Emergent intensity invariance in a physiologically inspired model of the grasshopper auditory system

Jona Hartling, Jan Benda

1 The sensory world of a grasshopper

Strong dependence on acoustic signals for ranged communication
- Diverse species-specific sound repertoires and production mechanisms
- Different contexts/ranges: Stridulatory, mandibular, wings, walking sounds
- Mate attraction/evaluation, rival deterrence, loss-of-signal predator alarm
→ Elaborate acoustic behaviors co-depend on reliable auditory perception

Songs = Amplitude-modulated (AM) broad-band acoustic signals
- Generated by stridulatory movement of hindlegs against forewings
- Shorter time scales: Characteristic temporal waveform pattern
- Longer time scales: High degree of periodicity (pattern repetition)
- Sound propagation: Signal intensity varies strongly with distance to sender
- Ectothermy: Temporal structure warps with temperature
→ Sensory constraints imposed by properties of the acoustic signal itself

Multi-species, multi-individual communally inhabited environments
- Temporal overlap: Simultaneous singing across individuals/species common
- Frequency overlap: No/hardly any niche speciation into frequency bands
- "Biotic noise": Hetero-/conspecifics ("Another one's songs are my noise")
- "Abiotic noise": Wind, water, vegetation, anthropogenic
- Effects of habitat structure on sound propagation (landscape - soundscape)
→ Sensory constraints imposed by the (acoustic) environment

Cluster of auditory challenges (interlocking constraints → tight coupling):
From continuous acoustic input, generate neuronal representations that...
1)...allow for the separation of relevant (song) events from ambient noise floor
2)...compensate for behaviorally non-informative song variability (invariances)

3)...carry sufficient information to characterize different song patterns, recognize the ones produced by conspecifics, and make appropriate behavioral decisions based on context (sender identity, song type, mate/rival quality)

How can the auditory system of grasshoppers meet these challenges?
- What are the minimum functional processing steps required?
- Which known neuronal mechanisms can implement these steps?
- Which and how many stages along the auditory pathway contribute?
→ What are the limitations of the system as a whole?

How can a human observer conceive a grasshopper's auditory percepts?
- How to investigate the workings of the auditory pathway as a whole?
- How to systematically test effects and interactions of processing parameters?
- How to integrate the available knowledge on anatomy, physiology, ethology?
→ Abstract, simplify, formalize → Functional model framework

2 Developing a functional model of the grasshopper auditory pathway

2.1 Population-driven signal pre-processing

"Pre-split portion" of the auditory pathway:
Tympanal membrane → Receptor neurons → Local interneurons

Similar response/filter properties within receptor/interneuron populations (Jan Clemens 2011)
→ One population-wide response trace per stage (no "single-cell resolution")

Stage-specific processing steps and functional approximations:

Initial: Continuous acoustic input signal $x(t)$

Filtering of behaviorally relevant frequencies by tympanal membrane
→ Bandpass filter 5-30 kHz

$$x(t) * h_{\mathrm{BP}}(t); \qquad f_{\mathrm{cut}} = 5\,\mathrm{kHz},\, 30\,\mathrm{kHz} \tag{1}$$

Extraction of signal envelope (AM encoding) by receptor population
→ Full-wave rectification, then lowpass filter 500 Hz

$$|x(t)| * h_{\mathrm{LP}}(t); \qquad f_{\mathrm{cut}} = 500\,\mathrm{Hz} \tag{2}$$

Logarithmically compressed intensity tuning curve of receptors
→ Decibel transformation

$$20 \cdot \log_{10} \frac{x(t)}{x_{\max}} \tag{3}$$

Spike-frequency adaptation in receptor and interneuron populations
→ Highpass filter 10 Hz

$$x(t) * h_{\text{HP}}(t); \qquad f_{\text{cut}} = 10\,\text{Hz} \tag{4}$$

2.2 Feature extraction by individual neurons

"Post-split portion" of the auditory pathway:
Ascending neurons (AN) → Central brain neurons

Diverse response/filter properties within AN population (Jan Clemens 2011)
- Pathway splitting into several parallel branches
- Expansion into a decorrelated higher-dimensional sound representation
→ Individual neuron-specific response traces from this stage onwards

Stage-specific processing steps and functional approximations:

Template matching by individual ANs
- Filter base (STA approximations): Set of Gabor kernels
- Gabor parameters: σ, ϕ, f → Determines kernel sign and lobe number

$$k(t) = e^{-\frac{t^2}{2\sigma^2}} \cdot \sin(2\pi f t + \phi) \tag{5}$$

→ Separate convolution with each member of the kernel set

$$c_i(t) = x(t) * k_i(t) = \int_{-\infty}^{\infty} x(\tau) \cdot k_i(t - \tau)\, d\tau \tag{6}$$

Thresholding nonlinearity in ascending neurons (or further downstream)
- Binarization of AN response traces into "relevant" vs. "irrelevant"
→ Heaviside step-function $H(c - \theta)$ (or steep sigmoid threshold?)

$$b_\theta(t) = \begin{cases} 1, & c(t) \geq \theta \\ 0, & c(t) < \theta \end{cases} \tag{7}$$

Temporal averaging by neurons of the central brain
- Finalized set of slowly changing kernel-specific features (one per AN)

- Different species-specific song patterns are characterized by a distinct combination of feature values → Clusters in high-dimensional feature space
→ Lowpass filter 1 Hz

$$f_\theta(t) \;=\; b_\theta(t) \,*\, h_{\mathrm{LP}}(t); \qquad f_{\mathrm{cut}} \;=\; 1\,\mathrm{Hz} \tag{8}$$

3 Two mechanisms driving the emergence of intensity-invariant song representation

3.1 Logarithmic scaling & spike-frequency adaptation

Song signal $s(t)$ with variable scale α and fixed-scale additive noise $\eta(t)$

$$\alpha \,\cdot\, s(t) \,+\, \eta(t) \tag{9}$$

3.2 Threshold nonlinearity & temporal averaging

4 Discriminating species-specific song patterns in feature space

5 Conclusions & outlook