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REVIEW

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Pulses, patterns and paths: neurobiology of acoustic behaviour in crickets

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Abstract Crickets use acoustic communication for pair formation. Males sing with rhythmical movements of their wings and the mute females approach the singing males by phonotaxis. Females walking on a trackball rapidly steer towards single sound pulses when exposed to split-song paradigms. Their walking path emerges from consecutive reactive steering responses, which show no temporal selectivity. Temporal pattern recognition is tuned to the species-specific syllable rate and gradually changes the gain of auditory steering. If pattern recognition is based on instantaneous discharge rate coding, then the tuning to the species-specific song pattern may already be present at the level of thoracic interneurons. During the processing of song patterns, changes in cytosolic Ca^{2+} concentrations occur in phase with the chirp rhythm in the local auditory interneurone. Male singing behaviour is controlled by command neurons descending from the brain. The neuropil controlling singing behaviour is located in the anterior protocerebrum next to the mushroom bodies. Singing behaviour is released by injection of cholinergic agonists and inhibited by γ-butyric acid (GABA). During singing, the sensitivity of the peripheral auditory system remains unchanged but a corollary discharge inhibits auditory processing in afferents and interneurons within the prothoracic auditory neuropil and prevents the auditory neurons from desensitisation.

Keywords Phonotaxis · Pattern recognition · Calcium imaging · Command neuron · Corollary discharge

Abbreviations SP: Syllable (or pulse) period · SPL: Sound pressure level · ACh: Acetylcholine · GABA: γ-butyric acid

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Introduction

Communication strategies to attract or find a mate are central to any sexually reproducing animals. At the sender side, they involve a variety of species-specific signals such as optical (fireflies, birds), chemical (moths and fish), electrical (fish), vibratory (spiders, insects) or acoustical (birds, fish and insects) displays. At the receiver side, these are processed by matched sensory filters and pathways that in turn may activate specific signalling responses and/or guide locomotion. Signal display and processing are shaped by natural selection to environmental constraints but also by sexual selection to species-specific conditions (Bradbury and Vehrenkamp 1998). Among acoustically communicating insects (e.g., grasshoppers, cicadas, crickets, bushcrickets, moths) there are about 2,600 species of crickets most of which use calling songs in pair formation (Walker and Masaki 1989). Already in the 18th century, naturalists (Roesel von Rosenhof 1749) have been interested in the conspicuous acoustic behaviour of crickets (Fig. 1), the neurobiological analysis of it started with the work of Huber (1955, 1964), Wohlers and Huber (1978), Hoy (1978) and Popov and Shuvalov (1977).

Male crickets generate loud almost pure sinusoidal sound signals by rubbing their front wings together. Depending on the behavioural context, they produce a species-specific calling song to attract females, a rivalry song to fend off other males or a courtship song as part of their mating behaviour. During calling in *Gryllus campestris*, each closing movement of the wings generates a sound pulse (or syllable) of about 20 ms duration at 4.6–4.8 kHz and 100–105 dB SPL (Nocke 1972a). Three to five of these sound pulses (also called syllables) are grouped into chirps (120–200 ms duration) repeated at 2–3 Hz (Fig. 1). Other crickets like *Teleogryllus* produce even more complex songs and repeat the sound pulses at a different rate during the intervals between the chirps. Since only male crickets sing, acoustic communication among the sexes is unidirectional. Singing males

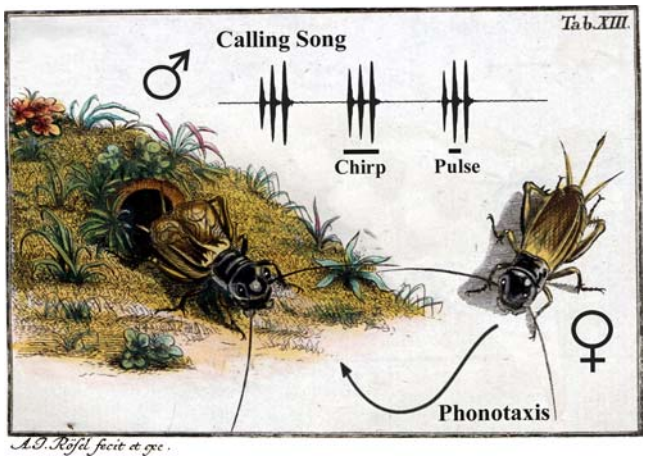

Fig. 1 Acoustic behaviour of *Gryllus campestris*. A male sings in front of its burrow by rubbing the elevated front wings together. The calling song consists of single sound pulses (syllables) grouped into chirps. Attracted by the calling song a female performs phonotaxis and walks towards the singing male using acoustic cues for orientation. Modified after Roesel von Rosenhof (1749)

receive no feedback about the success of their calling behaviour until a female arrives and consequently they have to be enduring singers. Males and females perceive sound patterns with ears located on the front legs. Females are attracted by the male's calling song and walk (Regen 1913) or fly (Ulagaraj and Walker 1973) towards singing males using the acoustical cues of the song for orientation, a behaviour called phonotaxis.

The auditory behaviour of crickets offers itself as a fascinating model to behavioural neurobiologists with a number of fundamental questions both at the receiver's and sender's side:

At the female side: How is the phonotactic behaviour of the females tuned to the species-specific temporal pattern and how is the sound source localised? What are the neuronal filter mechanisms underlying auditory pattern recognition?

At the male side: How is the motor pattern underlying singing generated and how does the central nervous system control it? Listening continuously to a loud self-generated song may deteriorate the animal's own auditory processing. How do singing males therefore deal with the self-generated auditory feedback they persistently produce?

Here I take the opportunity offered by the editors to focus on the behavioural measurements, neurophysiological experiments and imaging techniques that my collaborators and I used to approach cricket auditory behaviour from a system to a molecular level. Fundamental principles of sensory processing and motor control could be revealed emphasising the role of crickets as a model system in neurobiology.

Auditory behaviour as revealed with a sensitive trackball system: temporal tuning of phonotaxis

Cricket phonotaxis has only rarely been observed in its natural environment. For lab-based quantitative studies different devices have been developed e.g. walking wheels (Stabel et al. 1989) and treadmills including compensated closed-loop (Weber et al. 1981; Schmitz et al. 1982; closed-loop with respect to turning behaviour) or non-compensated open-loop systems (Doherty and Pires 1987; Schildberger and Hörner 1988). The performance of the latter treadmills was limited by inertia of the spheres and the closed-loop system compensated only the average speed of the walking animal. These limitations have recently been overcome with a trackball system allowing the measuring of rapid steering responses of walking crickets with high temporal and spatial accuracy, which even resolved the stepping-cycle of individual legs (Hedwig and Poulet 2004, 2005).

We analysed the temporal tuning of phonotaxis in females (*G. bimaculatus*) walking on our trackball system (Fig. 2a). In a dark sound proofed chamber females were exposed to sound patterns presented from a left and right speaker with systematically varied syllable periods (SP) (Thorson et al. 1982) (Fig. 2b). The deviation towards an active speaker was measured as an indicator of phonotaxis. Since the animals could not change the orientation of their body in the sound field their acoustic responses could be averaged over many trials.

When tested at 75 dB sound pressure level (SPL, rel. to 20 μPa), females responded best in the range of SP34–42 (Fig. 2c). The phonotactic response decreased to shorter and longer syllables and the animals only weakly steered towards very short (SP10) or to very long syllable periods (SP74–98). The temporal tuning curve measured with the new trackball system closely corresponded to previous analyses (Thorson et al. 1982; Doherty 1985a,b; Weber and Thorson 1989). Phonotactic behaviour appears to be tuned towards the temporal pattern of the males calling song, which covers syllable periods in the range of 30–45 ms (Doherty 1985b). The crucial parameter evaluated by the pattern recognition system seems to be the syllable period (Thorson et al. 1982). However, other temporal parameters like pulse duration and chirp interval may also contribute to the attractiveness of a song (Doherty 1985a; Stout and McGhee 1988). Therefore a more comprehensive testing of periodical pulse patterns is currently performed (see Hennig 2003).

Localisation: orientation emerges from reactive steering

How do crickets localise a sound source? Pattern recognition and localisation require different processing of auditory information. Whereas pattern recognition benefits from summing the input from both ears to increase

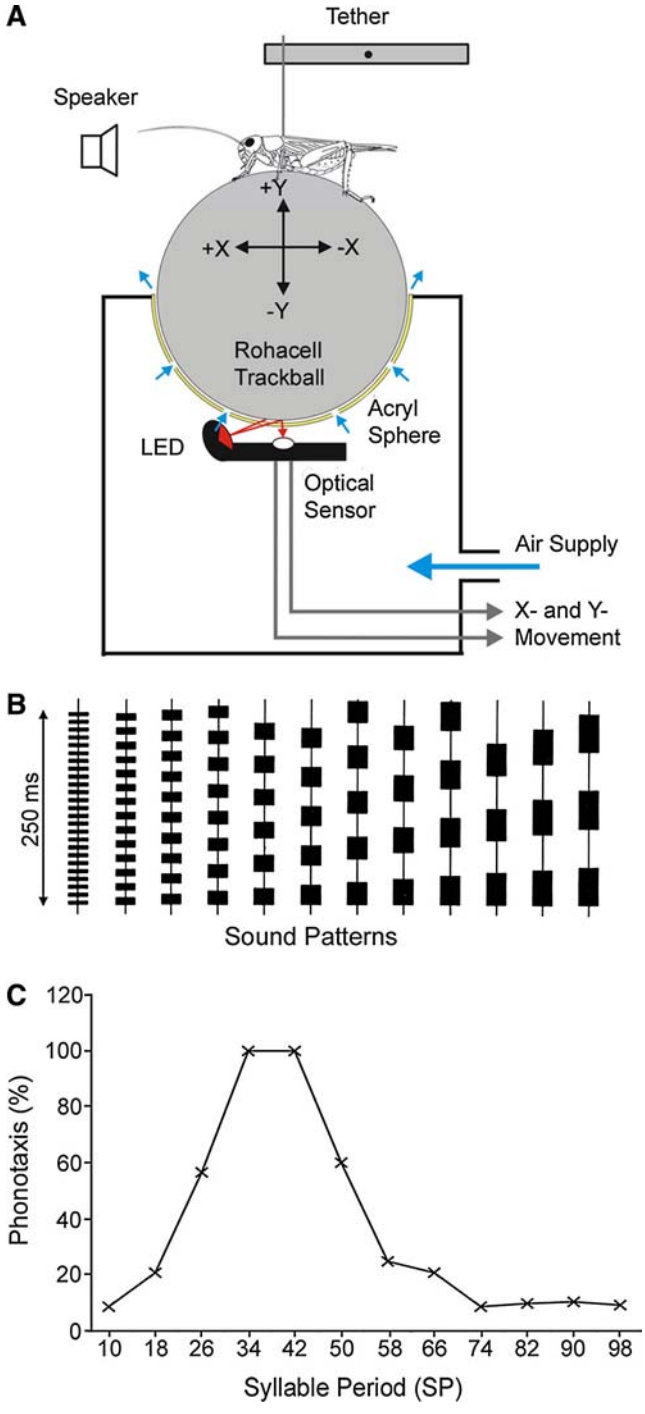

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Fig. 2 **a** Trackball system for analysing cricket phonotaxis. A female *(Gryllus bimaculatus)* is tethered on top of a lightweight trackball, which floats in an air stream. Whenever the animal walks it rotates the trackball with the legs. An optical sensor at the bottom of the trackball monitors the forward–backward (*X*) and left–right (*Y*) movements of the trackball with high spatial resolution (120 µm). The data are used to calculate the translational and steering velocity of the walking cricket. Two speakers aligned at 45° to the animal's length axis present acoustic stimuli. **b** Sound patterns to analyse temporal tuning of phonotaxis. 250 ms long chirps with 50% duty cycle and SPs ranging from SP10 (5 ms pulse duration and 5 ms interval) to SP98. Stimuli were presented at 75 dB SPL for 30 s and the animal's deviation towards the active speaker was quantified. **c** Tuning curve of phonotaxis demonstrates the strongest response to SP34–SP42, which corresponds to the natural range of SP. Phonotaxis declined at shorter or longer syllable periods

the signal to noise ratio and to enhance the receiver's performance, localisation requires a comparison between left and right inputs (Helversen and Helversen 1995). Both processes therefore have to be separated either temporally or spatially in serial or parallel pathways. In crickets, the most parsimonious hypothesis for orientation suggested that the animals always turn towards the louder sound (Huber et al. 1984), akin to fly-larvae performing photo taxis (Fraenkel and Gunn 1961). This could explain a meandering walking pattern based on consecutive turns to the side at which the ear perceived the sound loudest.

Neurophysiological evidence indicated that information ascending from both ears is kept separated in the CNS. The brain therefore seems to house one pattern recognition network in each of its sides (Schildberger 1984; Pollack 1986). It has been suggested that during serial processing, the output of both recognition networks is compared by integrating information over several sound pulses and that the animals then steer towards the better pattern (Stabel et al. 1989; Helversen and Helversen 1995). Recordings with previous treadmills seemed to support this assumption since females appeared to turn after listening to 1–2 chirps from a new direction, indicating that they integrated auditory information for 500 to 1,000 ms (Schmitz et al. 1982; Schildberger and Hörner 1988).

When we exposed crickets to a split-song paradigm with consecutive sound pulses presented from opposite sides, the animals walked straight ahead as demonstrated by Weber and Thorson (1988). At sound intensities of 75 dB SPL both ears will be stimulated and the simplest interpretation corresponding to a left and a right recognition network in the brain, would be that the animals chose the direction between the speakers where the sound pattern was optimal for each recognition network (Fig. 3a). High temporal resolution plots of the steering velocity during split-song presentation, however, demonstrated that the animals rapidly changed the direction of walking and steered to the left and right sound pulses (Fig. 3b). Averages of the response revealed steering to single sound pulses with a latency of only 55–60 ms (Fig. 3c). Such responses to single sound pulses - and especially responses to the first pulse of a chirp - cannot directly be initiated by proposed pattern recognition mechanisms like template matching (Hoy 1978), band-pass filtering (Schildberger 1984) or cross-correlation analysis (Hennig 2003) that are based on the temporal structure of the song and that require at least two sound pulses to identify the syllable rate. Steering towards individual sound pulses also implies that the animals overall walking path simply depends on the number of sound pulses perceived from the left and right side. This was tested with split-songs in which for each pulse the side of presentation was selected randomly but in each test a constant ratio of pulses was presented from

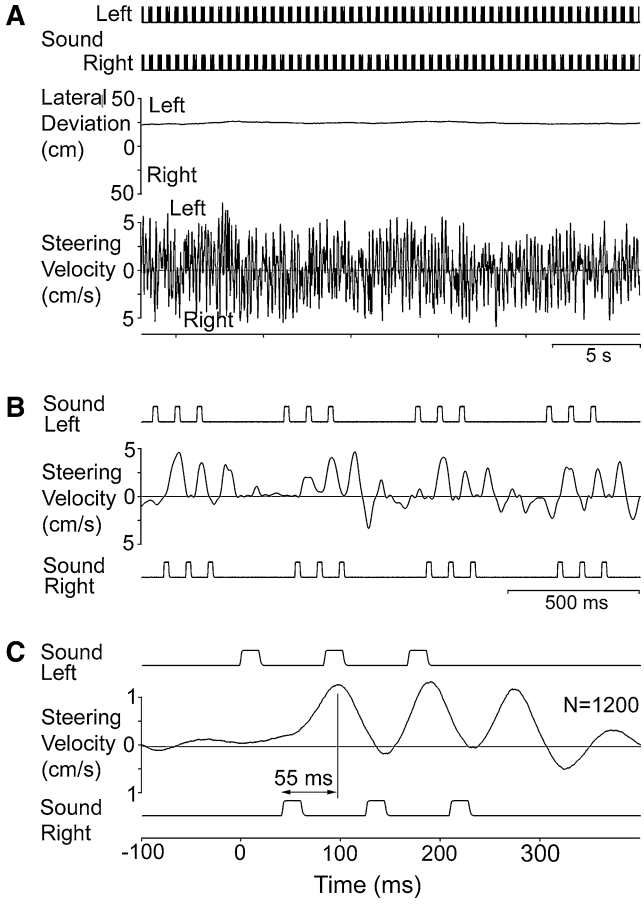

Fig. 3 Rapid steering responses in phonotactic walking crickets. **a** A split-song paradigm presented consecutive sound pulses from opposite sides (*top*). The animal walked straight ahead to a position between the speakers, as shown by the lateral deviation (*middle*). The steering velocity demonstrates rapid steering responses to the left and right side (*bottom*). **b** A plot at high temporal resolution revealed fast steering responses towards individual sound pulses presented from both speakers. **c** Averaging the steering velocity demonstrates the temporal dynamics of the response. Steering to individual pulses occurs after a latency of only 55–60 ms

the left or right side (Hedwig and Poulet 2004). In such tests, the overall lateral deviation of the animals clearly depended on the ratio of sound pulses perceived from either side. The apparently complex auditory orientation in *G. bimaculatus* therefore emerges from a rapid reflex-like steering response towards consecutive sound pulses which also occur in flying crickets (Pollack and Hoy 1981). On the trackball system the animal's overall walking path results from integrating these steering responses over time; under natural conditions the first turning response might bias the animal's further walking direction.

Pattern recognition and localisation: modulating the gain of auditory steering

Steering responses towards single sound pulses question the necessity of pattern recognition at all. Cricket phonotaxis, however, is tuned towards the species-specific song, which leaves no doubt for the functional necessity of a recognition process. Analysing the interaction between recognition and localisation/steering therefore was crucial for an understanding of the auditory-to-motor pathway.

The interaction of pattern recognition and steering can be revealed at the beginning of a song sequence. The onset dynamics of phonotaxis indicates for how long the animals integrate auditory information before they respond with a steering manoeuvre. Analysing many bouts of phonotaxis elicited by split-song paradigms demonstrated, that crickets steered to the first sound pulse of a song (Poulet and Hedwig 2005). Steering responses then gradually increased in amplitude and saturated after 4 chirps i.e. 2 s. A steering response towards the first pulse of a song cannot depend on the activation of a pattern recognition process. It rather indicates a reactive non-selective steering behaviour. However, since the steering response gradually increased in amplitude, pattern recognition obviously modulates the gain of steering on a slow time scale. We therefore tested, how the animals respond to non-attractive sounds inserted into the animal's natural sound pattern. In *Teleogryllus oceanicus* and in *G. bimaculatus* constant sound pulses, when presented on their own, elicited no or a very small steering response, demonstrating that the steering pathway is not activated (Fig. 4a). However, when the same non-attractive pulses were inserted into the species-specific song pattern, the animals strongly steered towards them (Fig. 4b).

These steering responses were generated in response to unstructured sound pulses. Therefore pattern recognition and localisation cannot be linked by direct consecutive serial processing of the temporal features of a sound pattern. Proposed recognition mechanisms in the brain should not process non-attractive test pulses and thus prevent a response towards them. Furthermore, the models of temporal pattern recognition are too slow to be directly involved in rapid steering. We therefore propose that pattern recognition changes the gain of non-selective auditory steering (Fig. 4c). The modulation of steering happens on a time scale of seconds and could be due to facilitation of synaptic transmission in a combined recognition-steering pathway or to a pattern recognition process modulating the steering pathway by a neuromodulator. Although pattern recognition networks appear to be located within the brain (Boyan 1980; Schildberger 1984), the targets of the modulation or facilitation may be descending interneurons (Böhm and Schildberger 1992; Staudacher 2001) or local thoracic networks involved in walking. As a consequence of the slow time course modulation, pattern recognition may allow females to pursue song patterns that deteriorate when spreading in the environment and to tolerate transient irregularities in male song production.

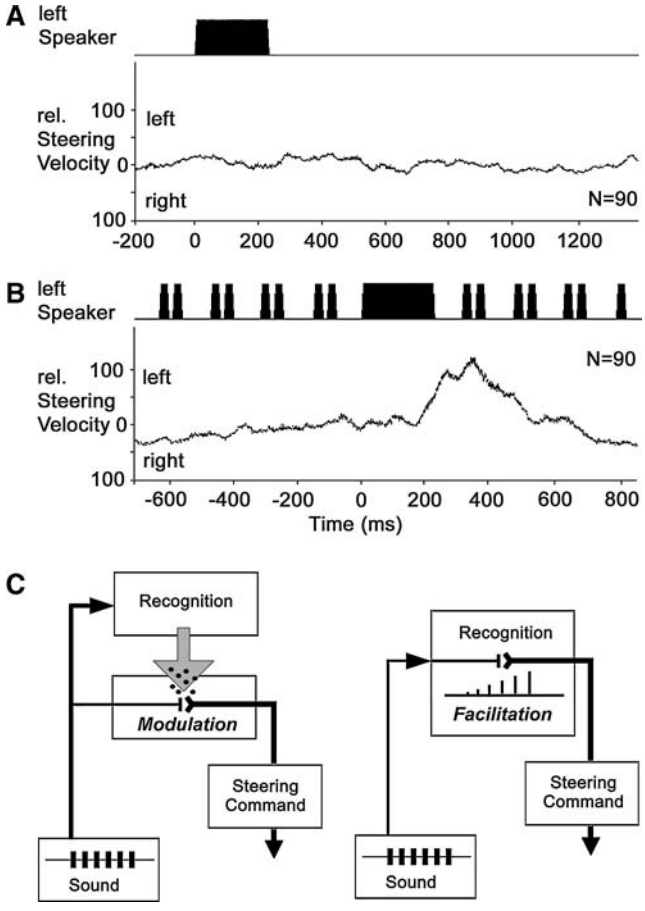

Fig. 4 Modulation of auditory responsiveness during phonotaxis in *Teleogryllus oceanicus*. **a** When presented with a test pulse (220 ms duration, 75 dB SPL) the animals showed no or only a weak phonotactic response. **b** Then a complete song was presented with the same test pulse inserted into the chirp or trill part. It now evoked a strong response. This indicates a modulation of auditory steering during phonotaxis and that temporal filters for pattern recognition are not directly involved in the animals steering (Ingham and Hedwig, unpublished). **c** Organisation of pattern recognition and steering in crickets. Pattern recognition controls the gain of auditory steering by neuromodulation (*left*) or facilitation of synaptic processing activated by the species-specific song pattern leads to a gradual increase in the gain of the steering-recognition pathway (*right*). From Poulet and Hedwig (2005)

Temporal filtering based on instantaneous discharge rate coding?

How can we link the auditory behaviour of the females to the processing of sound pulses and patterns in the nervous system? The auditory pathway of crickets consists of only a few processing stages (Schildberger et al. 1989). The ears comprise about 60 primary auditory afferents linearly arranged in the auditory organ (Michel 1974). Their axons project to the auditory neuropil in the prothoracic ganglion (Eibl 1978; Esch et al. 1980) and forward information to local and ascending interneurons. The local Omega neurons ON1 have their dendrites at one side of the ganglion and axonal output branches at the contralateral side. They are connected by mutual inhibition (Selverston et al. 1985) and may be involved in directional processing (Huber 1983) or even pattern recognition (Wiese and Eilts-Grimm 1985). Ascending auditory interneurons (AN1 and AN2) are directly driven by the afferent activity (Hennig 1988) and inhibited by ON1 (Horseman and Huber 1994). The ascending interneurons terminate in the dorsal lateral protocerebrum where auditory information is passed on to local brain neurons (Boyan 1980; Schildberger 1984). Early studies described a tonic representation of sound patterns by auditory afferents (Nocke 1972b) and thoracic neurons and concluded that these have no temporal filter properties but just copy any sound pattern (Wohlers and Huber 1982; Huber 1983). The copying properties of the interneurons were derived from the average number of spikes elicited by different chirp patterns (see Fig. 2) or from relative changes in spike activity (Schildberger 1984). However, to what degree could the dynamics of neural activity as expressed in the instantaneous discharge rate contribute to pattern recognition? The instantaneous discharge rate codes intensity changes of sensory stimuli and is most important for temporal summation of postsynaptic potentials. Notably, the recognition of the species-specific song pattern has to emerge from the *continuous* flow of auditory activity in time. An external temporal reference, like a stimulus onset marker (that neurobiologists can use for their data analysis) is not available for processing in the CNS. For other behaviours, the importance of instantaneous discharge rate coding is evident (Roeder 1964; Nolen and Hoy 1984; Koch 1999) and it appears that the same coding principle could also be crucial for auditory pattern recognition in crickets.

When exposed to the same sound patterns as used for behavioural tests (see Fig. 2b) summed recordings of the auditory nerve and intracellular recordings of ON1 demonstrated characteristic temporal response properties (Nabatiyan et al. 2003). Afferent activity was highly synchronised at the beginning of all sound pulses and copied pulses even at high syllable repetition rates (SP10). With increasing duration of the sound pulses (SP42–98) this afferent activity acted as a pulse onset detector and highlighted the beginning of each pulse with a clear phaso-tonic response lasting 5–10 ms. The amplitude of this onset response was very similar for all SP-patterns and did not indicate any temporal filtering. In contrast to the whole nerve recordings in ON1 pulses presented at a high repetition rate (SP10, 18) were not reflected in the instantaneous discharge rate. Clear peaks in the discharge rate in response to each sound pulse occurred at SP34 and SP42 and then at the beginning of all longer sound pulses (SP50–98) (Fig. 5a). When the number of discharge peaks was considered which reached a certain amplitude (here set to 200 Hz) this local thoracic neuron acted like a low-pass filter. It did not mirror the high syllable repetition rates in its instantaneous spike rate. The pulse patterns SP34 and SP42 elicited the greatest number of such discharge

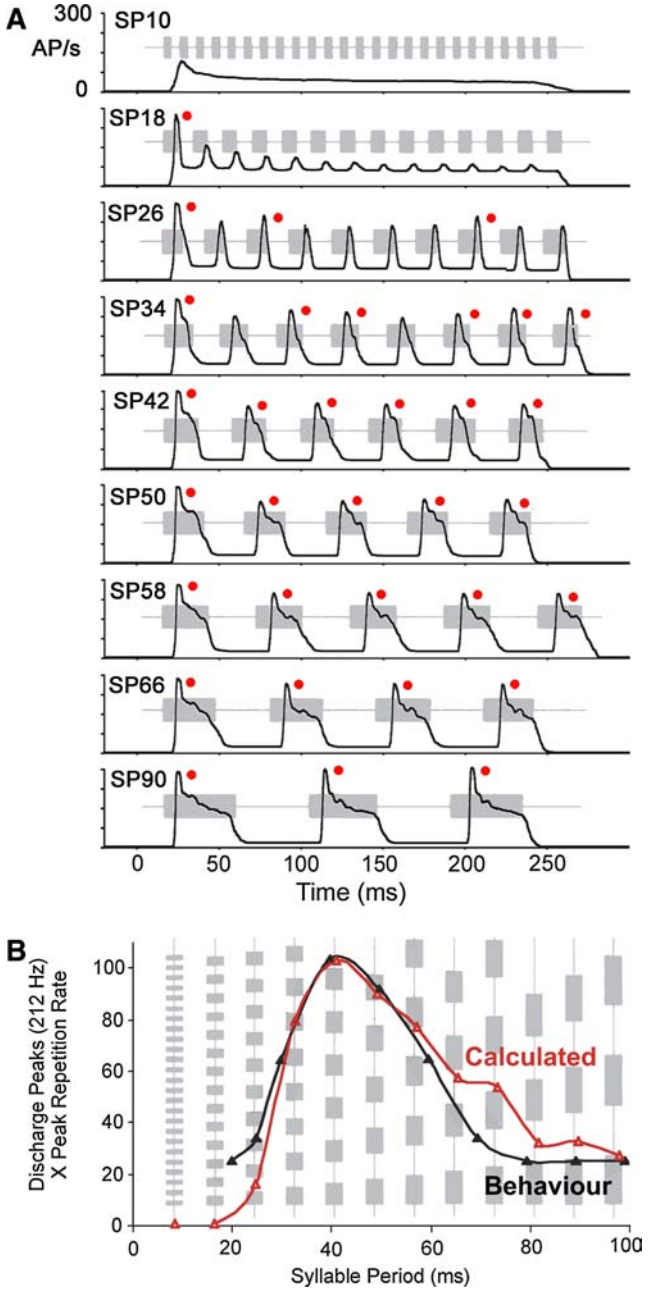

Fig. 5 Temporal filtering by instantaneous discharge rate coding in ON1. **a** Instantaneous discharge rates were calculated for the ON1 neuron in response to sound patterns also used to analyse phonotactic behaviour (see Fig. 2**b**). The instantaneous discharge rate was averaged over 100 trials to reveal the dynamics of the spike response. When exposed to SP10 and SP18 ON1 spiked almost tonically. Peaks in the discharge rate reaching 200 Hz and more gradually occurred with increasing syllable duration. The total number of discharge peaks reaching a threshold criterion of 200 Hz was maximum at SP34 and SP42 and then declined due to the lower number of pulses presented. **b** If the number of discharge peaks and their repetition rate is considered the tuning curve of phonotactic behaviour (*black*, redrawn from Doherty 1985b) and discharge activity of the ON1 neuron (*red*, modified from Nabatiyan et al. 2003) closely matched

peaks and were represented best in the activity pattern of the neuron. With a further increase in syllable period (SP50–98), the number of pulses presented during each chirp decreased and with it the number of discharge peaks (peaks reaching the threshold criterion are indicated with red dots in Fig. 5a). A postsynaptic neuron that is driven by spike activity like that of ON1 will respond best to incoming high frequency spike sequences and will automatically exhibit band-pass properties. Although pattern recognition in Teleogryllus species may be more complex at least in *G. bimaculatus*, there is no need for a serial low-pass and high-pass filter process in the brain (Schildberger 1984). The response patterns of band-pass neurons may purely derive from thoracic processing and emerge from a gradual increase in the spike rate response to sound patterns from SP10–34 and from the gradual decline in the number of sound pulses presented per chirp from SP42–98. Thus, when the instantaneous discharge rate of ON1 is considered and the frequency of the discharge peaks is taken into account, a band-pass response similar to the tuning of phonotaxis is already established at the level of thoracic processing (Fig. 5b, details in Nabatiyan et al. 2003). With instantaneous discharge rate coding, the network would need only one further synapse in the brain for the recognition process and could integrate information on the basis of individual sound pulses as is obvious from the behavioural experiments (Hedwig and Poulet 2004, 2005). However, to check its validity for cricket phonotaxis, instantaneous discharge rate coding as described here will need further testing and considering the trial-by-trial variability of neural responses.

Spatio-temporal calcium^{2+} dynamics in the omega neuron (ON1)

In order to understand the filter characteristics of the auditory neurons, it is crucial to analyse the synaptic input from the network and also their intrinsic cellular properties. Ca^{2+} ions play an essential role in regulating the function of neurons and directly and indirectly participate in signal processing (Berridge 1998). Links between changes in cytosolic Ca^{2+} and signal processing are analysed in a number of invertebrate sensory systems (e.g., fly visual system (Borst and Egelhaaf 1992; Single and Borst 2002), olfactory processing in bees (Galizia and Kimmerle 2004) and the cercal system of crickets (Ogawa et al. 2001) but apart from a study by Sobel and Tank (1994), no further attention has been paid to central auditory neurons of invertebrates. Using a highly sensitive CCD camera with on-chip gain control, we analysed the spatio-temporal Ca^{2+} dynamics in ON1. After intracellular loading with fluorescent indicators, the neurons were exposed to acoustic stimuli and changes in fluorescence were imaged (Baden and Hedwig 2005).

Increasing the intensity of the sound stimulus from 60–80 dB SPL demonstrated four regions of Ca^{2+} increase within ON1 (Fig. 6a). These are the distal and proximal dendrites and the distal and proximal axonal

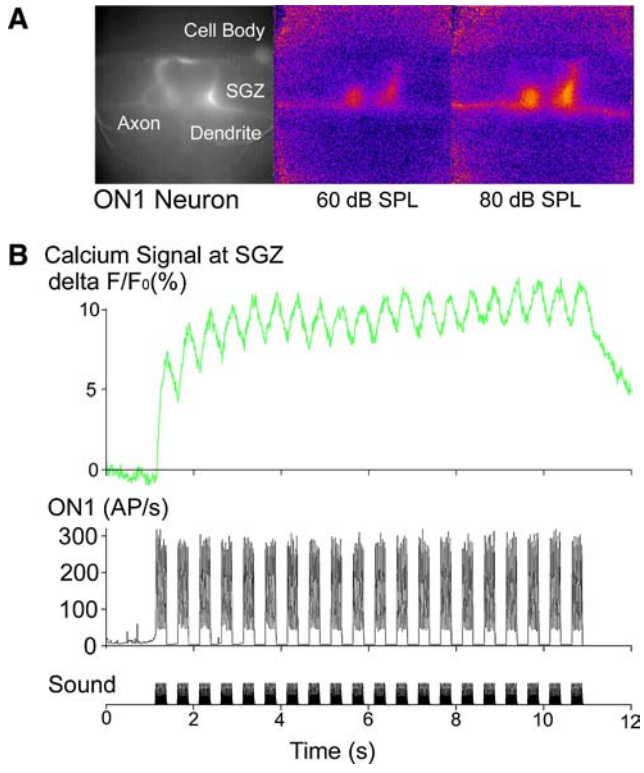

Fig. 6 Imaging of cytosolic Ca^{2+} changes in ON1. **a** Structure of ON1 in vivo after staining with Oregon Green BAPTA-1 (*left*). The dendrite, axon and spike-generating zone (SGZ) are clearly discernible, the cell body is out of focus. Upon acoustic stimulation (250 ms chirp, SP42, 4.8 kHz at 60 dB SPL) imaging demonstrates an enhanced Ca^{2+} level at the dendrites and axonal branches (*middle*). The Ca^{2+} signal increased with sound amplitude (80 dB SPL, right) and points towards distal and proximal entry sites of Ca^{2+} related to synaptic inputs (dendrites) and spike activity (axon), respectively. **b** Prolonged stimulation with SP42 (75 dB SPL) revealed a maintained increase in the Ca^{2+} signal superimposed by a fast modulation in response to individual chirps, measured at frame rates of 90 Hz. The instantaneous discharge rate of the simultaneously recorded ON1 is given below together with the sound pattern, from Baden and Hedwig (2005)

arborisations. Since input and output regions of ON1 are localised at different sides of the prothoracic ganglion (Selverston et al. 1985), these local changes in Ca^{2+} accumulation appeared to be related to synaptic input and output processing. At the dendrites and axonal arborisations, Ca^{2+} may enter via voltage gated Ca^{2+} channels and at the dendrites additionally via ionotropic transmitter receptors (Oertner et al. 1999). A hotspot of gradual Ca^{2+} accumulation and decay appeared at the transition between the dendritic and axonal region of the cell, the putative spike generation zone. Since Ca^{2+} triggers a potassium current, which may support a mechanism akin to selective attention to louder sound signals (Pollack 1988), this very local accumulation could be of specific functional importance for spike generation and processing of acoustic patterns.

Previous studies (Sobel and Tank 1994) indicated a gradual increase and decrease of cytosolic Ca^{2+} upon acoustic stimulation. Natural sound patterns in *G. bimaculatus* are characterised by a chirp rate of 2–3 Hz and a syllable rate of about 25–30 Hz. To reveal fast Ca^{2+} changes, we simultaneously imaged ON1 and recorded its spike pattern while acoustic stimuli of different syllable periods were presented. Playing a sound pattern similar to the species-specific song (SP42, Fig. 2b) demonstrated the dynamics of the Ca^{2+} signal in the axonal and dendritic regions of the cell. At the spike generating zone, a modulation of the signal in the chirp rhythm was present which was superimposed on a gradually increased level of Ca^{2+} (Fig. 6b). Each chirp elicited a signal peak of about 20% amplitude of the slow signal change. Thus changes in Ca^{2+} may influence auditory processing in ON1 not only at a slow time scale, but with a much faster dynamic. Experimental modulation of the calcium transients will reveal the extent to which they contribute to processing and tuning within the cricket's auditory system.

Central control of singing behaviour

At the sender side of the cricket communication system, the central topics are motor control and sensory-motor interaction during sound production. Singing male crickets rhythmically open and close their front wings and rub the scraper and file of the sound producing apparatus against another. A motor pattern-generating network located in the thoracic ganglia (Kutsch and Otto 1972; Hennig and Otto 1995) activates the thoracic singing muscles. The network is driven by descending commands from the brain as demonstrated by extracellular electrical stimulation of single fibres in the connectives (Otto 1971; Bentley 1977) and activation of neuropils in the frontal protocerebrum (Huber 1964; Otto 1971). Since successful stimulation sites in the brain were located in the vicinity of the mushroom bodies and the central body it was suggested that these brain structures might control the singing motor pattern (Huber 1960). Using sharp microelectrodes I probed the protocerebrum and tested single interneurons by intracellular current injection for their ability to activate singing behaviour. These experiments led to the identification of a command neurone (Wiersma and Ikeda 1964; Kupfermann and Weiss 1978; Edwards et al. 1999) in the brain that controls the release of the calling song (Hedwig 2000).

Activity of the command neurone has an immediate effect on behaviour in crickets set-up for neurophysiological experiments. When intracellular current injection increased the spike rate to 60–80 spikes/s the crickets raised their wings and started the calling song. Singing behaviour was maintained for the duration of the increased spike activity and then gradually waned (Fig. 7a). This effect occurred very reliably and demonstrated that the activity of this brain neuron is sufficient to release the calling song. During spontaneous singing, suppressing the interneurone's spike activity by hyperpolarizing current stopped the ongoing motor pattern. The interneurone activity is therefore

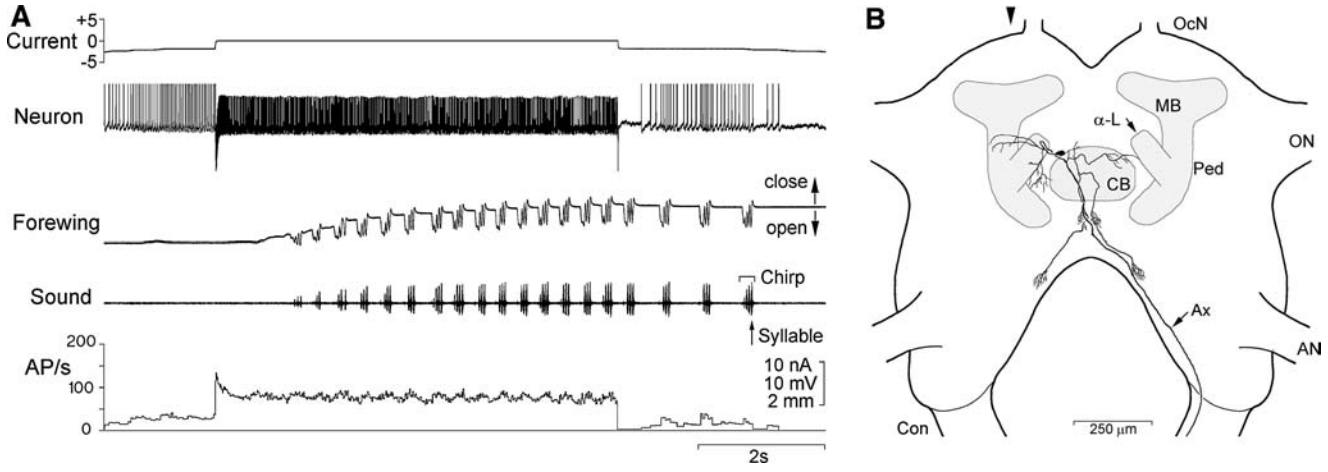

Fig. 7 Command neuron controlling calling song. **a** Intracellular recording of the command neuron in the brain of *Gryllus bimaculatus*. Increasing the neurons spike activity by intracellular current injection to 60–80 Hz elicits the generation of calling song. The cricket lifts its wings and starts to sing. Singing stops at the end of stridulation when the spike rate of the neuron declines again. **b** Structure of the command neuron in the brain. The cell body is located at the dorsal surface of the ganglion. Dendrites branch in the anterior protocerebrum and are particular profuse between the α-lobe and Pedunculus of the mushroom bodies (see Fig. 8**a**). The axon descends in the contralateral connective and gives off collaterals in the Tritocerebrum

also necessary for the release of calling song and meets the criteria for the identification of command neurons (Kupfermann and Weiss 1978). Although the spike activity exhibited a weak phasic modulation in the chirp rhythm there was no evident functional coupling to the timing of the sound pulses. Analysing the correlation between the interneurone discharge rate and the cycle periods of chirps and syllables demonstrated that the repetition rate of chirps increased with the interneurone discharge rate whereas the syllable rate remained unchanged (Hedwig 2000). It confirmed that the brain does not deliver precisely timed commands for the generation of the motor pattern (Otto 1971; Bentley 1977). Activating the command neuron never elicited a transition to rivalry or courtship song. As in grasshoppers, these song types may be controlled by different sets of descending brain interneurons (Hedwig and Heinrich 1997).

Intracellular staining revealed two mirror image command neurons, one in each half of the brain with cell bodies at the dorsal surface of the protocerebrum. Dendrites were located ventral to the central body complex and were profuse in the lateral protocerebrum (Fig. 7b). Histological sections located the dense dendritic branching between the α-lobe and the Pedunculus of the mushroom body (Fig. 8a) and identified this area in the anterior protocerebrum as a putative brain neuropil for the control of calling song behaviour (Fig. 8b). Electrical brain stimulation sites which released singing were arranged around this neuropil (Fig. 8c, from Huber 1960) and it appears likely that the command neuron was directly driven in these experiments.

The identification of the calling song command neuron demonstrated that in crickets and grasshoppers, different brain areas are involved in the control of singing. In grasshoppers, command neurons, which each control a different species-specific motor pattern, have their dendritic arborisations in a dorsal brain neuropil (Hedwig 1994, 2001). In both groups, the singing behaviour is based on central pattern generators, which are probably driven towards precise timing of motor activity by sexual selection. The stereotypy of the singing behaviour and the spatial separation of motor pattern generation (thorax) and coordination of behaviour (brain) may have favoured a control of singing by specialized descending brain neurons.

Pharmacological release of singing

The arborisation pattern of the calling song command neuron in the brain opened up the possibility to analyse the neurochemical control of singing behaviour. Small amounts (0.5–1.0 nl) of neuroactive substances were injected into the anterior protocerebrum and the resulting behaviour was analysed (Otto 1978; Wenzel and Hedwig 1999).

Microinjections of acetylcholine (ACh, 10^{-3} mol l^{-1}) into the protocerebrum reliably released the calling song. Successful injection sites for the release of singing were located in the anterior protocerebral neuropil (Fig. 8d) where the dendrites of the calling song command neuron are located (Fig. 8a,b). After a short latency the animals lifted their wings and started singing (Fig. 8e). Specific activation of nicotinic or muscarinic ACh receptors led to different response times and duration of singing. Injection of nicotine caused short bouts of singing after a short latency whereas injection of muscarine led to a gradual build up of singing behaviour over 60 s, which then lasted for about 2.5 min. These effects may correspond to the

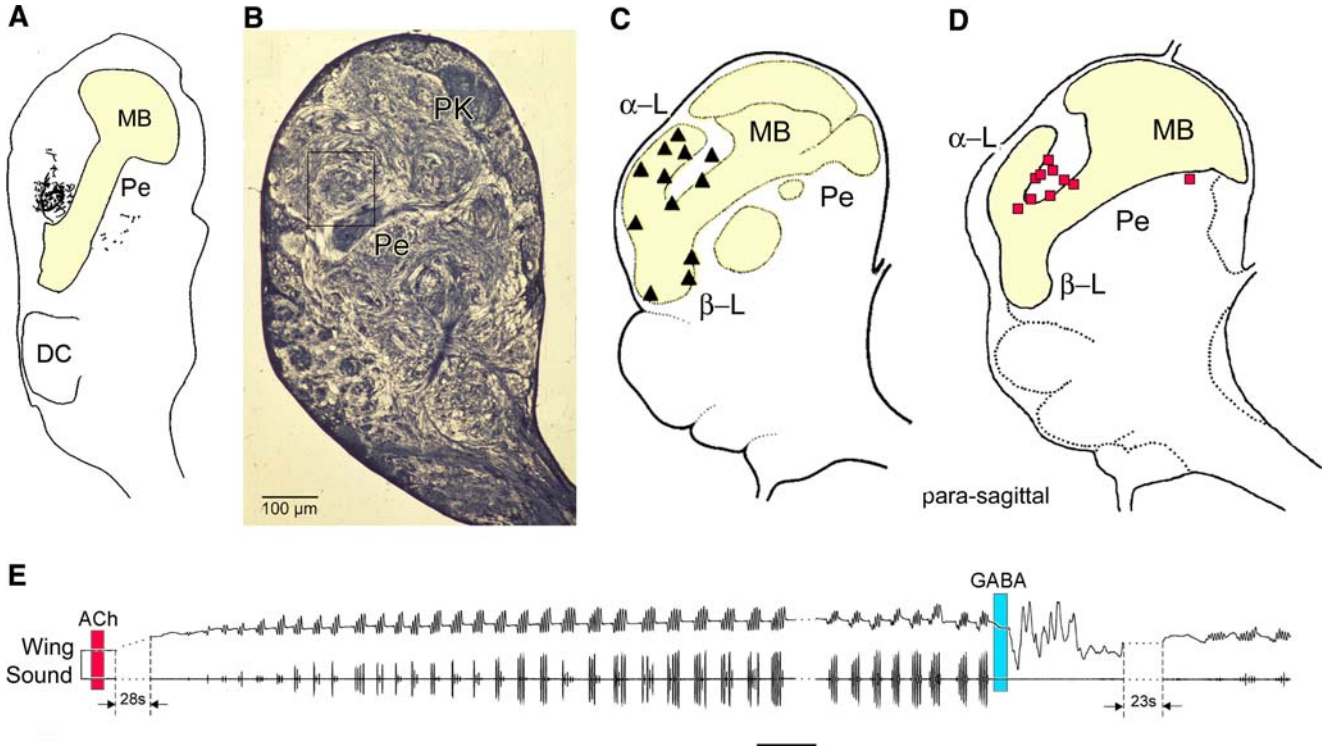

Fig. 8 Brain neuropil involved in the control of singing. **a** The calling song command neuron has profuse dendritic branches in the frontal protocerebrum between the α-lobe and Pedunculus. **b** A para-sagittal histological sections of a haematoxylin stained brain points to a dense circular neuropil in front of the Pedunculus as a putative area controlling singing behaviour in crickets. Level of sectioning indicated in by arrowhead in Fig. 7b. **c** Positions of electrodes in the anterior protocerebrum in brain stimulation experiments releasing calling song in *Gryllus campestris* (modified from Huber 1960). **d** Injection sites of cholinergic agonists, which elicited calling song in *Gryllus bimaculatus* (from Wenzel and Hedwig 1999). **e** Sequence of calling song elicited by injection of 1–2 nl of ACh (10^{-3} mol l^{-1}) into the singing neuropil in the anterior protocerebrum. Continuous singing starts after 28 s and is consecutively blocked by an injection of GABA (10^{-3} mol l^{-1}) into the same area of neuropil

direct effect of ligand coupled nicotinic ACh receptors and G-protein second messenger activated pathways of muscarinic ACh receptors. Blocking the decay of ACh by deactivating the activity of ACh-esterase with Eserine proved to be very effective and released singing for 30–60 min (Otto 1978; Poulet and Hedwig 2001). Although calling song was most frequent, all three song types and transitions between them could be evoked by injection of ACh or cholinergic agonists. Once released, calling song stridulation could be blocked by subsequent injection of γ-butyric acid (GABA) at the same site (Fig. 8e). When inhibitory pathways in the brain were blocked by picrotoxin, motor activity increased in general and different song patterns were briefly produced. Since the pharmacological injection sites in the brain were clearly separated from the motor pattern generating networks in the thorax, the experiments demonstrated the neurochemical sensitivity of the cephalic control system of singing, i.e. the command neurons or the presynaptic neurons driving these. As in grasshoppers (Hedwig and Heinrich 1997), different song types could be elicited from the same neuropil in the anterior protocerebrum, which provides further evidence for its significant role in the control of cricket singing behaviour.

Dealing with self-generated sounds: auditory processing in singing crickets

With the neurochemical tools for the release of singing behaviour at hand, it was an obvious challenge to analyse sound processing in singing crickets. It had been apparent to philosophers and scientist for many centuries, that visual processing during the perception of moving objects should be different to processing during active eye movements since we maintain the constancy of our visual sensations (Grüsser 1986). The question behind this observation is central to any sensory modality and is fundamental to sensory neuroscience: "How do animals process self-generated sensory information as compared to sensory stimuli perceived from their external environment?" Addressing this question, Sperry (1950) and von Holst and Mittelstaedt (1950) formulated their ideas about corollary discharge mechanisms and efference copies, that are generated by the central nervous system

to interact with expected self-generated sensory feedback. Singing male crickets are ideal models to analyse this problem. In order to attract females and provide them with a localisation cue, male crickets (*G. campestris*) sing their loud calling song of 100–105 dB SPL (Nocke 1972a) for many hours. During singing, their own auditory system is exposed to the self-generated sound signals. This might have a detrimental effect on their auditory pathway and reduce their auditory sensitivity—unless they process self-generated sound signals differently to sounds perceived from the environment. Laservibrometric measurements of the tympanic membrane in singing crickets (*G. bimaculatus*) revealed that the tympana oscillated like the membrane of a microphone to self-generated sounds as well as to external sounds. The amplitude of these oscillations was 4–5 times larger than tympanic membrane vibrations in response to sound pulses of 90 dB SPL. Also the primary auditory afferents were activated in response to the self-generated sound pulses. There was no indication that male *G. bimaculatus* changed the responsiveness of their tympanal membrane or auditory afferents during singing (Poulet and Hedwig 2001). Intracellular recordings of the afferents and interneurons in the auditory neuropil of the prothoracic ganglion demonstrated spike activity in both types of auditory neurons during singing (Poulet and Hedwig 2002, 2003a). This excitation could have masked an additional inhibitory input. Advantageously, crickets can be made to "sing" silently by removing one of the front wings. This prevents any self-generated auditory feedback and continuous acoustic stimulation can be used to analyse response properties within the auditory pathway. Intracellular recordings in such silently "singing" crickets, in which the movements of the remaining wing indicated the animal's behaviour, revealed an inhibition of auditory processing in afferents and interneurons in phase with the animal's singing activity. At the axon terminals the afferents received a depolarising input, typical for a primary afferent depolarisation (PAD) that has an inhibitory function in many sensory systems (Clarac and Cattaert 1996) by presynaptically shunting the axon membrane (Fig. 9a). As a consequence, spikes are reduced in amplitude and synaptic transmission between the auditory afferents and postsynaptic interneurons becomes less effective. In parallel the local auditory interneurone ON1 (Fig. 9b) and the ascending neurons AN1 and AN2 (Poulet and Hedwig 2003b) received IPSPs in phase with sound generation. The neurons responded to test sound pulses in the chirp intervals, but the auditory response was suppressed during chirp production. Both types of inhibition persisted even in fictively singing crickets, in which all thoracic and abdominal sensory and motor nerves were cut (except the auditory nerve). The inhibition was therefore not mediated by non-auditory sensory pathways. It rather appeared that a corollary discharge (Sperry 1950; Bell and Grant 1989) from the central pattern-generating network of the thoracic ganglia inhibited processing in the auditory pathway in phase with sound production

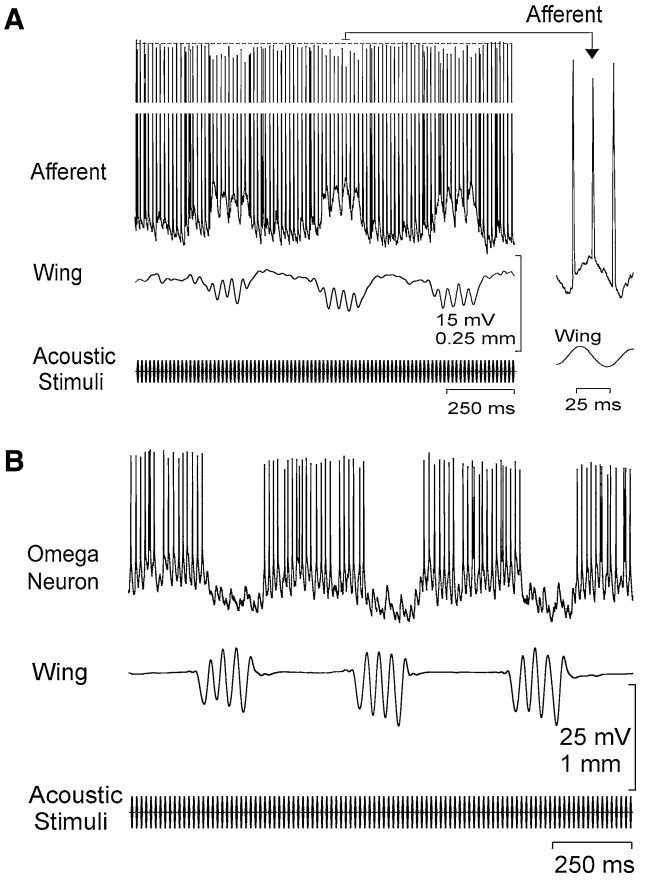

Fig. 9 Corollary discharge inhibition of auditory processing in singing crickets. One front wing was removed to prevent sound production; singing activity is monitored by the opening–closing movements of the remaining front wing. A continuous sequence of sound pulses (4.5 kHz, 7.5 ms duration, 7.5 ms interval, 75 dB SPL) is presented to activate the auditory pathway. **a** Intracellular recording of an auditory afferent close to the axonal terminals in the auditory neuropil of the prothoracic ganglion. The afferent responds with a continuous sequence of spikes to the acoustic stimulation. In phase with chirp generation the afferent neuron is presynaptically inhibited. It receives a rhythmic primary afferent depolarisation, which shunts the membrane and leads to a decrease in spike amplitude. **b** Intracellular recording of ON1 reveals a postsynaptic inhibition in phase with sound production. The neuron spikes during the chirp intervals in response to acoustic stimulation. IPSPs, which occur in phase with the wing movements, suppress the auditory response of ON1 (from Poulet and Hedwig 2002)

(Fig. 10). Although the inhibition of auditory neurons during singing is not complete, it prevents the auditory pathway from desensitisation (Poulet and Hedwig 2002, 2003) and allows crickets to listen out for singing conspecifics or predators while they are calling for a mate. The cellular basis of this corollary discharge has recently been identified (Poulet and Hedwig 2006).

Future prospects

Our analysis of cricket auditory behaviour has demonstrated fundamental principles in neuroscience like

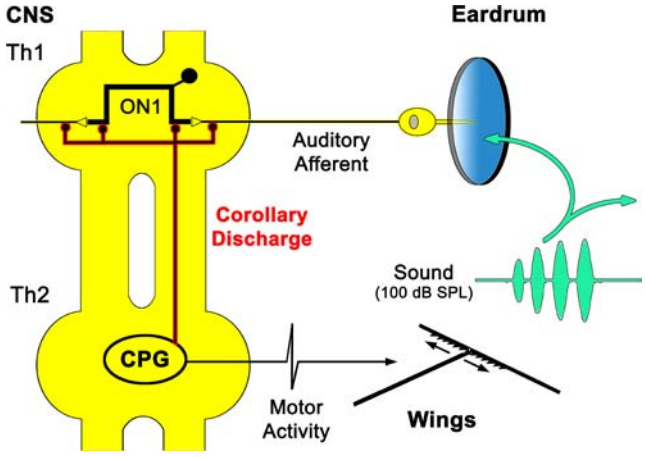

Fig. 10 Corollary discharge inhibition in crickets. During singing, the animal's self-generated sound pulses activate the ears. Auditory afferents respond to the sound pulses and drive auditory interneurons, e.g. ON1. Synaptic transmission between afferents and ON1 is reduced by presynaptic inhibition of the afferent terminals. Additionally ON1 is inhibited postsynaptically. This twofold inhibition of auditory processing is timed to the generation of sound pulses and prevents the cricket's auditory pathway from desensitisation. Inhibition is mediated by a corollary discharge from the central pattern generator in the thoracic ganglia

command neurons, corollary discharge mechanisms, a possible code for pattern recognition and calcium dynamics in an identified auditory neuron. Future approaches will focus on pattern recognition and steering in phonotactic walking crickets. In combination with bio-inspired models of cricket neural networks (Webb 2002), we will be able to test our hypothesis of auditory information processing in artificial neural networks. Further advances in imaging techniques and genetic/molecular approaches to neural function in crickets will boost our methods to unravel the neural principles underlying a fascinating acoustic communication system.

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