Physiologically inspired model of the grasshopper auditory system

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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 Pre-split pathway: Population pre-processing

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

Extraction of signal envelope (AM encoding) by receptor population
- Full-wave rectification + lowpass 500 Hz

Logarithmically compressed intensity tuning curve of receptors
- Decibel transformation

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

3 Post-split pathway: Feature extraction

Template matching by individual ascending neurons
- Separate convolution with each of a set of Gabor kernels
- Pathway splitting: Single population response into several separate branches
- Expansion into a higher-dimensional sound representation

Thresholding nonlinearity in ascending neurons (or further downstream)
- Step-function (or sigmoid) threshold
- Binarization of response values into "relevant" vs. "irrelevant"

Temporal averaging by neurons of the central brain
- Lowpass 1 Hz
- Finalized set of slowly changing kernel-specific features

- Different (species-specific) songs are characterized by a distinct combination of feature values

4 Pre-split intensity invariance: Logarithm-highpass mechanism

5 Post-split intensity invariance: Threshold-lowpass mechanism

6 Conclusion and outlook