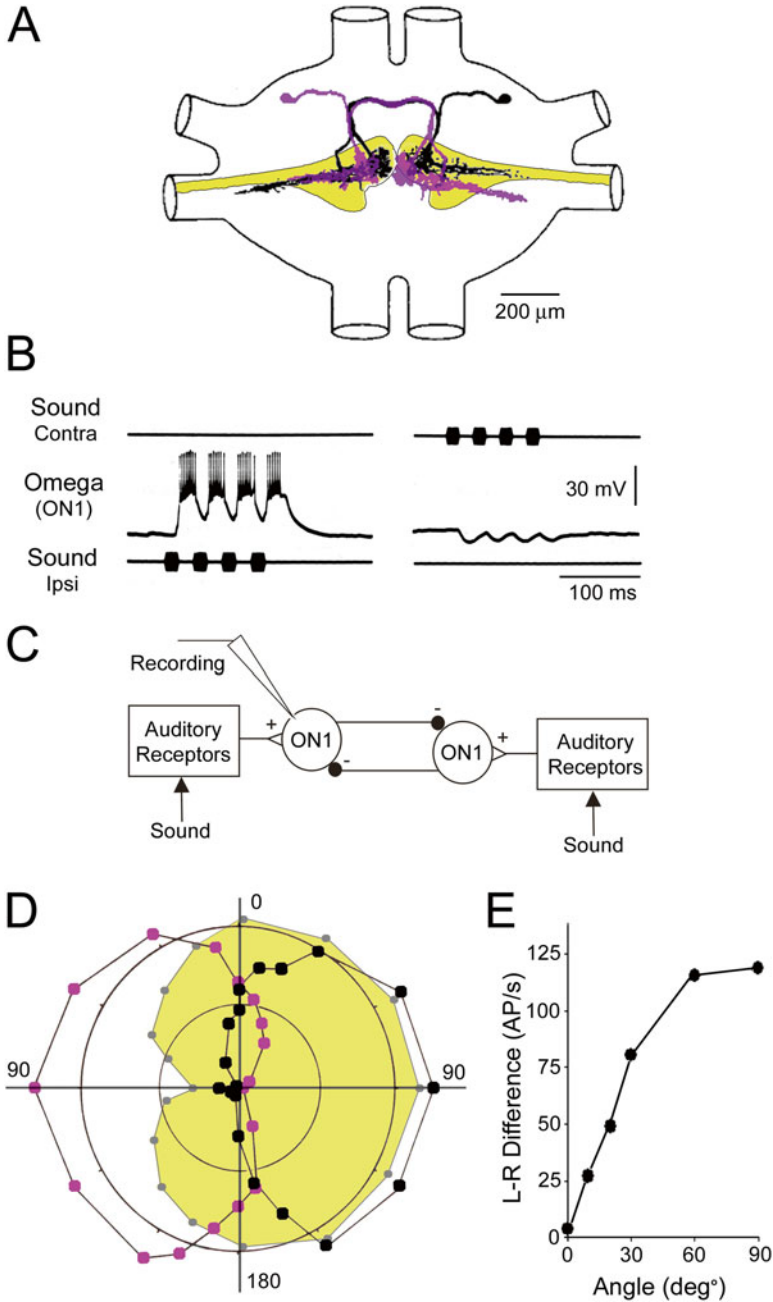
Fig. 8.5 Directional processing. Bilateral auditory contrast enhancement by reciprocal inhibition in the cricket auditory pathway. (**A**) Projection of auditory afferents (*yellow*) and of the left (*magenta*) and right (*black*) omega neurons (ON1) in the prothoracic ganglion. Dendritic and axonal arborizations of the neurons overlap with the afferent projections. (**B**) Acoustic stimulation of the ipsilateral ear elicits EPSPs and a spiking response whereas stimulation of the contralateral ear

crickets (Pollack and Hoy 1981) or as indicated by the short latency steering responses of phonotactically walking crickets (Hedwig and Poulet 2004). In the locust, interneurons receiving auditory inputs evoke flight motor and steering responses (Boyan 1984; Baader 1991), and a particular multimodal neuron, can trigger hind leg motor responses (Pearson et al. 1980). As another possibility, directional information is processed in the brain and leads to precise descending directional steering commands. Such commands have not yet been identified at the neural level.

8.5 Frequency Processing

8.5.1 Hearing Ranges and Organization of Afferents

Hearing in insects covers the sonic and ultrasonic ranges (Pollack and Imaizumi 1999). Sound frequency may be used to discriminate among predators, heterospecifics, and conspecifics but also to distinguish rivals from mating partners (von Helversen and von Helversen 1997; Pollack 2015). Frequency processing starts with a biomechanical frequency segregation in the sound-sensitive structures of the ear (see Windmill and Jackson, Chapter 6), which provides the basis for frequency tuning of auditory afferents in various types of ears (Hedwig and Pollack 2008). In moths, which have only a few primary auditory neurons, each afferent represents the full hearing range of the species (about 5 kHz to more than 100 kHz) and there is no basis for frequency discrimination in the auditory pathway (Surlykke 1984). In contrast, in the hearing organ of bushcrickets, up to 40 or more sensory neurons are each specifically tuned to a different sound frequency. Their cell bodies are arranged strictly tonotopically in the hearing organ as are their central axonal projections in the auditory neuropil (Fig. 8.6A, B; Oldfield 1983; Römer 1983). The overall hearing range, from about 2 kHz to 80 kHz or higher, is much broader than that of a single sensory neuron and provides the basis for subsequent frequency processing within the CNS (Stölting and Stumpner 1998).

Fig. 8.5 (continued) causes only IPSPs (inhibitory postsynaptic potential). (**C**) Diagram for the reciprocal inhibition circuit in the auditory pathway. Each ON1 also inhibits contralateral ascending interneurons, which are not shown. (**D**) Directional response of the right auditory afferents (*yellow*) and of the left (*magenta*) and right (*black*) ON1 neuron. (**E**) The difference in bilateral ON1 activity of the animal, calculated from the data in (**D**), indicates in the frontal range (±30°) a linear relation to the angle of incidence with a slope of about 3 AP/s per degree. Inner and outer circles in (**D**) indicate 50 AP/s and 100 AP/s activity level for ON1; the maximum left–right response difference of the afferents corresponds to an intensity difference of 25 dB [ON1 structure and afferent projections redrawn from Wohlers and Huber (1985); intracellular recording of ON1 from Wohlers and Huber (1982) with permission; afferent activity redrawn from Boyd and Lewis (1983); ON1 activity redrawn from Wiese and Eilts-Grimm (1985)]
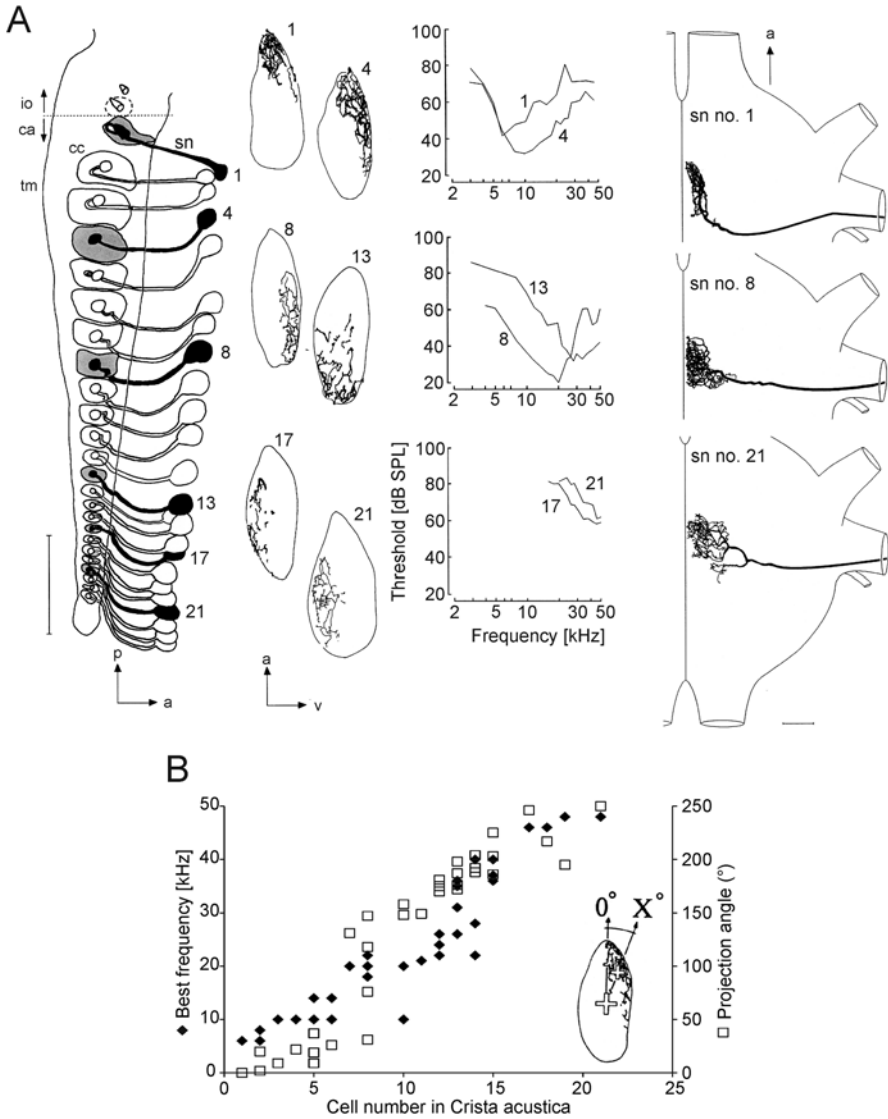
Fig. 8.6 Tonotopy. Arrangement of sensory neurons in the hearing organ (crista acustica) and projection of the sensory axons into the prothoracic ganglion of the bushcricket (*Pholidoptera griseoaptera*). (**A**) Six out of 24 cells in the crista acustica are marked (*black*) and their projection in the auditory neuropil (sagittal sections) and their frequency tuning are shown. Numbers refer to the position in the crista acustica. For three cells, the view of the prothoracic projection in the horizontal plane is given. ca, crista acustica; io, intermediate organ; tm, tectorial membrane. (**B**) Frequency of peak sensitivity ("best frequency") and projection angle ("X°") within the auditory neuropil (see inset; orientation as in **A**) for various sensory neurons recorded in different individuals of *P. griseoaptera* [Modified after Stölting and Stumpner (1998) with permission]

Grasshoppers and crickets have two hearing ranges peaking at lower sonic and ultrasonic frequencies. Even though there are three or four classes of sensory neurons in grasshoppers, their sensitivity clearly is highest either at low or at high frequencies (Halex et al. 1988; Jacobs et al. 1999). The hearing range of crickets is similarly organized to that of grasshoppers (Imaizumi and Pollack 1999). There is a categorical processing of frequencies in crickets, which show positive phonotaxis to sound signals in the sonic range and negative phonotaxis to ultrasonic signals, as in bat avoidance behavior (e.g., Wyttenbach et al. 1996). A number of further taxa, however, are not yet well studied. Cicadas can have extremely complex amplitude- and frequency-modulated calling songs (Gogala et al. 2004). Ears with more than 1,000 auditory afferents and the responses of interneurons indicate sophisticated frequency processing in the CNS (Fonseca et al. 2000; Fonseca 2014). Also in parasitoid flies, with about 50–250 sensory neurons per ear, both physiological (Stumpner et al. 2007) and behavioral (Rosen et al. 2009) results demonstrate frequency discrimination.

8.5.2 Afferent Activity Is Sharpened by Presynaptic Inhibition

In the CNS, frequency processing occurs as early as at the terminals of the afferent neurons, which are subject to frequency-specific presynaptic inhibition. Presynaptic inhibition modulates the efficiency of synaptic transmission. It is mediated by GABAergic (GABA = γ-aminobutyric acid) inputs to the afferent terminals, which cause a depolarization of membrane potential (primary afferent depolarization [PAD]) due to an increased chloride conductance. The conductance increase reduces the amplitude of the invading spikes, with the result that the release of neurotransmitter is also reduced (Watson et al. 2005). Close to the axon terminals of bushcricket afferents, PADs occur that are tightly coupled to the invading spikes (Fig. 8.7A; Baden and Hedwig 2010). These depolarizations are of central origin, although the responsible presynaptic neurons are not yet known. On acoustic stimulation, the spiking response is superimposed on a maintained PAD during which the spike amplitudes decrease. The generation of PADs is sensitive to picrotoxin, which blocks GABAergic synapses.

Ultrastructural studies (Fig. 8.7B; Hardt and Watson 1999) show input synapses to afferents from GABA-immunoreactive processes of unidentified central interneurons. In bushcrickets PADs are driven mainly, but not exclusively, by stimuli from the same side as the respective sensory neuron. This can be demonstrated by removing the ipsilateral ear, which removes all spiking activity of sensory neurons, revealing small-amplitude PADs on their terminations. These PADs then have to be of contralateral origin. Comparing the Ca^{2+} response of the afferent terminal before and after the ipsilateral ear is removed (Fig. 8.7C, D) demonstrates that tuning of the PADs in some afferents is similar to the tuning of their spike activity. In others, however, the frequency range of PADs is below or above that of the excitation, indicating that presynaptic inhibition may sharpen frequency-specific synaptic transmission of afferent activity to postsynaptic neurons.
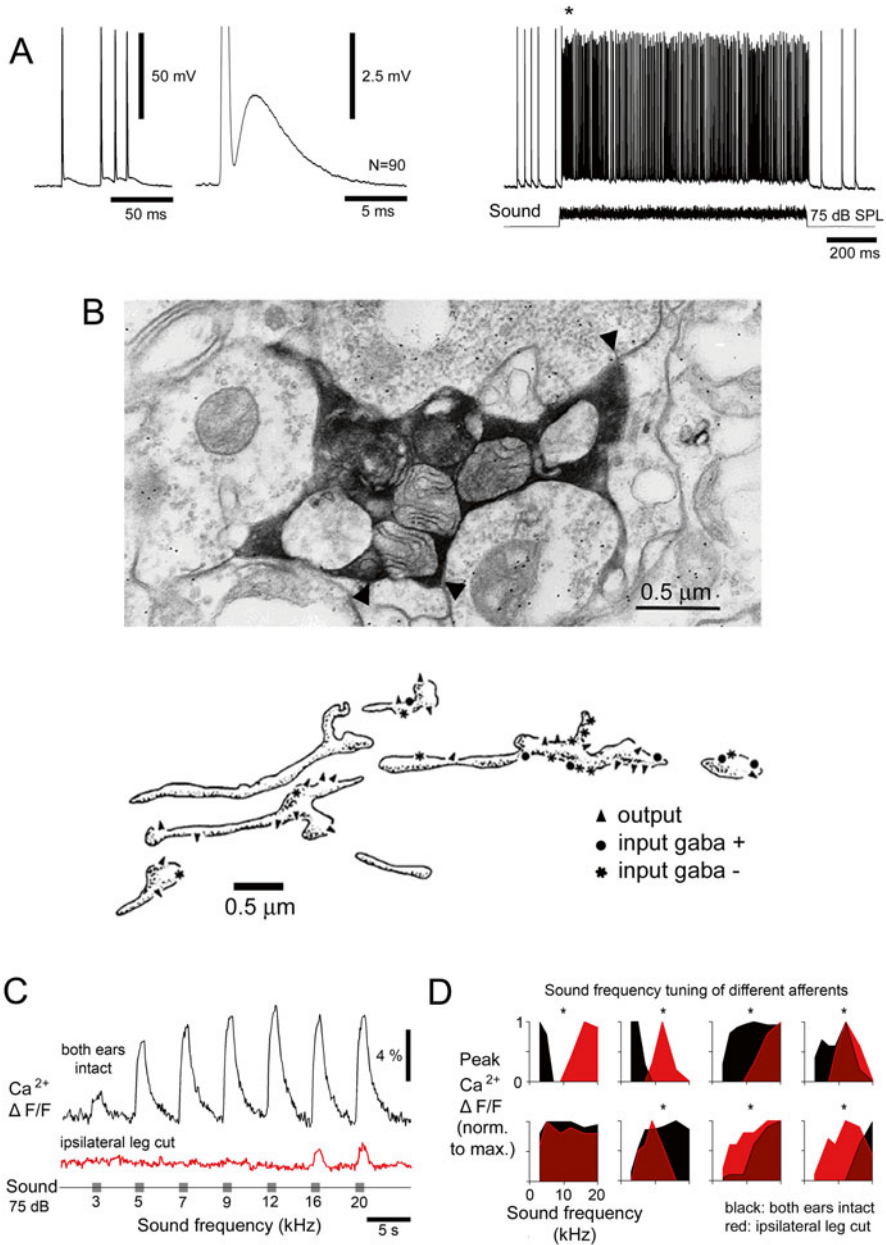
Fig. 8.7 Presynaptic inhibition. (**A**) Intracellular recording of a bushcricket (*Mecopoda elongata*) auditory afferent close to its axonal terminals in the prothoracic ganglion. *Left*: A graded primary afferent depolarization (PAD) of 2.5 mV is coupled to the end of each spike. *Right*: On maintained acoustic stimulation [white noise, 75 dB sound pressure level (SPL), 1 s] spikes ride on top of the PAD and spike amplitude is reduced, most pronounced at the stimulus onset (see asterisk). (**B**) *Top*: Ultrastructural evidence for GABA-immunoreactive processes forming synapses (*arrowheads*) on the terminals of an auditory afferent (*black*) tuned to 6 kHz in the bushcricket *Tettigonia cantans*.

8.5.3   Interneurons

While a tonotopic ordering of the central projections occurs in species with differently tuned sensory cells (grasshoppers, crickets, bushcrickets), this is less clear for interneuronal arborizations. Dendrites of some interneurons show overlap with restricted regions of the afferent projection (Römer et al. 1988); however, as interneurons also connect to other interneurons, they may branch throughout the entire neuropil, even when they receive only restricted auditory input. In crickets, correlations between low- or high-frequency tuning and anatomical characteristics of a number of mostly second-order or higher interneurons such as soma position and axonal projection in a connective have been described (Atkins and Pollack 1987).

In addition to presynaptic inhibition of afferents, frequency-specific synaptic inhibition occurs at the level of thoracic interneurons (Römer et al. 1988). Pharmacological experiments in a bushcricket revealed that this inhibition is picrotoxin sensitive; its elimination further reveals excitation by sound stimuli that initially elicited purely inhibitory responses (Fig. 8.8A–D; Stumpner 1998). Inhibitory synaptic processing therefore contributes to sharpening the frequency tuning of neurons. Among closely related species of phaneropterine bushcrickets, species-specific tuning of interneurons may be determined entirely by differences in the strength of inhibitory input (Stumpner 2002). A sharpening of frequency tuning will also occur if a neuron reaches threshold only when presynaptic firing rate is high enough to produce sufficient temporal summation and if the presynaptic firing rate depends on carrier frequency, as has been described for a bushcricket brain neuron (Ostrowski and Stumpner 2010). The Q_{10dB} value is a measure of the sharpness of tuning, that is, the higher the value, the sharper the tuning. Whereas afferents may have Q_{10dB} of up to 4, interneurons can reach a Q_{10dB} of 7. However, the Q_{10dB} values of many afferents and interneurons are in the same range of 0.5–2 (Hennig et al. 2004). The sharpness of tuning may be relevant for reducing interneuronal responses to ambient noise as compared to conspecific signals, especially in species-rich communities (Schmidt et al. 2011).

Frequency-specific inhibition also leads to complex intensity response functions of interneurons (Fig. 8.8C, F). A neuron that, at its preferred carrier frequency, receives a tonic excitation that increases with sound intensity may show an optimum-type response and a strong decrease of its activity at higher sound intensities

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Fig. 8.7 (continued) *Bottom*: Reconstruction through branches of a 20-kHz afferent shows the distribution of output synapses (*arrowheads*) and input synapses from fibers that were labeled (gaba+, dots) or unlabeled (gaba–, stars) by GABA antibodies. (**C**) Cytosolic calcium change measured in the axonal terminals of an intact afferent (*black trace*) demonstrates a broad frequency tuning of the response. After the ear and spike-generating structure were removed (*red trace*), the remaining response is tuned to high frequencies only. (**D**) Different tuning of the calcium signal imaged in intact (*black*) and spike-generating zone-deprived (*red*) afferents demonstrates a different tuning of the presynaptic signal that may sharpen frequency-specific synaptic transmission. *Asterisks* indicate significant differences [(**A**), (**C**), and (**D**) from Baden and Hedwig (2010) with permission; (**B**) from Hardt and Watson (1999) with permission]
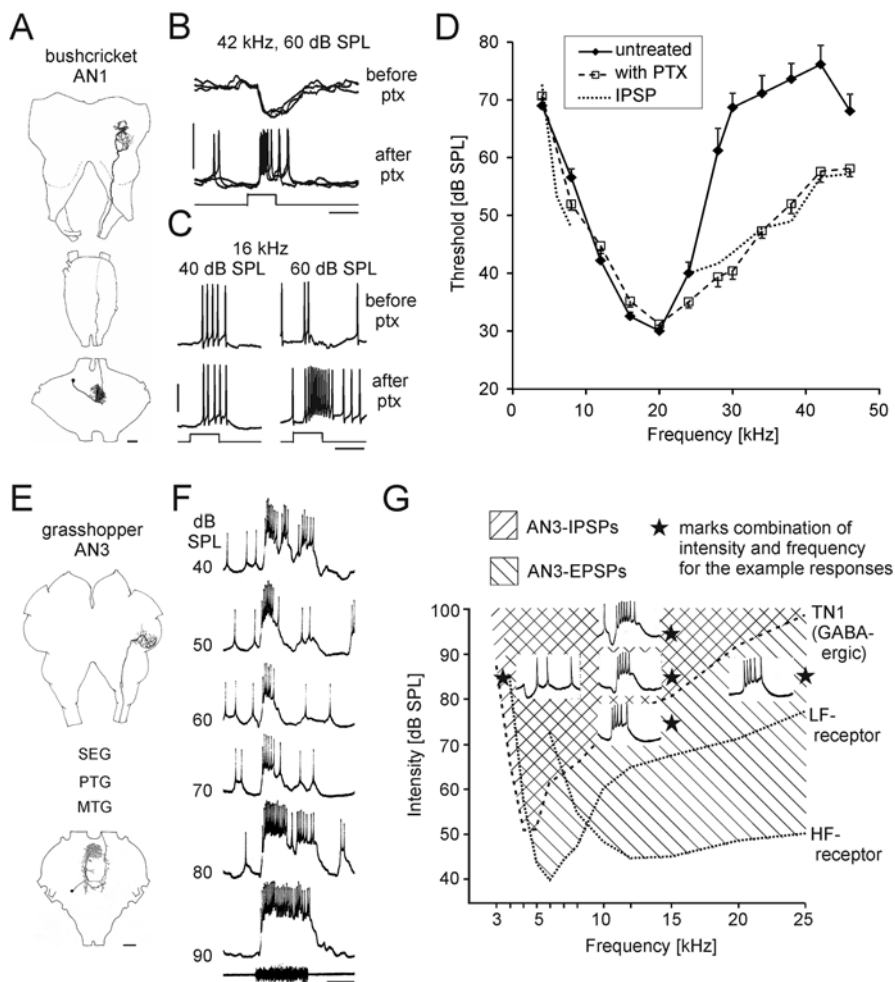
Fig. 8.8 Frequency processing. "Complex" responses to carrier frequencies and intensities in auditory interneurons. (**A–D**) Ascending auditory interneuron AN1 of the bushcricket *Ancistrura nigrovittata*. (**A**) Structure of the AN1 neuron in the prothoracic and subesophageal ganglion and the brain. (**B, C**) Responses to a 42-kHz stimulus and a 16-kHz stimulus before and after application of the chloride-channel blocker picrotoxin (ptx); bars: 50 ms, 25 mV. (**D**) Frequency tuning of AN1 before and after application of picrotoxin; means + SE, $n = 12$–13. Mean threshold for inhibition before ptx application shown as stippled line (IPSP, $n = 2$–9. [Modified from Stumpner (1997, 1998) and combined with new data]. (**E–G**) Ascending auditory interneuron AN3 of the grasshoppers *Chorthippus biguttulus* and *Locusta migratoria* (**G**). (**E**) Anatomy of the AN3 neuron in the metathoracic ganglion complex and the brain. MTG, mesothoracic ganglion; PTG, prothoracic ganglion; SEG, subesophageal ganglion. (**F**) Responses of AN3 to white noise stimuli of increasing intensity. (**G**) Thresholds of the presumed excitatory inputs to AN3 from low-frequency (LF) and high-frequency (HF) sensory neurons mediated via intercalated interneurons, and threshold of the GABAergic inhibition mediated via the TN1 interneuron. *Insets* show the occurrence of simple and complex responses in AN3 depending on frequency and intensity (*asterisks*) [(**E**), (**F**) from Stumpner (1988) and Stumpner and Ronacher (1991), respectively, (**G**) modified after Römer et al. (1981) with permission]

(Stumpner 1997). Such a response function is due to additional inhibitory inputs that are tuned to other frequencies and therefore become effective only at higher sound intensities (Fig. 8.8B–D). Blocking the inhibition reveals an underlying tonic excitation (Fig. 8.8B, C). The intensity-dependent responses may be even more complex in grasshoppers (Fig. 8.8E–G). When stimulated with white noise pulses of increasing intensity, the neurons show a first maximum at low intensities and then a reduced activation at intermediate intensities that is followed by a second peak of activation at high sound intensities (Fig. 8.8F, G). Such a bimodal response pattern can derive from a low- and a high-frequency evoked excitation in combination with a less sensitive inhibition at low frequencies. In grasshoppers, candidate neurons have been described that explain such a response pattern (Fig. 8.8G; Römer et al. 1981; Sokoliuk et al. 1989).

For insects with broadband communication signals, such as many bushcrickets and grasshoppers, frequency analysis may allow determination of the distance to the signaler. This is possible because in addition to the geometric spreading of acoustic energy with distance, excess attenuation occurs for higher frequencies (Römer and Lewald 1992). Therefore, the tonotopic organization of the sensory input also allows for a "coding of distance" as the activation pattern of the afferent population by a broadband signal will depend on the distance of the signaler. In the bushcricket *Mygalopsis marki*, different interneurons respond optimally to stimuli originating at different distances from the receiver (Römer 1987).

In some cases, the main frequency component of an insect's communication signals may overlap with the spectra of signals produced by predators and therefore neurons may respond to both signals. Even when the spectral content of conspecific and predator signals is different, central neurons may still respond to both due to convergence of sensory input (Ostrowski and Stumpner 2010). In these cases, differences in temporal patterns and additional context-specific sensory information need to be evaluated to allow for correct decisions (Nakano et al. 2013). When the frequency spectra do differ, the strength of synaptic input from afferents may be much stronger for ultrasound than for sonic conspecific signals (Pollack and Imaizumi 1999). Furthermore, local processing within a neuron's extended dendrites may allow segregation of signals differing in spectral content and temporal pattern (Triblehorn and Schul 2013; Prešern et al. 2015), implementing a form of auditory scene analysis or stream segregation analogous to mechanisms described for vertebrates (Moss and Surlykke 2010).

8.6   Pattern Recognition

8.6.1   Pattern Recognition: A Sequence of Feature Detection Steps

Hearing insects show typical motor responses to specific acoustic signals generated by conspecifics, predators, or prey, indicating that their auditory pathway detects and recognizes these signals as significant events within the auditory scene

(Bregman 2008). The underlying processing mechanisms are generally referred to as "feature detection" (Hoy 1978) or "pattern recognition" (von Helverson 1984; Stumpner and Ronacher 1994). Both processes are used within an operational context and their interrelationship may need to be considered. In the visual system, steps of feature detection (feature extraction) are thought to be necessary in a process underlying more complex pattern recognition (Barlow 1969). In a similar way, auditory pattern recognition may be regarded as a process involving several feature-detecting mechanisms (often called "filtering") in the frequency, the amplitude, and also the time domain, that is, when pulse intervals are crucial for communication. Different auditory patterns need to be processed and recognized, as species-specific signals that differ in carrier frequency and temporal structure are used for calling, courtship, and rivalry behavior and for response and disturbance signaling (Alexander 1962; Gerhardt and Huber 2002). For mate attraction, insects use bidirectional or unidirectional acoustic communication; so in this context either sex or (more commonly) just the females perform pattern recognition (Heller and von Helverson 1986; Robinson and Hall 2002). Otherwise, males need to employ pattern recognition for chorusing, intermale spacing, or phonotaxis to other singing males as in case of satellite males.

Frequency analysis is performed at the first level of auditory processing by the biophysical properties of the hearing organ and refined within the central auditory pathway (see Sect. 8.5). The processing of sound pulses is supported by the synchronous onset activity and the phaso-tonic responses of auditory afferents (Ronacher and Römer 1985; Nabatiyan et al. 2003) and by central mechanisms selecting the loudest signal (see Sect. 8.3). Already the activity of single auditory afferents represents fine-scale differences of intraspecific communication signals (Machens et al. 2003) and the afferent population provides the CNS with all the information available for temporal pattern recognition. However, the analysis of species-specific temporal sequences of sound pulses is not achieved in the peripheral auditory system and rather requires neural processing within the CNS. In several insect groups, ascending thoracic auditory neurons (Fig. 8.2) and their projection patterns within the brain have been characterized and local auditory brain neurons have been identified (e.g., Ostrowski and Stumpner 2010; Kostarakos and Hedwig 2012). A careful interpretation indicates that circuits for temporal auditory processing are preferentially housed in the ventral protocerebrum; however, a specific auditory brain region cannot be identified across the groups of acoustically communicating insects.

Although cicadas employ the most complex frequency- and amplitude-modulated signals, little is known about central auditory processing (Huber 1983; Fonseca 2014). In acridid grasshoppers, the amplitude modulation/temporal structure of the broadband songs appears to be crucial for pattern recognition (von Helverson and von Helverson 1983, 1987, 1998). Ascending thoracic neurons with spike activity patterns that monitor the continuity of the song pattern have been identified (Ronacher and Stumpner 1988), as well as neurons representing the basic pulse-pause unit of the song by bursting spike activity (Creutzig et al. 2009). Processing mechanisms in the brain, however, have not yet been explored.

8.6.2 Calling Song Pattern Recognition in Crickets

Neural mechanisms underlying temporal feature detection of pulse patterns are best explored in the CNS of crickets and bushcrickets. In their calling song-male crickets generate sound pulses within a very narrow carrier frequency spectrum (4–6 kHz) and combine these pulses to form complex chirp and trill patterns (Otte 1992). Conspecific females that are ready to mate approach singing males or a speaker broadcasting the calling song. In field crickets (*G. campestris*, *G. bimaculatus*, *T. oceanicus*), female phonotactic behavior is tuned to the 25–35 Hz pulse repetition rate of the male calling song as the dominant parameter for pattern recognition. It may also depend on the processing of pulse duration and chirp intervals (Doherty 1985; Hennig 2009). Elucidating the neural mechanisms underlying the response toward the species-specific pulse rate has been a major aim in behavioral neurobiology. Mechanisms such as resonant oscillations (Bush and Schul 2006), low-pass/high-pass filters (Schildberger 1984), template matching (Hoy 1978; Hennig 2003) and a delay-coincidence mechanism (Weber and Thorson 1989) have been proposed (Kostarakos and Hedwig 2012, 2015).

There is no evidence that temporal feature detection of the songs occurs at the thoracic level of the cricket CNS (Schildberger et al. 1989; Pollack 2001). However, local (ON1) and an ascending interneuron (AN1) indicate a first broad filter mechanism as they respond better and transfer more information when stimulated with sound pulses with an amplitude modulation rate below 30 Hz, which covers the range of pulse patterns for phonotactic behavior of crickets. The physiological mechanism may be due to the nature of the afferent synaptic inputs; it is not related to the reciprocal inhibition of ON1 neurons underlying directional processing (see Sect. 8.4; Marsat and Pollack 2004, 2005), which had been proposed by Wiese and Eilts-Grimm (1985). A response decrement of another ascending neuron (AN2) has been linked to phonotactic behavior (Stout et al. 2011), but details of the processing are not yet revealed.

In crickets, only one ascending auditory interneuron (AN1) forwards activity to the brain that reliably represents the temporal structure of the calling song (Wohlers and Huber 1982) (see Fig. 8.2). Its axon terminates in the ventral anterior protocerebrum. Based on intracellular recordings of local auditory brain neurons, Schildberger (1984) proposed that a combination of low-pass and high-pass neurons could constitute the feature-detecting mechanism that leads to the 30-Hz pulse-rate tuning of female phonotaxis. Detailed neuronal processing mechanisms underlying this filtering process were not revealed.

By using a cricket preparation that allows standing and phonotactic walking on a trackball (Fig. 8.9A), a group of local auditory interneurons has been identified that are closely linked to the output structures of the AN1 neuron (Kostarakos and Hedwig 2012). One identified neuron (B-LI2) simply copies the auditory stimulus pattern, whereas the spike patterns of other neurons (B-LC3 and B-LI4) exhibit a tuning that matches female phonotactic behavior (Fig. 8.9B). One particular interneuron (B-LI4) is inhibited at low and high pulse rates and spikes only at the
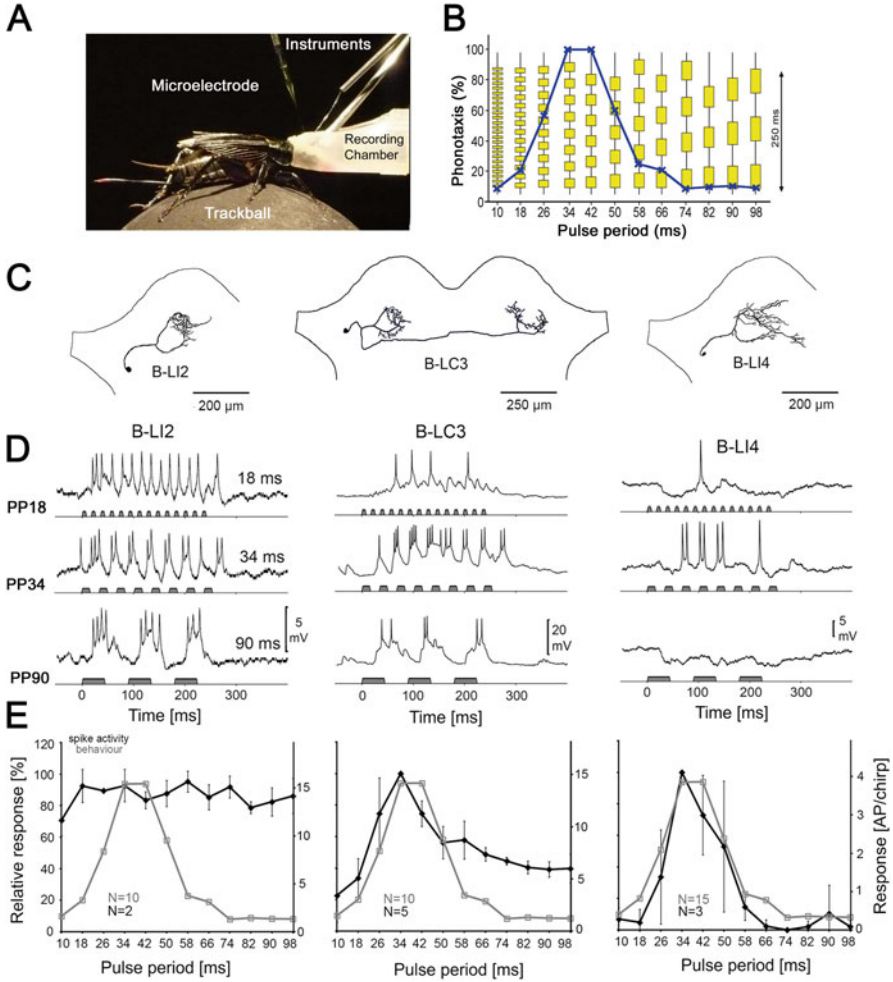
Fig. 8.9 Pattern recognition in a cricket. (**A**) Tethered female cricket (*G. bimaculatus*) positioned on a trackball for recording auditory brain neurons. (**B**) Auditory test patterns with different pulse periods and temporal tuning (*blue line*) of female phonotaxis. (**C**) Local brain neurons involved in the processing of the pulse pattern; their arborizations match the ring-like axonal arborizations of AN1 (see Kostarakos and Hedwig 2012). (**D**, **E**) Spike activity of brain neurons in response to different pulse period patterns. B-LI2 copies the sound pattern, whereas B-LC3 and B-LI4 show a tuning of their spike responses (*black line*) that matches the female phonotactic behavior (*gray line*). B-LI4 receives inhibitory and excitatory inputs and only spikes in response to the species-specific pulse period. The tuning of this neuron reveals response properties of a feature detector for the pulse period [(**C**)–(**E**) from Kostarakos and Hedwig (2012) with permission]

species-specific pulse rate. Its spiking activity closely matches the tuning of the female phonotactic behavior. The B-LI4 neuron may therefore be regarded as a feature detector for the species-specific pulse rate. Analyzing the timing of the neuronal responses reveals that some local brain neurons respond with a very long

latency and only when the second sound pulse occurred (Zorović and Hedwig 2011; Kostarakos and Hedwig 2012). As the processing of any pulse rate requires at least two pulses, these responses are consistent with a coincidence detection mechanism, in which the response to the first pulse is delayed by the species-specific pulse period to coincide with the response of the second pulse (Weber and Thorson 1989; Kostarakos and Hedwig 2012). The underlying neural circuitry and the nature of the delay mechanism that explains the tuning toward the pulse periods has been described while this chapter was in press (Schöneich et al. 2015).

8.6.3   Pattern Recognition in Duetting Bushcrickets

The brain must also account for acoustic signaling behaviors that operate over longer time periods. Bushcrickets often use simple, double-pulse song patterns in the sonic and/or ultrasonic range for communication. However, in some groups with acoustically duetting mates (e.g., Phaneopterinae), male songs can be quite complex as they include both temporally patterned chirps and specific trigger pulses that are crucial to elicit the female response song (Heller and von Helversen 1986). The duetting behavior between the sexes relies not only on differences in carrier frequency but also on differences in temporal patterns. During calling, male *Ancistrura nigrovittata* (Phaneropteridae) produce chirps (pulse groups), which last about 200 ms and contain 5–9 sound pulses of 16 kHz. Chirps are produced every 800–900 ms (Fig. 8.10A) and about 350 ms after the end of a chirp a single "trigger pulse" is emitted. Females do not respond to the chirps. However, 25–30 ms after the trigger pulse, the female generates a brief ultrasonic click with her wings, which will guide the male towards her (Heller and von Helversen 1986; Dobler et al. 1994a). The female response depends strongly on the pattern of the male chirp and also on the time interval between the chirp and the trigger pulse; intervals of 250–450 ms are most efficient (Fig. 8.10B). Behavioral tests indicate that females have an expectation of the time when the trigger syllable should occur. Very motivated females respond at approximately the correct time after a chirp even if the trigger pulse is omitted (Dobler et al. 1994b). The short latency of the female's response to the male's trigger pulse does not allow for complex pattern analysis. Rather, processing and recognition of the preceding chirp signal may set an internal time window, which subsequently enables the female's short latency response to the trigger pulse. On the other hand, males will respond to female replies only if these occur within a restricted temporal "window" after the trigger syllable (Heller and von Helversen 1986).

Neural processing in the CNS of both sexes must account for these time windows, but how can this be realized? In the brains of bushcrickets, local auditory interneurons have been identified in the anterior lateral protocerebrum, with specific response properties matching the carrier frequency and timing of the communication signals (Ostrowski and Stumpner 2010, 2013). In males as well as in females, a particular neuron (LBN9) is inhibited when the bushcricket hears a male chirp at
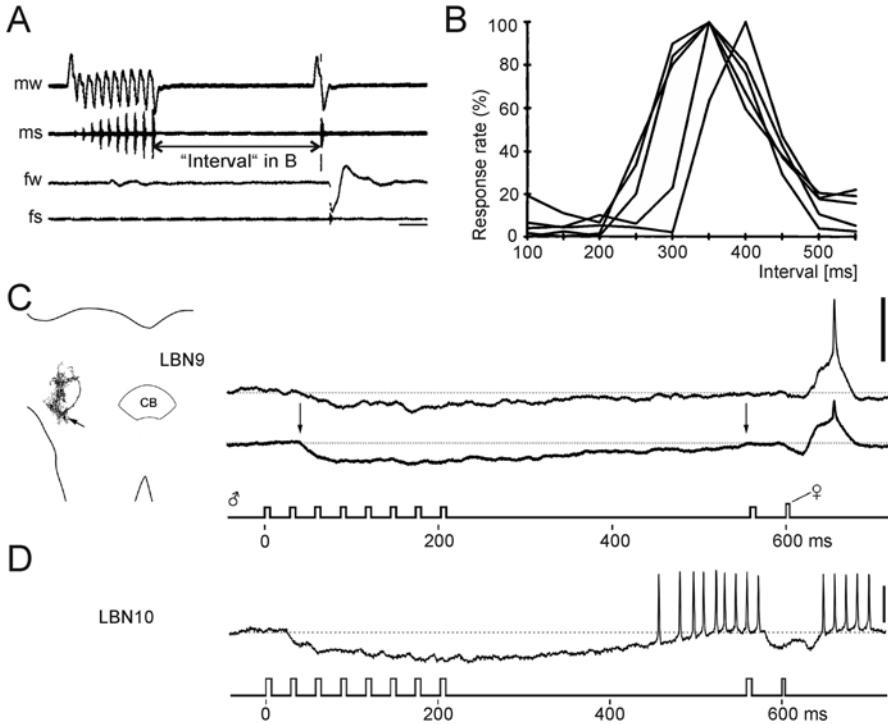
Fig. 8.10 Pattern recognition in a bushcricket. Behavioral and interneuronal responses in the bushcricket *Ancistrura nigrovittata*. (**A**) Natural duet, wing movements of male (mw) and female (fw) and sound produced (ms, fs). Upward is wing opening. Scale bar = 100 ms. The *arrow* ("Interval" in **B**) shows the interval varied in the diagram of (**B**). (**B**) Responses of females to models of the male song. Each female is represented by one line. Responses are tightly linked to the separate "trigger" pulse by the male song and occur only if the interval between trigger pulse and preceding group of pulses is between 250 and 450 ms. (**C, D**) Responses of brain neurons to artificial duets. (**C**) Morphology of the local brain neuron LBN9 and responses (*upper*: single response; *lower*: average of five responses) showing a long-lasting inhibition by the pulse group. (**D**) Responses of LBN10 showing a postinhibitory activation at about the time when the trigger pulse occurs in natural songs [(**A**) modified after Dobler et al. (1994b); (**B**) modified after Heller and von Helversen (1986); (**C**) from Ostrowski and Stumpner (2013); (**D**) from Ostrowski (2009); with permission]

16 kHz and is excited by a later-occurring female pulse at 24–28 kHz (Fig. 8.10C). The inhibition begins with a latency of 40 ms, builds up during the chirp, and is maintained for another 300 ms after the end of the chirp. The long duration of the inhibition thus matches the delay between the onset of the chirp and the trigger pulse. If a trigger pulse (16 kHz) is then presented, it also elicits an inhibitory response; however, a subsequent pulse at 27 kHz that, like a female response, follows the trigger pulse by 30 ms leads to excitation and spiking of the neuron. Other local brain neurons show a similar long-lasting inhibition. In one of these (LBN10; Fig. 8.10D; Ostrowski 2009), the inhibition gradually fades and is fol-

lowed by postinhibitory spiking activity. Although the functional significance of the long-lasting inhibition cannot yet be specified in detail, its time course closely matches the time window for the male trigger and the female response pulse and may be directly involved in the processing of the trigger pulses.

8.6.4 Pattern Recognition and Auditory Motor Responses

In phaneropterine bushcrickets, the very short latency female responses to the male trigger pulse indicates a functional separation of the circuitry underlying pattern recognition and that controlling the auditory motor response. The initial recognition of the male chirp seems to prime the female auditory pathway to allow for a rapid reflex-like motor response, that is, moving the wings for sound production. The single trigger pulse has no specific temporal structure and is characterized simply by its duration and frequency. Thus at this stage, a complex mechanism for pattern recognition that might involve the brain is not required, and the female motor response may be controlled by a fast local thoracic network. Such an organization would indicate a functional similarity to phonotactic steering in flying and walking crickets (Pollack and Hoy 1981; Hedwig and Poulet 2004).

8.7 Dealing with Noise due to Movement and Self-Generated Sounds

8.7.1 Effects of Motor Activity on Auditory Processing

Insect hearing organs evolved from mechanosensitive proprioceptors and they are not completely decoupled mechanically from the animal's tracheal system and body. As a consequence, they respond not only to airborne sound but can also be activated by vibrations due to the insect's muscle activity and movements of appendages. Such self-generated stimulation of the hearing organs causes activity of auditory afferents that is not related to acoustic stimulation. It can also lead to failure of auditory responses. Both effects pose a problem for central processing and make the coding of acoustic signals less reliable. Motor activities such as breathing, flight, passive leg movements (Hedwig 1988, 1989; Lang and Elsner 1989), or walking (Schildberger et al. 1988; Zorović and Hedwig 2011) have significant effects on the representation of auditory signals in spike patterns of afferents and interneurons. This is especially relevant when the neuronal representation of the communication signals is used for auditory orientation and pattern recognition.

Effects of motor activity on auditory processing can be resolved only in experiments that do not restrain the insect's behavior but rather consider motor activity as the natural functional condition for auditory processing. Recordings from auditory
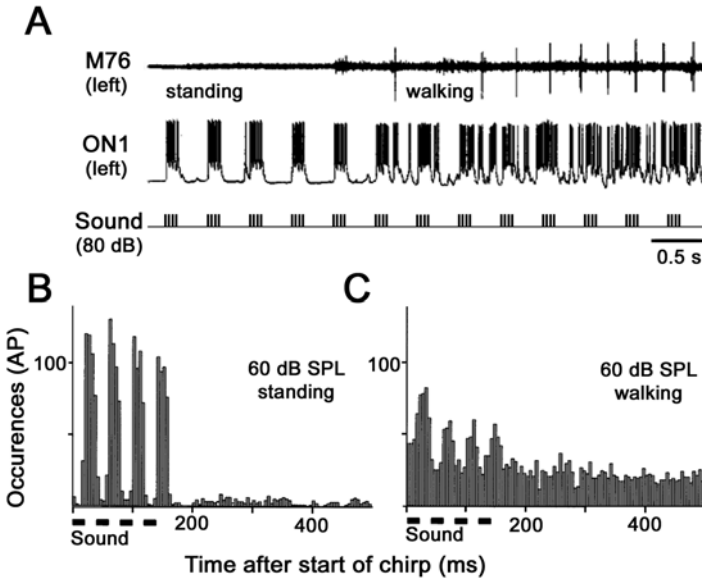
Fig. 8.11 Neural noise during walking in a cricket (**A**) Activity of a *G. campestris* ON1 interneuron in response to acoustic stimulation with calling song (80 dB SPL) in a standing and then walking cricket as indicated by the activity of a leg muscle M76. (**B**) The peri-stimulus-time-histogram (PSTH) of auditory evoked spike activity in a standing cricket gives a clear representation of the chirp pattern presented at 60 dB SPL. (**C**) Walking motor activity causes substantial background activity in the auditory pathway. The auditory response is reduced and the representation of the sound stimulus less reliable [From Schildberger et al. (1988) with permission]

neurons in the thoracic ganglia and the brain have been obtained in tethered crickets that were either standing or freely walking on a trackball system. When the insect is quietly standing and is exposed to a model of the species-specific calling song, a reliable representation of the acoustic signal occurs in the spike pattern of the thoracic ON1 neuron (Fig. 8.11A; Schildberger et al. 1988). The neural activity pattern, however, changes dramatically with the onset of walking. The walking motor activity, which will also move the hearing organ in the front leg, causes additional spikes in the interneuron and it reduces the reliability of the stimulus representation. While the insect is standing, each pulse of the sound pattern is clearly represented in the corresponding peristimulus time histogram with a response about 20 times higher than the background activity. During walking, the background spike activity increases and at the same time the response to the sound pulses decreases by about 50 % and now is only about twice as high as the background activity (Fig. 8.11B). This effect of walking on auditory processing is carried forward to the brain. Even local brain neurons show a less reliable representation of acoustic signals during walking (Zorović and Hedwig 2011). How the pattern recognition networks deal with these noisy input is not yet resolved, but once pattern recognition is activated in crickets, the system is noise tolerant and transiently responds even to nonattractive sound pulses (Poulet and Hedwig 2005).

8.7.2 Dealing with Self-Generated Sounds

All acoustically signaling species face an even more fundamental challenge: How can the signalers deal with the self-generated sound to prevent desensitization of their auditory pathway and avoid a mix-up of self-generated and external acoustic signals? A peripheral mechanism operates in cicadas, which fold their tympana during singing by contracting a detensor tympani muscle and thereby increase the auditory threshold by 20 dB (Hennig et al. 1994). In stridulating acridid grasshoppers that produce broadband signals (von Helversen 1997), the self-generated sounds and accompanying mechanical vibrations lead to an activation of the auditory afferents that also depolarizes the auditory interneurons (Hedwig and Meyer 1994). Sound stimuli presented during stridulation are masked by the self-generated afferent activity, and as a consequence interneuronal responses are strongly reduced (Hedwig 1984; Wolf and von Helversen 1986). Intracellular recordings did not provide any evidence for a central neural mechanism that modulates auditory processing and reduces interneuron responses during singing (Hedwig 1990).

The situation is different in crickets (*G. bimaculatus*), which may produce puretone calling songs at approximately 100 dB SPL for many hours to attract a mate, exposing their own ears to long-lasting and intense self-generated sound. There is no evidence that peripheral processes alter the sensitivity of the hearing organ (Poulet and Hedwig 2001); rather a central mechanism is employed. A central corollary discharge, that is, a signal that is generated by the motor system and forwarded to the sensory pathway, modulates self-generated auditory activity at the level of the auditory afferents and thoracic interneurons, demonstrating a concept proposed and discussed for visual pathways (von Holst and Mittelstaedt 1950; Sperry 1950). Its efficiency can be demonstrated in silently singing crickets when one of the front wings is removed to prevent sound production. At the same time, the animals are exposed to a sequence of acoustic pulses, that activate the auditory system. The auditory afferents reliably respond to the sound pulses but intracellular recordings close to the axonal terminals demonstrate that synaptic transmission is affected by a presynaptic mechanism (Fig. 8.12). The axonal arborizations close to the afferent terminals receive a PAD of 2–3 mV, which in many sensory pathways indicates presynaptic inhibition (see Sect. 8.4). The depolarization is coupled to the closing phase of the wing movements. It decreases the amplitude of the invading spikes and thereby the efficiency of synaptic transmission whenever the cricket would generate a sound pulse.

Thoracic interneurons (ON1 and AN1) respond reliably to the sound stimuli in the chirp intervals (Fig. 8.12B, C), but during the chirps, they receive a strong postsynaptic inhibition that suppresses any spike activity (Poulet and Hedwig 2002, 2003a, b, 2006). The inhibition is phase-coupled to the closing movement of the wings and it reduces spike activity to self-generated sound pulses. Presynaptic and postsynaptic inhibitions are mediated by a bilateral pair of corollary discharge interneurons that make monosynaptic connections to the afferents and the auditory interneurons (Fig. 8.12D, E). The inhibition provided by this interneuron reduces the
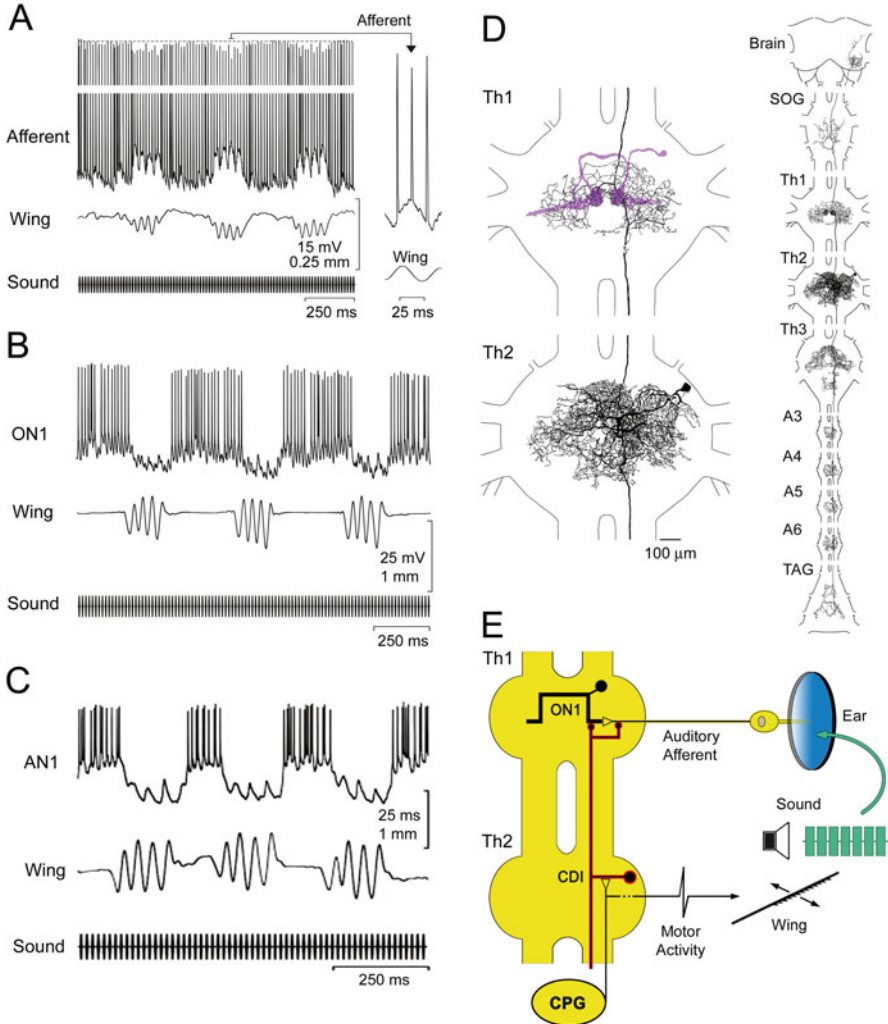
Fig. 8.12 Dealing with self-generated sound during singing. (**A–C**) Activity of auditory neurons in "silently" singing crickets in which one front wing is removed and the movement of the other wing is recorded (see **E**). The crickets cannot generate any sound but are exposed to a continuous sequence of sound pulses (4.5 kHz, 75 dB SPL). (**A**) An auditory afferent spikes in response to the acoustic stimuli; in phase with the wing movements the afferent receives PADs, which reduce spike height. (**B, C**) Auditory evoked spike activity in the ON1 and AN1 neurons occurs in the chirp intervals; the auditory response is inhibited during the singing wing movements. (**D**) Structure of the corollary discharge interneuron in the Th1 and Th2 thoracic ganglia and in the complete CNS (right). The structure of an ON1 neuron is indicated in magenta. (**E**) Proposed circuit for the underlying neuronal mechanisms. The corollary discharge interneuron is activated by the singing central pattern generator (CPG) and inhibits the auditory pathway in phase with sound production [(**A**)–(**C**) from Poulet and Hedwig (2003a,b); (**D**) from Poulet and Hedwig (2006); (**F**) from Hedwig (2006), with permission]

spike activity of auditory interneurons during singing and may serve to prevent the auditory pathway from desensitization (see Sect. 8.3). The corollary discharge inter-neuron has its dendrites in the mesothoracic ganglion; its axonal arborizations in the prothoracic ganglion are particularly dense and match the auditory neuropil. The interneuron may be driven directly by the singing central pattern generator housed in the abdominal ganglia, but direct evidence is so far missing.

8.8   Summary

Auditory systems evolved in a variety of insect taxa for sound processing in the context of predator avoidance and intraspecific communication. The insects' rather simple nervous systems allow analyzing neural mechanisms of auditory processing at the level of neuropils, identified neurons, and even the synaptic connections in circuits. Neurobiological studies successfully revealed principles underlying direc-tional processing and frequency processing and, more recently, the mechanisms involved in complex corollary discharges and pattern recognition. With increasing complexity of the auditory processing task, a single-cell recording approach to char-acterize and manipulate the activity patterns of individual neurons may have its limits. Double intracellular recordings to reveal the flow of information within an auditory pathway are very challenging and in case of local small brain neurons, they may not be feasible at all.

Future research would greatly benefit from a molecular–genetic approach, but so far, the genome has not yet been sequenced for any acoustically communicating species using tympanic hearing organs. Such future developments may provide molecular–genetic tools to introduce calcium indicators or voltage reporters into the nervous system, generating transgenic lines with genetically encoded indicators expressed in specific subsets of neurons. Combined with intracellular recordings of identified neurons, these techniques should provide a most efficient toolbox for research. Imaging of neural assemblies in combination with electrophysiological recording of the synaptic and spike activity of identified neurons would enormously foster a detailed understanding of neural mechanisms underlying auditory process-ing at the level of neurons and networks. Based on such information, reliable and robust computational models could be developed to synthesize and synergistically combine the response properties of identified neurons and to test the functional properties of the modeled networks in silico. This could allow a comprehensive and detailed understanding of the way auditory circuits function and how they may have been shaped during evolution to match the processing of species-specific acoustic communication signals.

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