

The Senses - Audition - Coding Strategies in Insects

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Abstract

Insects process acoustic information to select specific motor programs for survival and reproduction. In contrast to the supercomputers available to vertebrates and mammals, insects face severe limitations in computational power due to their small and simple nervous systems. Given this constraint we here first explore the repertoire of acoustic behaviors of insects and then summarize their specific limitations and special attributes with respect to hearing. Second, we give an overview of known coding schemes available for coding strategies. Finally, we proceed to specific examples to illustrate coding strategies in small neural circuits such as ratio coding of acoustic signals, flip-flop circuits used by both sexes, context dependent coding in a three-neuron network and evolutionary flexibility of pattern recognition in a large species group.

A wing would be a most mystifying structure if one did not know that birds flew. ... Yet without knowing this, and without understanding something of the principles of flight, a more detailed examination of the wing itself would probably be unrewarding.

Barlow (1961).

The Making of Coding Strategies

Nervous systems process information to control behavior. For instance, through the recognition of behaviorally relevant objects, such as a worm captured by a frog. But energetic costs and hardware capacity limit what can be processed (Sterling and Laughlin, 2015): A supercomputer with 100 Billion neurons like a mammal’s brain can perform sophisticated calculations but is also expensive to build and maintain. Insects manage to survive and reproduce with numerically small nervous systems. Given this limited computational capacity, we expect insects to fully exploit nature’s toolbox of solutions, to have come up with ingenious tricks and work-arounds. What are the coding strategies with which insects achieve their goals?

Acoustic Behaviors in Insects – Maximal Performance With Minimal Resources

The goal of hearing in insects is survival and reproduction - acoustic cues are used to avoid predators and to find food and mating partners (Fig. 1). Given this essential contribution of hearing to fitness, the neural circuits that process acoustic signals must be

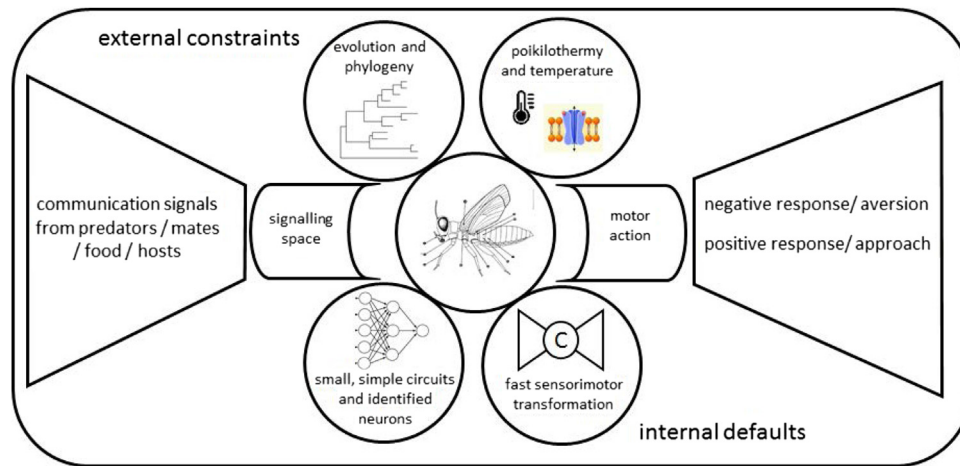


Figure 1 A simplified sketch of the internal and external world of an insect in the context of acoustic communication. From left to right: Insects receive a multitude of acoustic signals from different sources and in different contexts making up the signaling space to be processed. Ears of insects originated independently in different body parts. Internally, important defaults for neuronal processing and coding are small circuits, identified neurons and a fast sensorimotor transformation. External factors such as evolutionary history and change as well as temperature variation constitute important constraints on auditory processing that are reflected in neuronal processing and coding. Motor action flows into two classes of behaviors, positive or negative responses. Indicated by lines, from [Hoy and Robert \(1996\)](#). Insect modified from [Hoy and Robert \(1996\)](#), with permission.

streamlined to perform at low costs. Consequently, the neural codes implemented in the insect auditory systems are often energy efficient ([Niven and Laughlin, 2008](#)) and operate on minimal hardware – sometimes reduced to a single neuron per ecologically relevant sound category. For instance, notodontid moths detect the ultrasonic echolocation calls of bat predators using a single auditory receptor neuron ([Fullard et al., 2003](#)).

Ecology and Performance

Despite this frugality and minimalism, insect auditory systems achieve exceptional performance, often at the limit of what is physically possible: For instance, active processes in the fly ear tune the sensitivity of hearing close to limits imposed by thermal noise (([Nadrowski et al., 2008](#)), Römer this volume). Likewise, a cricket female can localize a singing male with an accuracy of 1 degree, rivaling the performance of vertebrate specialists like bats or barn owls with orders of magnitudes more neurons ([Schöneich and Hedwig, 2010](#)). Accuracy is crucial since it reduces predation risks by minimizing the time spent and distance traveled to reach the male: Female crickets leave their hiding places and expose themselves to aerial and ground-based predators. Acoustic communication is also costly for the sender – singing males expose themselves to predators or parasites, which localize them by the song to eat or lay their eggs, respectively ([Conner and Corcoran, 2012](#)). These risks can be so high as to outweigh the benefits of singing, resulting in silent crickets ([Zuk et al., 2006](#); [Pascoal et al., 2014](#)). Sensitivity and accuracy are also essential for avoiding predators. Crickets and moths can detect the echolocation ultrasound calls of bats with high sensitivity and perform evasive flight maneuvers ([Dunning and Roeder, 1965](#)). Some moth species even jam the bat's echolocation system by producing confusing ultrasound signals of their own ([Conner and Corcoran, 2012](#)). Ecological demands therefore enforce high performance under limited resources ([Fig. 1](#)).

Communication and Signals

Many insect species produce calling and courtship songs. Song not only exposes the sender to potential mating partners and predators – it also signals the sender's species, sex, and physiological status ([Fig. 1](#)). Spectral and temporal properties of the song are evaluated by the auditory system to assess the sender and inform mating behavior. Accurate song pattern recognition minimizes communication costs and avoids futile interactions with mating partners of the wrong species or sex, or of poor quality. Pattern recognition needs to be robust to environmental noise. Yet, nervous system parameters notoriously vary as a result of changes in ambient temperature, since body and ambient temperature are tightly coupled in the poikilothermic insects and the biochemical processes underlying nervous system function speed-up with temperature ([Roemschied et al., 2014](#)). Common behavioral responses to song are phonotaxis or copulation. But courtship can also involve complex acoustic interactions, such as the call-response behavior of males and females in *Chorthippus biguttulus* ([von Helversen, 1972](#); [von Helversen et al., 2004](#)), multimodally coordinated acoustic duets in *Drosophila virilis* ([LaRue et al., 2015](#)), or choruses among groups of male katydids (Römer this volume). The diverse acoustic behaviors of insects betray sophisticated sensorimotor transformations that combine accurate pattern recognition with reliable evaluation of signal timing and location. The need of insect nervous systems to be fast, reliable, robust, correct, and choosy under the constraints of minimal energy and hardware makes them ideal models to study how simple nervous systems achieve high performance.

Insects and Their “Special” Attributes

Small Brains, Computational Basics and Identified Neurons

How is information about the external (and internal) world encoded and transformed into behavior in the nervous system of insects? Insects unlike vertebrates or mammals, have small brains and are forced to use computational algorithms and processing implementations that are likely stripped to their computational basics. A possible materialization of this concept is found in the prevalence of “identified neurons” in insect. These possess individual physiological and morphological attributes that identify these cells from one individual to the next and even across species and higher taxonomical orders (Boyan and Ball, 1993; Neuhofer et al., 2008), hence they represent plesiomorphic traits conserved over millions of years. Typically, these single, cellular units possess considerable processing power, arguably the computational equivalent to ganglia and nuclei of vertebrate brains that are – in contrast to the mini-brains of insects – built from millions of neurons operating in parallel. Coding strategies in insects are therefore limited by small brains and computational power.

Hearing for Communication and Limitations by Noise

As a consequence of the limited computational capacity of insect brains, insect hearing is not geared toward a paramount perception of the physical world but focused on specific goals. These goals are restricted to the world of communication in which insects can take the role of a sender, of a receiver, or of both. There are countless examples for communication between sexes or between predators and prey that embrace interactions between individuals for mate choice, predator evasion, prey finding and host localization, agonistic interactions and territorial spacing (Römer this volume). To achieve these goals, insects have to accomplish the three fundamental tasks of hearing: to detect acoustic signals, to identify acoustic objects, and to localize sound sources (see processing of sound below). The context of communication also brings up the issue of noise. There are three fundamental types of noise that can impact insect hearing: abiotic noise from the outside world, biotic noise mostly from other communicating insects of the same or different species, and intrinsic noise of neurons and synapses (Ronacher et al., 2008). To summarize, insect hearing is bound to the world of communication in which insects strive for specific, clearly defined goals. This restriction creates a defined context within which insect behavior can be quantified to explore their computational power.

Innate Behavior and Dedicated Circuits

Insect behavior is typically stereotyped and can be well quantified, because the behavior associated with the computation of acoustic information for motor actions is largely innate. This means that insects possess prior knowledge about acoustic objects acquired during evolution that works like a build-in memory function of processing circuits. There are several consequences from this for the understanding and investigation of coding strategies. Processing of acoustic information is performed by dedicated circuits directed toward a specific goal and without the involvement of learning sensory templates, as common in birds or humans. This is not to say that experience does not play a role for communication behavior (Bailey and Zuk, 2008, 2009) and the responses of high-order auditory neurons of *Drosophila* are also known to be shaped by sensory and social experience (Li et al., 2018; Deutsch et al., 2019). But this plasticity is largely restricted to circuits at the sensorimotor interface. Implementing and running such dedicated circuits is beneficial for insects: Neural networks that consist of few neurons are cheap to operate and to develop. Basic circuits have to be retained but are not required to change which avoids the cost of plasticity. Innate behavior simplifies computations toward specific and a-priori known goals which greatly reduces the costs for the operation of neuronal circuits.

Fast Sensorimotor-Transformation From Input Representation to Motor Action

Insects are small and with their dedicated circuits require only few synapses for object identification or localization (Fig. 2). The sensorimotor interface is tapered toward command neurons with a subsequent motor circuit that is hierarchically organized. Motor commands from the brain descend by individual neurons to circuits close to motoneurons to trigger actions or modulate peripheral, acoustic reflexes (Namiki et al., 2018; Hedwig and Poulet, 2004). Together, sensory processing and motor action involve relatively few synapses and facilitate fast responses.

Temperature Dependence and Compensation

Insects are poikilotherms and fluctuations in temperature create challenges in terms of varying signals for emission, but also in terms of changing conditions for sensory processing (Fig. 1). Insects employ at least two strategies to cope with variability from temperature effects. The first strategy assumes that sender and receiver are both within close range and are thus exposed to the same temperature. The second strategy is to extract and evaluate temperature independent cues from a signal (e.g., grasshoppers) and is apparently escorted by compensating temperature effects of single sensory cells already at the periphery ((Roemschied et al., 2014), Römer this volume). Variability due to temperature changes have fostered different strategies and at least in part, are compensated by neuronal properties and computational algorithms.

Evolution: Rich in Innovation, Diversity, Transitions and Transformations

The evolutionary history of hearing in insects started more than 200 million years ago and is rich in innovation and diversity. From the very beginning, insect hearing likely served predator evasion and mate choice (Fig. 1). Most prominently, the appearance of bats

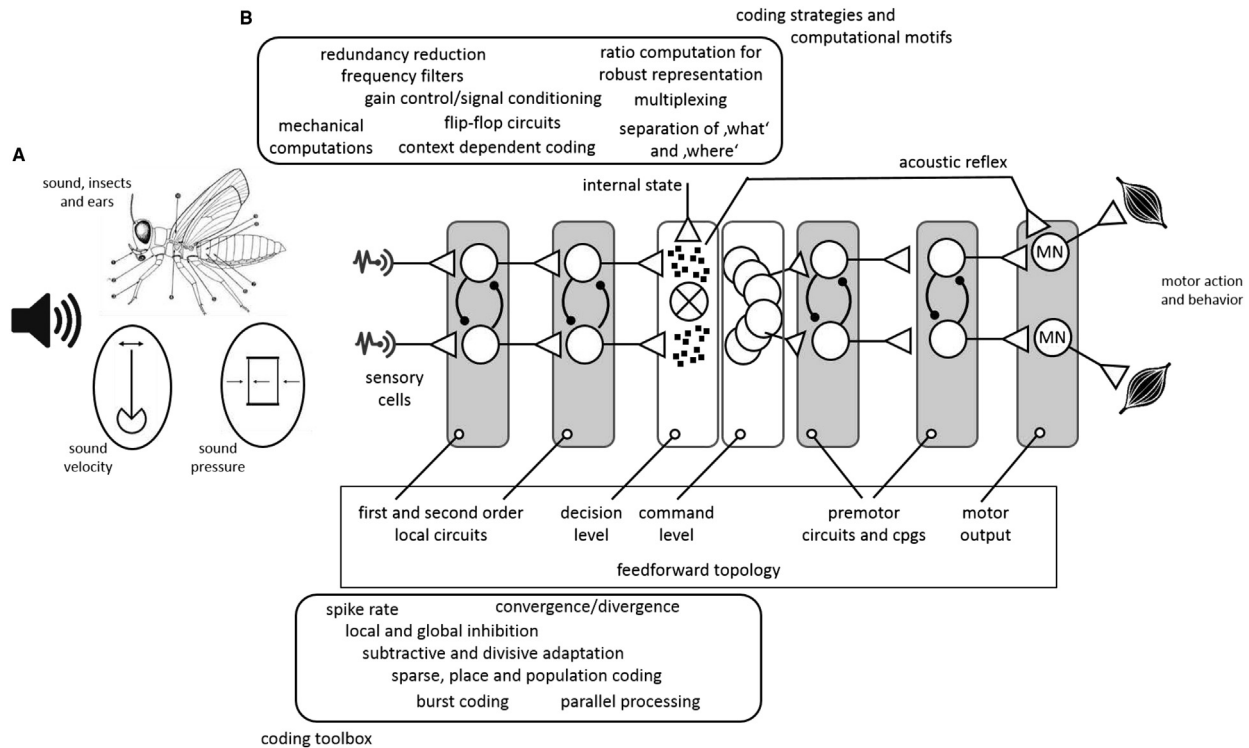


Figure 2 The layout and topology of auditory pathways of insects, processing tools and coding strategies. (A) Insects exhibit two types of ears, sound velocity receivers and tympanic sound pressure receivers. Ears may be located on almost any part of the body. (B) Auditory pathways are usually bilateral with two or three local circuits up to decision and command level for motor action and comprise a simple feedforward topology. Circuits may be housed in individual or fused ganglia. Motor circuits are similarly simple and may involve acoustic reflexes. Upper and lower boxes exemplify coding strategies or computational motifs and typical examples from the mechanistic coding/processing toolbox. Insect modified from [Hoy and Robert \(1996\)](#), with permission.

changed the acoustic world dramatically as many insects had to adapt or invent ears to accommodate a new category of signals. For mate choice as the basis for maintaining species isolation signals and their recognition adapted and changed to produce an impressively rich signaling space across a wide spectrum from low frequency vibrational to ultrasonic frequencies. Due to changing selection pressures signaling - and thus the recognition of signals - was repeatedly lost and re-invented during evolutionary history (Römer this volume). This evolutionary flexibility in insect hearing is at least in part due to the mechanical construction of their bodies equipped with an exoskeleton. The whole body of insects may serve as a substrate to produce acoustic signals by shaking body parts or rubbing them against one another. At the same time, the sensory inventory to monitor internal mechanical forces required for orchestrating movement can be easily converted into a perceptual machinery to detect mechanical pressure exerted by the radiation of sound waves. In terms of coding strategies, circuits and algorithm are likely to emerge during evolution that can be flexibly adjusted at a minimal cost and that enable fast transitions to a changing signaling space and object recognition requirements during speciation ([Fig. 1](#)).

How Insects Process Sound

Sound is a mechanical wave carried by the motion of particles in a substrate. Insects are armed with various types of ears to detect these motions ([Fig. 2A](#)). There are sensory organs for sensing vibrations (if sound is transmitted in a dense substrate), filiform hairs and antennae for detecting sound velocity, and tympanic ears for perceiving sound pressure in air ([Göpfert and Hennig 2015](#)). The structural diversity of ears in insects is truly impressive and given the exoskeletal structures equipped with mechanosensory receptors serving a proprioceptive function, ears evolved on almost any part of an insect's body. Most insects possess bilateral ears, others feature one or more "cyclopean ears" ([Yager, 1996](#)). Mechanotransduction is accomplished by scolopidia or chordotonal sensilla and is at least in some insects known to utilize active amplification for increased sensitivity ([Göpfert and Hennig 2015](#), [Albert this volume](#), [Römer this volume](#)). Insects truly explore the available physical properties of sound. Besides the diversity of different ear types, insect ears also differ impressively by the number and function of sensory cells: while some possess literally only one sensory cell per ear (notodontid moth), others accommodate up to 2000 receptors (cicadas) or turn their antennal ear into a multimodal sensory device ([Göpfert and Hennig 2015](#)).

Leaving the local movement of particle motion aside that accounts for sound velocity, a sound pressure wave has two dimensions, sound pressure amplitude over time. Like vertebrates, insects create two dimensions from sound amplitude by separating frequency information from temporal information. The acoustic signal is then decomposed into the frequency and the time domain for further processing (Römer, Albert, this volume). For processing in the frequency domain, insects as vertebrates employ mechanical devices to perform a spectral analysis of an acoustic signal. Although the mechanical properties of tympanic membranes could serve as a substrate for high frequency resolution (Olson and Nowotny, 2019), the ability of insects to perform a fine scale spectral analysis is limited and typically only one or two categorial classes of sound emerge (Stumpner and Helversen, 2001). The tuning for frequencies varies between species, but evidently a major gain of frequency tuning is the implementation of peripheral filters to reduce noise (Römer this volume). While vertebrates and mammals often exhibit exquisite spectral resolution, insects appear to ignore much of the available information and send only what is needed to further processing stages (Sterling and Laughlin, 2015). Consequently, much of object recognition is performed by processing in the time domain, for which sound pressure amplitude is translated into intensity dependent spike rates of sensory cells. However, spectral information through a series of frequency filters in the ear can be used in other ecologically important contexts, such as estimation of distance to signalers, intensity discrimination, novelty detection, or improvement of the signal-to-noise ratio (Pollack and Imaizumi, 1999; Römer, 2015, this volume) for temporal processing.

Peripheral computations for directional hearing in insects provide a remarkable example for a widely used, cheap and reliable implementation of a coding algorithm – mechanical computations. By internal, mechanical coupling of both tympanic ears, pressure receivers are turned into pressure difference receivers as sound pressure will act on both, external and internal, sides of a tympanum. By that, the directional response differences are greatly enhanced and equip insects with a sense for directional hearing that would not be available with the standard tympanic ear of vertebrates that operates as a pressure receiver (Huber et al., 1989). This solution is also used by many vertebrates from frogs to birds (Christensen-Dalsgaard, 2011) with the exception of mammals (Grothe and Pecka, 2014). In insects, the small interaural time differences in the microsecond range cannot be exploited by neuronal processing, but localization becomes possible due to the amplification of interaural intensity differences by pressure difference receivers. Notably, for further auditory processing, interaural intensity differences are first enhanced by contralateral inhibition and then translated into differences in spike rate but also differences in spike time, that is the arrival time of action potentials at neurons computing sound direction (Krahe and Ronacher, 1993). Differences in the relative timing of contralateral inhibition with ipsilateral excitation in different interneurons further enhance the directional cues in spike rate and time (Römer et al., 1981; Römer and Dronse, 1982). By that, insects arrive at the same solution for coding directional cues as vertebrates do by using interaural intensity and time differences. In a nutshell, insect ears use the full capacity of available physical properties for sensing sound. Mechanical devices perform the initial computations to provide a basis for further processing in the frequency and time domain.

Diversity of Auditory Pathways and Topologies

Given the multitude of insects able to hear and the overwhelming diversity of ears, it appears as a formidable challenge to provide a résumé of auditory pathways and underlying network topologies as part of a review that aims at the principles of what these circuits do. Given the tasks of the ‘what’ of acoustic object identity and the ‘where’ of object localization (Pollack, 2000), the general layout of auditory pathways, sketched across several taxonomical units of genera, families and orders, is one of a bilateral, feedforward topology (Fig. 2) with repeated, local circuit interactions between both sides and within one side. In addition, at least at the peripheral stage of processing there is also a central, not bilateral and thus unpaired network for frequency processing (Lefebvre et al., 2018). Local circuits and upstream projections in different species each may be implemented by individual cells, as for instance in crickets (local and ascending first order neurons) (Clemens et al., 2015b), or by populations of neurons as in grasshoppers and *Drosophila* (Pacheco et al., 2019; Patella and Wilson, 2018; Stumpner and Ronacher, 1991). Within local circuits inhibition (Hennig et al., 2004; Yamada et al., 2018) is a common neuronal interaction. At least for some species, only two to three local circuits exist from the sensory periphery up to the brain. At the sensorimotor interface the result of sensory processing and decision making is passed onto command neurons (Zorovic and Hedwig, 2012). The precise topological and physiological basis at this transition point is still unclear; direct synaptic connections are possible, but not demonstrated. Indirect chemical transmission or the involvement of neuromodulators is also possible, at least pharmacological manipulations allow to elicit specific parts of the behavioral repertoire (Heinrich et al., 2012). From command neurons to motor action again a bilateral organization with local circuit interactions is known to accommodate premotor circuits and central pattern generators for specific behaviors (Fig. 2). Notably, auditory processing and coding has found a sensory shortcut to modulate directly a local reflex, important for directed behavior (Hedwig and Poulet, 2004).

Given the goals and limitations of insect auditory perception and pathways, evolution is expected to favor coding strategies that (1) use dedicated circuits to achieve specific goals, (2) keep computational and operational costs low, (3) implement fast sensorimotor transformations from input representation to motor action, (4) minimize the detrimental effects of noise and temperature dependence, (5) are flexible and not rigid in implementations as evolutionary change may require fast adaptations and transitions, and that (6) shift processing tasks to mechanical devices that save cost and gain speed of performance.

Processing of sound for directional hearing and signal recognition in insect audition generally requires only few synapses and indicates an efficient use of coding strategies. We now ask first, what are known coding schemes that help us to understand coding strategies. Then, we will explore the computational power of small networks from specific examples.

From a Neuronal to a Computational Toolbox

The coding strategy for an organism in a given modality depends on its goals, its available resources, potential costs and benefits, and finally on physical and phylogenetic constraints. For insects, the small size of their neuronal networks constrains computational capacity. On the other hand, insects code for specific goals in the auditory domain, which may help to streamline coding operations. Coding strategies may be expected to serve three purposes, (1) that of the representation of incoming information, (2) the extraction of features and cues of relevant objects, and (3) fast and efficient sensorimotor transformation. In order to comprehend coding strategies in the auditory world of insects it is less helpful to compare mechanistic implementations in different species, because of the heterogeneous and diverse phylogenetic background evidenced by the multitude of different auditory pathways. Rather, the computational algorithms should be identified starting with the computational themes observed in peripheral processing (Hildebrandt et al., 2015). Some of these general coding principles may also apply for sensory processing and the representation of information across auditory, visual and olfactory modalities in insects, such as the reduction of redundancy for efficient coding (Sterling and Laughlin, 2015; Weber and Machens, 2015).

In peripheral sensory processing in insects four computational themes can be identified (Hildebrandt et al., 2015): sensitivity control, recoding of pattern representation, frequency filtering and directionality processing. Associated with these themes is a set of preprocessing motifs, commonly observed in nervous systems such as adaptation and negative feedback, feed forward inhibition, sparsening and decorrelation, lateral inhibition, frequency pooling and parallel processing. These motifs are carried by a number of available operations out of the computational toolbox in nervous systems.

Coding in the sensory periphery of insects is dominated by spike rate coding by a time dependent firing rate with high rates of action potentials. Toward the extraction of cues the spike rate declines rapidly and information is represented by relatively large (>10–20) populations, for instance in the auditory pathway of grasshoppers, noctuid moths, and *Drosophila* (Boyan et al., 1990; Stumpner and Ronacher, 1991; Patella and Wilson, 2018), or by few neurons firing few spikes, as in the neurons coding song features in crickets (Clemens et al., 2015b; Schöneich et al., 2015). A similar reduction of spike rate is also observed in the ascending sensory pathways of mammals (Casseday and Covey, 1996; Covey and Casseday, 1999). Sparse codes may represent object information by single or few spikes, by single cells or both. For instance, temporal sparseness in single neurons coding with few spikes is matched by the ascending neurons in the locust and the local neuron LN4 in crickets (LN4 in Fig. 5C, E) (Clemens et al., 2011; Schöneich et al., 2015). Sparseness by coding with few neurons is known, for instance in crickets ascending or local neurons (Fig. 5, AN1 and AN2, LN4) (Clemens et al., 2015a). Activity patterns in a larger population where only few neurons are active at any given time is observed in locusts (Clemens et al., 2011). Associated with spike rate coding is adaptation which controls neuronal sensitivity and gain, suppresses background noises, and improves the fidelity of representation (Hildebrandt et al., 2015, Römer this volume). With this relatively simple computational toolbox insects accomplish remarkable efficiency and performance even with very small networks of limited capacity (see sections below).

Other known coding schemes are less prominent in insects, such as the formation of neuronal maps that is mostly limited to peripheral representations. However, frequency maps in the first three layers of sound processing in *Drosophila melanogaster* are also known (Patella and Wilson, 2018). A lack of sensory surface maps is not unusual (Grothe, 2018). Yet, a possible ultimate reason for this rarity of map-like representations in insects may lie in the fast sensory to motor transformation and/or the extreme convergence toward command neurons for decision making. Burst coding for predator detection in single neurons ((Marsat and Pollack, 2012), see below) is known, but with respect to coding it may play a less prominent role than in many vertebrate systems (Krahe and Gabbiani, 2004). The parallel role of spikes also suggests that some neurons multiplex information, which is consistent with the need to fully exploit limited hardware. For instance an ascending neuron in crickets encodes different sound features in isolated spikes and bursts (Wimmer et al., 2008). Other coding schemes such as temporal or factorial coding do not seem to play a prominent role for auditory processing in insects. The antagonistic representation of information as observed in receptive fields of the visual system of vertebrates may, although in a much simpler form, be present in onset excitations and onset inhibitions, seen in the auditory pathway of grasshoppers (Stumpner and Ronacher, 1991).

Insects often exhibit fast sensory-to-motor transformations. Information converges onto few, individual command neurons that may be viewed as the read out of the decision making machinery that blends external information with internal state or motivation (Hedwig, 2000; Heinrich et al., 2012). Notably, crickets achieve fast sensory-motor transformation of acoustic information by peripheral reflexes that are modulated by descending brain neurons (Fig. 2, (Hedwig and Poulet, 2004)). Insects benefit from parallel processing for efficient coding of information, but there is also evidence for serial processing of information. While some insects (grasshoppers) separate conflicting information such as object identification and object localization in parallel processing schemes (von Helversen and von Helversen, 1995), crickets appear to use a conventional serial scheme (Hennig et al., 2004). The latter may be the result of old phylogenetic constraints where object identification evolved before object localization (Strauß and Stumpner, 2014).

Coding Strategies – Examples for the Computational Power of Small Networks

We will now illustrate particular coding strategies employed by insect auditory systems. These examples show how small insect circuits achieve exceptional performance – by using computational shortcuts, by reusing circuits, by employing complex adaptive codes, and lastly by maintaining evolutionary plasticity while retaining robust functions.

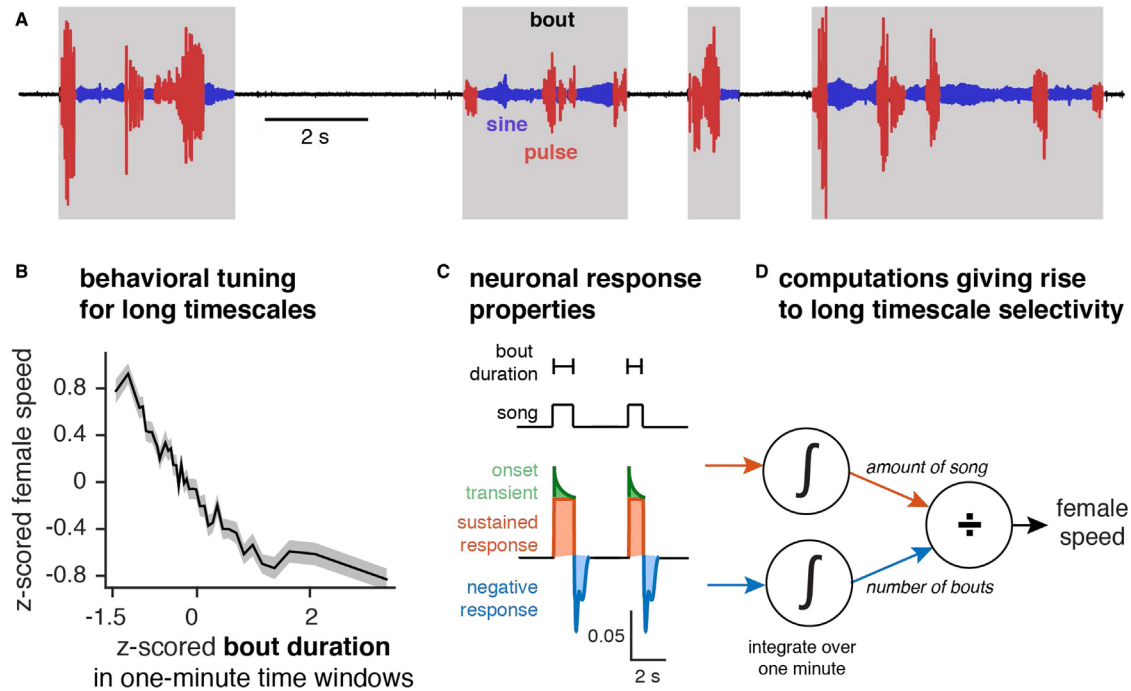


Figure 3 Computational short cuts for extracting information across long timescales in song. (A) *Drosophila melanogaster* males produce song in bouts. Each bout is typically composed of two major modes – sine (blue) and pulse song (red). Sine song corresponds to a sustained sinusoidal oscillation of around 150 Hz; Pulse song consists of trains of pulses with two distinct shapes, interleaved by a species-typical interval of 35–45 ms. Males control the mode composition and duration of bouts based on dynamic sensory cues from the female. (B) Female flies reduce their walking speed when hearing the male song. This locomotor response is strongest for courtship epochs with long song bouts (x-axis indicates the average duration of bouts in a one-minute time window, z-scored for each individual). Line and shaded area correspond to mean and standard error over all time windows for each bin. (C) Schematic of a typical neuronal response to song in the early auditory system of *Drosophila*. Responses consist of three phases: an onset transient at the beginning of each bout (green), a sustained positive response (orange) that copies the bout structure, and a negative response component (blue) that marks the end of each bout. (D) From these response properties, a simple readout mechanism for producing the female tuning in B can be devised: Positive and negative response components can be separated using rectification. The onset transient can be removed via saturation. The integral over positive components corresponds to the amount of song and the integral over negative components corresponds to the number of bouts in the integration time window. The ratio of both integrals yields the behaviorally relevant song feature – the average duration of bouts in the integration time window – and well predicts female responses to song. Panels (A–D) reproduced with permission from Clemens et al. (2015a).

Computational Shortcuts for Encoding and Decoding on Long Timescales

Communication signals often exhibit structure on multiple time scales. For instance, human speech is composed of sentences, which are composed of words, which themselves are composed of phonemes. Signal structure on timescales of seconds exceeds the time scales of most neuronal processes – for instance the time constants of cellular membranes and ion channels are typically shorter than 100 milliseconds. The operations that connect these intrinsic neuronal time scales with the long timescales of features in communication signals are therefore poorly understood (for exceptions see: Pollack, 1988; Römer and Krusch, 2000). Many insect songs have a multi-scale structure, rendering insects ideal model systems for uncovering the computational principles of processing at long timescales.

For instance, *Drosophila melanogaster* males arrange their courtship song into bouts that typically last 0.5–1.0 seconds (Clemens et al., 2015a) (Fig. 3A). Bout timing, duration, and composition are highly variable and arise from dynamical interactions between the male and the female (Coen et al., 2014; Coen et al., 2016; Clemens et al., 2018). Hearing the male song reduces female walking speed during the courtship chase and may lead to copulation (Coen et al., 2014). Behavioral experiments have shown that females evaluate song features spanning timescales from a few milliseconds to seconds (Clemens et al., 2015a; Deutsch et al., 2019). Notably, the average duration of bouts in a time window of tens of seconds is most predictive of female slowing in natural courtship, suggesting that females evaluate bout duration (hundreds of milliseconds) and integrate this information over longer time-scales (tens of seconds) to control their walking speed (Clemens et al., 2015a) (Fig. 3B).

An efficient algorithm for how bout duration can be evaluated and integrated has been proposed based on electrophysiological properties of auditory neurons in the fruit fly (Clemens et al., 2015a): Auditory neurons produce triphasic responses to individual bouts, with a positive onset transient, a sustained plateau phase, and a negative offset transient (Fig. 3C). Computational modeling has shown that these properties imbue single neuron responses with information about bout duration in a format that can be read out using common neuronal computations (Fig. 3D): The sustained part copies the bout structure, and its temporal integral

therefore contains information about the amount of song in the integration time window. By contrast, the offset transient is independent of bout duration and its temporal integral is therefore proportional to the number of bouts in the integration time window. Mathematically, the ratio between both integrals – amount of song and bout number – corresponds to the average bout duration in the integration time window and can be easily computed with excitatory and inhibitory synapses. The neurons performing these operations are not yet known, but a computational model of these processes reproduces the female responses to natural song with high accuracy, suggesting that the female brain may use a similar algorithm to evaluate the long timescale structure of the song to control walking speed during courtship.

Note that in the proposed algorithm - which is also known for frogs and bats - the duration of an *individual* bout is never explicitly represented in the brain (Covey and Casseday, 1999). Doing so would require sophisticated temporal computations that detect the beginning and end of each bout and then combine this information over long time scales. Rather, the *average* bout duration – which is the behaviorally relevant stimulus feature – is computed directly from simple song features like the amount of song and the number of bouts. This avoids the unnecessary and costly computation of complex intermediate features. Other insects employ this coding strategy, too: grasshoppers compute the duty cycle of the song to obtain a measure independent of temperature variation (von Helversen and von Helversen, 1994; Creutzig et al., 2009) and some crickets also evaluate pulse duty cycle rather than specific pulse rates (Hennig et al., 2016). Interestingly, the same coding strategy – relying on temporal or spatial averages of features instead of their exact, individual values, sequences, or distributions on longer time scales – underlies the recognition of visual and acoustic textures in the human brain (McDermott et al., 2013; Freeman and Simoncelli, 2011) suggesting that this computational strategy constitutes a universal shortcut.

Re-use of Circuits for Specific Computations – A ‘Flip-Flop’-Usage

In many species, the males sing but both males and females evaluate acoustic signals, either because females also produce signals or because detecting the song of other males may be of value – for instance to guide agonistic behaviors toward rivals. If the sex-specific behaviors rely on similar features – or even the same signal, then feature detectors can be re-used. Specific behaviors can then be driven from shared feature detectors using dedicated pre-motor circuits.

For instance, in *Drosophila melanogaster*, only males sing during courtship. Females are the intended receiver and evaluate the song to inform their behavior during courtship. However, nearby males may also detect the song and use it as a cue to also court that female or to induce agonistic behaviors. Interestingly, while the type of behavioral response to the pulse mode of the song (Fig. 4A) is sex-specific – males accelerate and sing, females reduce their locomotor activity – the feature tuning of these behaviors is similar in both sexes (Deutsch et al., 2019). Both male and female behavioral responses are strongest for pulse trains that match the conspecific song (Fig. 4B). Responses in a set of high-order auditory neurons in the fly brain – the pC2 neurons – match the behavioral tuning for the conspecific song in males and females (Fig. 4C). Optogenetic activation of the pC2 neurons drives singing only in males and sex-specific locomotor responses, suggesting that they connect to sex-specific pre-motor neurons (Fig. 4D). In *Drosophila*, sex-shared song detector neurons are thus re-used to drive sex-specific behaviors.

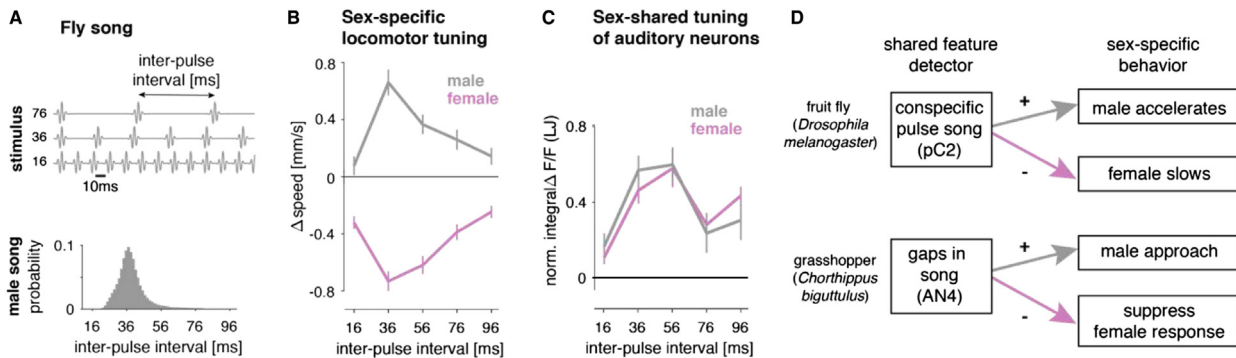


Figure 4 Re-use of circuits. (A) The pulse song of *Drosophila melanogaster* males consists of brief pulses produced at a species-typical interval. Top traces show examples of artificial pulse trains composed of one of the two species-typical pulse shapes and with different inter-pulse intervals. The bottom histogram shows the distribution of inter-pulse intervals in the male song with a mode around 36 ms. (B) Males and females change their walking speed upon playback of pulse song. This locomotor response has a sex-specific sign – males (gray) accelerate, females (magenta) slow – but the tuning for inter-pulse interval (and other song features) is shared between sexes – both sexes change their speed the most for inter-pulse intervals of 36 and 56 milliseconds. (C) High-order auditory neurons in the fly brain – called pC2 – are tuned to all conspecific features of the pulse song – including the inter-pulse interval. Tuning is similar in both sexes. This is consistent with the sex-shared auditory pC2 neurons being re-used in both sexes to determine the feature tuning of the locomotor response. Optogenetic activation of the pC2 neurons in males and females evokes sex-specific locomotor responses, confirming this hypothesis. (D) Schematic of examples for circuit re-use across sexes in fruit flies and grasshoppers. In fruit flies, pC2 neurons detect pulse song in both sexes and produce locomotor responses with a sex-specific sign. In grasshoppers, the AN4 neuron detects songs with gaps and could trigger approach behavior in males and a suppression of responses in females. Panels (A–C) reproduced with permission from Deutsch et al. (2019).

Another instance of the reuse of recognition circuits comes from the grasshopper *Chorthippus biguttulus*, which engages in an acoustic duet. Males sing with a species- and sex-specific calling song. Receptive females respond with their own, sex-specific song and males use the female reply to localize and approach her. Both males and females evaluate the temporal structure of the signals of the other sex to inform their behavior – females decide whether to answer the male call and males decide whether to approach the female (Stumpner and Ronacher, 1994; von Helversen and von Helversen, 1997). The early auditory system of grasshoppers is not sex-specific – the same sets of neurons process the song in males and females. Notably, these circuits are also not species-specific – these neurons thus constitute a generic set of feature detectors which is re-used across species and sexes to accommodate the recognition of species- and sex-specific affordances, and possibly also to detect predators (Neuhöfer et al., 2008). For instance, the ascending neuron (AN) 4 is specifically inhibited by song syllables that are interrupted by short (1–6 ms) gaps (see also: Kostarakos and Römer, 2018). Gaps are an acoustic feature that is informative to males and females: The male song is gapless, but the song of females contains gaps – gap detection can therefore contribute to sex discrimination. On the other hand, the song of heterospecific or injured males also features gaps. Gaps therefore discriminate suitable males – intact conspecifics – from unsuitable males – injured or heterospecific males (Kriegbaum, 1989). Thus, the gap detector AN4 can be re-used in both sexes to drive sex-specific behaviors: In males, its output could be used to drive the approach to female song; in females, it could be used to suppress replies to the songs of inferior males. In brief, re-use of neurons and circuits across contexts and tasks may be a general strategy employed by insects.

Context Dependent Coding and Gain Control at a First-Order Local Circuit in Crickets

In vertebrate systems, the coding properties of neurons or networks can depend on the stimulus statistics in complex ways (Carandini and Heeger 2012 see Chapters by M Pecka, C Schreiner, S Shamma in this volume). These stimulus-dependent and dynamic codes are thought to mostly arise from the complex and numerous networks of vertebrate brains. However, examples from insects show that simple and small networks can produce complex and dynamic codes. Recent evidence related to spatial coding in mammals suggest that even in mammals simple circuits can produce similar stimulus-dependent coding dynamics (see chapter by M Pecka).

For instance, stimulus-specific adaptation (SSA), during which responses to repeated signals are reduced while responses to novel stimuli remain unaffected, is thought to be a neural correlate of novelty detection in the auditory system and is expressed in the midbrain and in the cortex of vertebrates (Khouri and Nelken, 2015, see chapter by M Malmierca in this volume). However, its mechanisms are only beginning to be elucidated (see (Natan et al., 2015)). In contrast, a mechanism for SSA has recently been revealed in *Neoconocephalus* katydids: A first order T-shaped neuron (TN) 1 receives input from low- and high frequency afferents that are sensitive to communication signals (10–15 kHz) and bat echolocation calls (>25 kHz), respectively. TN1 quickly ceases to respond to fast trains of song pulses but maintains sensitivity to simultaneously presented bat signals. The same SSA, in combination with selective tuning may result in selective responses to conspecific signals despite intense heterospecific masking (Römer, this volume).

A combination of imaging, electrophysiology, and pharmacology suggests that this form of SSA arises via dendritic computations (Schul et al., 2012; Trübschhorn and Schul, 2013; Prešern et al., 2015): TN1 receives tonotopically organized input from low and high frequency afferents on separate dendritic branches. The frequency-specific inputs lead to a local accumulation of Na and Ca, which reduces the local sensitivity to subsequent inputs, for instance via Na-gated K-channels. This locally restricted dendritic plasticity confines adaptation effects to a specific frequency through the tonotopic organization of afferents. Thus, a complex computation can arise from a simple mechanism already within a single neuron, in this case at the level of a first-order interneuron postsynaptic to auditory sensory cells, and does not necessarily require high computing power and sophisticated neural networks.

Another example comes from crickets, in which a dynamic, stimulus-dependent code arises from nonlinearities in a network. The peripheral auditory system contains a three-neuron core network that receives afferent input and has two output neurons. The ascending neurons (ANs) 1 and 2 encode two ecological sound categories: AN1 receives input from low frequency afferents and encodes the temporal pattern of the calling song; AN2 is most sensitive to the ultrasound echolocation calls of bats and necessary and sufficient for bat avoidance, but it also receives input from the low frequency afferents (Nolen and Hoy, 1984; Hennig, 1988). The local omega neuron 1 (ON1) receives broad spectral input – and ON1's main function is to increase directionality of responses for sound source localization (Horseman and Huber, 1994) by inhibiting the two contralateral ascending neurons, AN1 and AN2.

The spectral and temporal tuning of the ANs can change dramatically depending on the spectral composition of the input (Clemens et al., 2015b): For pure tone carriers, both ANs can be relatively broadly tuned – for instance, AN1 often responds to intensity peaks in high carrier frequencies. The spectral tuning sharpens drastically for spectrally complex sounds composed of multiple frequencies – now AN1 and AN2 respond only to their preferred frequencies – song and bat calls, respectively. This sharpening reduces confusion about features from frequency ranges with different behavioral valence, and modeling suggests that saturating NIs in the periphery are sufficient to produce this adaptive sharpening. For AN2, the spectral context also changes temporal tuning, from a temporal low-pass filter for pure tone stimuli, to a band-pass filter for complex broadband stimuli. A model of the network suggests that the stimulus-dependent temporal tuning arises from an increase in inhibitory drive from ON1 to AN2 for broadband stimuli: ON1 is broadly tuned, inhibits AN2 with a delay and produces stronger responses for broadband stimuli, while excitation from afferent inputs increases only moderately. This relative increase in inhibition leads to the temporal bandpass filter (Rau et al., 2015). Inhibitory drive also increases for AN1 but does not yield a bandpass, since excitation and inhibition coincide. Note that the

two proposed mechanisms underlying adaptive tuning – saturating nonlinearities and increased, delayed inhibitory drive – are static. This form of adaptation does not require a parameter change in the network and can therefore respond instantaneously to changes in the stimulus statistics. Similar cross-frequency effects have so far only been reported from the more complex auditory networks of vertebrates, but – like for stimulus-specific adaptation – mechanisms are largely elusive due to the complexity and mechanistic redundancy of vertebrate cortical networks.

The mechanisms proposed to underlie the adaptive codes in insects – dendritically compartmentalized plasticity, saturating nonlinearities and delayed, broadly-tuned inhibition are ubiquitous in nervous systems and could therefore explain similar effects in more complex vertebrate networks (Whitmire and Stanley, 2016; Carandini and Heeger, 2012). The reduced mechanistic redundancy of the neuronal networks in insects therefore facilitates the identification of mechanisms and algorithms for sophisticated computations.

Swift Evolutionary Transitions, Preference Profiles and Neuronal Circuitry

The great diversity of song patterns in groups of closely related insect species illustrates the astonishing evolutionary plasticity of song production and song recognition networks in insects. Most insect species use pulsed songs for communication (Fig. 5A, see also 4A). The temporal structure of pulse songs can be fully described in a two-dimensional feature space with pulse duration and pulse pause as principal axes (Fig. 5B). Evolution of song recognition can be thought of as reshaping the set of preferred stimuli within this parameter plane. The computational principles of pulse song recognition are now well understood (Ronacher et al., 2014; Hennig et al., 2014). A model comprising common neuronal computations – a linear Gabor filter, a sigmoidal nonlinearity, and temporal integration – can produce all major types of preference functions (Fig. 5B). The Gabor filters determine the song preference in the network and are known from engineering (Gabor, 1946) and the nervous system (Hubel and Wiesel, 1959; Lewicki, 2002).

The filter shapes can arise through diverse mechanisms, e.g. through interactions between excitation and inhibition in a network or through cell-intrinsic properties (Rau et al., 2015). Electrophysiological studies in the brain of the cricket *Gryllus bimaculatus* have revealed an implementation in which this filter arises through a combination of these mechanisms (Kostarakos and Hedwig, 2012; Schöneich et al., 2015) (Fig. 5C). The network consists of five neurons which interact to produce the behavioral selectivity for the pulse song via a delay-line and coincidence detection principle: AN1 provides excitation onto local neurons (LNs) in the brain. LN2

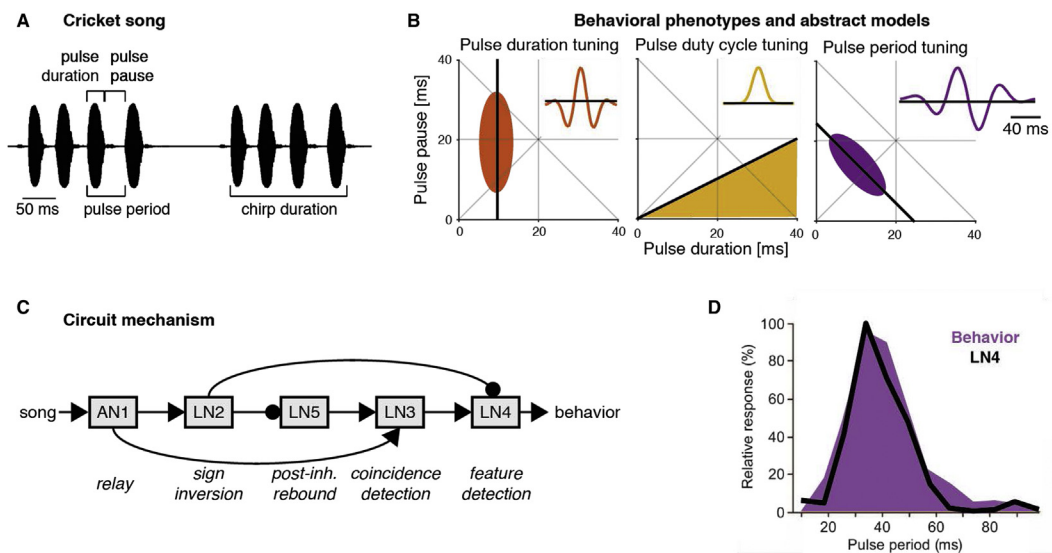


Figure 5 Evolutionary plasticity of song preference. (A) Song of *Gryllus bimaculatus* as an example of the general *Bauplan* of cricket song. Song is often produced in short regular packets of pulses called chirps. The chirp structure is fully characterized by the duration of the pulses and the pause between pulses. The sum of pulse pause and duration corresponds to the pulse period. The pulse duty cycle corresponds to the fraction of the pulse period filled by the pulse. (B) The female preference function for the pulse parameters can be estimated in phonotaxis experiments with artificial pulse trains in which pulse duration and pulse pause are systematically altered. Experiments in multiple species revealed three major types of preference functions: Tuning for pulse duration (left, brown), characterized by high selectivity for duration, and low selectivity for pause. Tuning for duty cycle, characterized by responses only for stimuli that exceed a minimal duty cycle (middle, mustard). And tuning for pulse period, characterized by high selectivity for pulse period and lower selectivity for other song features (right, purple). An abstract computational model that combines linear filtering of the pulse pattern and integration can reproduce the known types of preference functions. The temporal filter acts as a template for the pulse pattern and determines the song preference (filters shown as insets in each panel). (C) Five-neuron network for song recognition in the cricket *Gryllus bimaculatus*. Labels below each neuron indicate that neuron's function. Triangular and round arrow heads indicate excitatory and inhibitory synaptic connections, respectively. (D) Comparison of neuronal tuning for pulse period at the output neuron of the network, LN4 (black line), and in behavior (purple area). The network tuning matches the behavioral tuning. Panel D adapted from Schöneich et al. (2015).

inhibits LN5, which produces a post-inhibitory rebound potential at the end of each pulse. A coincidence detector (LN3) then combines this post-inhibitory rebound with direct excitation from AN1. LN3 will spike only when these two sources of excitation coincide, and synaptic delays in the network ensure that this happens only for the conspecific song pattern. Finally, the readout neuron LN4 further sharpens interval selectivity by responding only when excitatory input from LN3 is maximal (i.e., not to single pulses) (Fig. 5D). A computational model reveals that the network can be easily tuned to produce the preference function of other species by changing few physiological parameters like synaptic delays or the duration and magnitude of the post-inhibitory rebound in LN5 (unpublished results). This plasticity of the recognition mechanism could be the origin of the high evolutionary plasticity of acoustic communication in insects. Recognition principles and mechanisms for pulse song found in insects may also be relevant for understanding the evolutionary origin and overarching principles of vertebrate acoustic communication. For instance, resonant conductances, post-inhibitory rebounds, or interactions between excitatory and inhibitory synaptic inputs are mechanisms to attain duration or pause selectivity in the auditory systems of electric fish (Baker and Carlson, 2014), frogs (Rose, 2014), or mice (Aubie et al., 2012).

Overall, these examples demonstrate that insect auditory systems are capable of complex computations expected only from bigger brains. This performance is achieved by similar computational principles as those found in the brains of vertebrates. However, the minimal implementations found in insects exhibit reduced mechanistic redundancy, which facilitates the identification of candidate mechanisms.

Research Strategies and Open Questions

Past work has provided an enormous amount of insight into the evolutionary diversity and computational principles of auditory coding in insects. We believe that tackling the following open questions in the future will lead to a more complete understanding of the coding strategies employed by insects:

- (1) Detection of complex songs: The songs of most insect species follow a simple *Bauplan* with short pulses produced at regular intervals (Fig. 5A) and the computational principles for their evaluation as well as an example implementation are now known (Clemens and Hennig, 2013; Schöneich et al., 2015). However, several species deviate from this simple scheme, for instance by composing songs from multiple pulse patterns (Stumpner and Helversen, 1992; Bailey et al., 2017). How are these more complex signals recognized?
- (2) Integration over long time scales: It is rarely tested – but widely assumed – that the long and repetitive songs are integrated over time to inform behavior. Accordingly, compelling evidence for long-timescale integration is scant (but see (Clemens et al., 2015a; Clemens et al., 2014; Poulet and Hedwig, 2005)) and many existing behavioral data are consistent with moment-by-moment decision making. To what extent is song information integrated behaviorally? If so, how is this integration implemented in the brain?
- (3) Multimodal integration: During courtship, song is not the only sensory cue – the touch, sight, smell and taste of the communication partners also inform interactions and mating decisions (LaRue et al., 2015; Finck et al., 2016; Rybak et al., 2002; Haberkern and Hedwig, 2016; Vedenina and von Helversen, 2003). The theoretical principles underlying cross-modal integration are well-understood (Ohshiro et al., 2011; Angelaki et al., 2009), but how acoustic information is combined with other modalities is rarely explored in insects (but see (Rybak et al., 2002)).
- (4) Internal state: The motivation to court and to accept a mating partner are known to be modulated by internal state associated with age, hunger or sleep state, or mating history (Heinrich et al., 2012; Zhang et al., 2016; Calhoun et al., 2019). While recent studies provide demonstrate effects of social experience on auditory tuning in brain and behavior (Li et al., 2018; Deutsch et al., 2019), how internal state affects auditory computation mechanistically is poorly understood.

We believe that recent technological advances will further accelerate progress, by improving data collection, by allowing to collect new types data, or by making better use of data. These advances will exploit the advantages of insects as study systems - dedicated tasks, easily quantifiable behavior, small brains – to unveil novel neuronal circuits and coding strategies:

- (1) Cheap hardware (Geissmann et al., 2017; Chagas et al., 2017) combined with advances in computer vision now allows tracking not only the position of the body centroid but of individual body parts in unmarked, freely moving, socially interacting animals (Pereira et al., 2018; Mathis et al., 2018; Graving et al., 2019). This enables the highly detailed, pose-based analysis of acoustic interactions under naturalistic conditions. Moreover, tools for the automated annotation ((Arthur et al., 2013), see also (Coffey et al., 2019), (Cohen et al., 2019)) and classification (Clemens et al., 2018; Ding et al., 2019) of communication signals will unveil novel complexity and context-dependence in the behavioral and neuronal basis of acoustic interactions (Gomez-Marin et al., 2014; Berman, 2018; Brown and de Bivort, 2018).
- (2) Whole brain functional imaging and connectomics will provide systems-level representational and structural maps of auditory systems, enabling an unbiased and complete assessment of auditory representations and circuits, from sound detection and recognition all the way to motor output (Mann et al., 2017; Patella and Wilson, 2018; Aimon et al., 2019; Zheng et al., 2018; Pacheco et al., 2019).
- (3) Comparative studies that sample acoustic signals, behaviors and neural representations with high phylogenetic density and breadth will reveal transitions, transformations and evolutionary plasticity of acoustic communication systems in insects (Alexander, 1962; Otte, 1992).

- (4) CRISPR-Cas9 mutagenesis greatly facilitates bringing the powerful toolbox of genetic model organisms to other species and enables the functional study of neural circuit evolution with single-cell resolution, for instance by comparing the tuning and the activity of individual, homologous neurons across species (Seeholzer et al., 2018; Ding et al., 2019).
- (5) Experimental innovations will produce data sets of unprecedented size and complexity. Computational tools and models will be essential to cope with the volume of data, to merge different data sets and to extract meaning from them (Berman, 2018; Costa et al., 2016; Vogelstein et al., 2019; Wiltshcko et al., 2015; Pandarinath et al., 2018). Moreover, computational theory will be central for leveraging these technological innovations toward understanding brain function (Bialek, 2018).

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