Time-scale invariant processing:
How do grasshoppers solve this task?

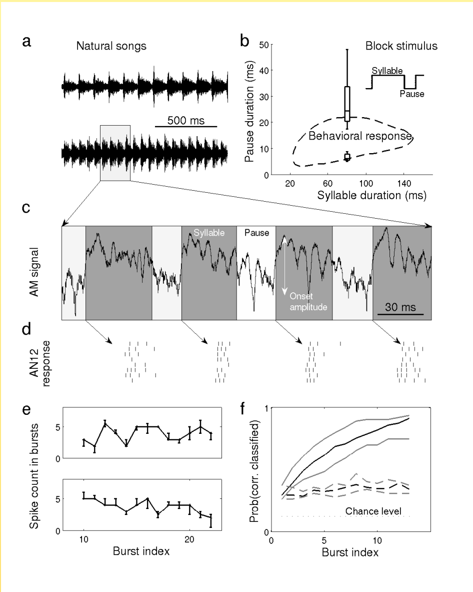
F. Creutzig[1,3], S. Wohlgemuth[2], J. Benda[1,3], A. Stumpner[4], B. Ronacher[2,3], A.V.M. Herz[1,3]

[1] Institute for Theoretical Biology, [2] Behavioral Physiology, Humboldt-Universität zu Berlin, 10115 Berlin, Germany, [3] Bernstein Center for Computational Neuroscience Berlin, [4] Institute for Zoology and Anthropology, Georg-August-Universität, 37073 Göttingen, Germany

1 Introduction

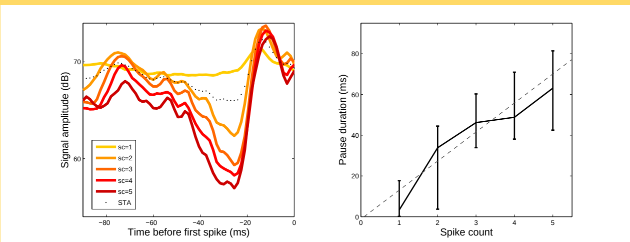
Time-scale invariant pattern recognition is a general task of auditory systems: Often, stretched or compressed temporal sequences - such as GOAL! or GGGOOOAAALLL!!! - need to be classified as equal. Communication signals of grasshoppers of the species *Chorthippus biguttulus* portray a particular example: Female grasshoppers respond to male mating songs that consist of specific repetitive syllable-pause patterns. Behavioral experiments with artificial stimuli show that the female reaction is not determined by the absolute syllable or pause duration but rather by the ratio between both durations. Here, we study the neural basis of processing natural mating songs (in n= 6 animals) and artificial songs (in n= 9 animals). We focus on the role of a single auditory ascending neuron (AN12). We postulate a plausible time-scale invariant decoding mechanism and relate this to the behavioral response of grasshoppers.

2 Stimulus and neuronal response



Grasshopper males communicate with calling songs: 2 examples are depicted as sound-pressure waves (a). The song is composed of 20-40 repetitions of a basic pattern: a period consisting of syllable plus subsequent pause. Behavioral experiments showed that a typical ratio of syllable and pause durations in artificial block stimuli elicit positive female response, depicted as the oval curve in (b), adapted from Helversen et al. (1994). The boxes show the response variability across 17 females at a given syllable duration of 80 ms. In natural songs, syllables and pauses can also be identified (c). The AN12 neuron responds with a burst at syllable onset (d). The spike count in bursts is reliable at any burst index, the given position within a song. Here, the responses to 2 songs are depicted (e). This spike count response pattern is sufficient to distinguish 8 different songs with 90% precision (f). Indeed, (59 ± 11)% of the variance of the spike-count distribution can be explained by a set of 6 different song features.

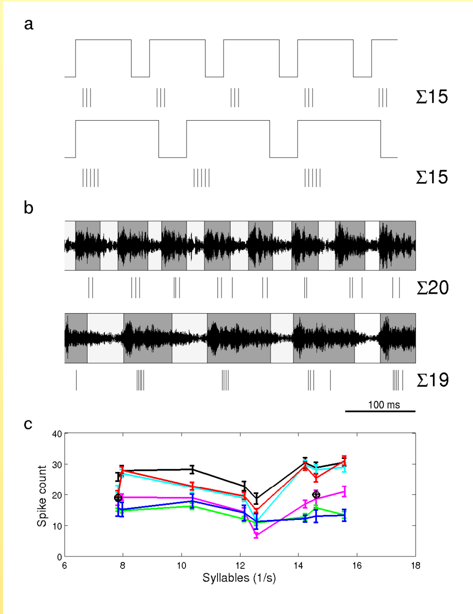
3 Spike count encodes pause duration



What are the relevant features of the stimulus by which spike count within a burst is determined? We constructed the burst-triggered average (BTA), the average stimulus preceding a burst with specific spike count ($sc = 1-5$), see (a). A shallow peak in stimulus intensity is sufficient to elicit 1 spike. For two and more spikes a sharp stimulus peak, interpreted as a syllable onset, is preceded by a period of relative quietness. Neither the slope nor the relative onset amplitude do have a systematic influence on the spike count. **Most of the spike count variance can be explained be the preceding pause** $(69 \pm 15\%$, $p < 10^{-5})$. Even more, the spike count encodes preceding pause duration linearly (b). Additionally, only the preceding onset amplitude adds significantly to the explained variance in each cell, $27 \pm 8\%$ $(p < 10^{-5})$.

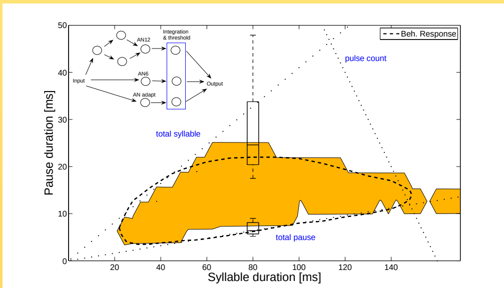
Supported by Boehringer Ingelheim Fonds and DFG (SFB 618)

4 A time-warp invariant read-out



Can this encoding mechanism be related to time-scale invariance? Time-scale invariance in this context means that the ratio between pause duration and period duration is kept constant. Does the grasshopper perform a complicated division? Not necessarily: A stretching of syllable and pause duration lead to fewer bursts events in one time frame compensated by higher spike count in bursts (a). Hence integration of the AN12 spike train over a given time is independent of spike count within a burst = pause duration (b). In all cells, the total spike count is invariant to the syllable frequency $(r = 0.00 \pm 0.32)$, see (c): the different cells are color-coded, the two black circles indicate the examples of (b). Such a neuronal mechanism, constituting a moving average, measures the syllable-pause ratio and is time-scale invariant.

5 Song feature integration sufficient to elicit behavioral response



Is this AN12 read-out adequate to explain the behavioural response of female grasshoppers? We suggest that the overall read-out is based on integration of 3 neurons and subsequent threshold operations. A possible neuronal read-out mechanism would integrate over certain song features: total pause duration, total syllable duration and number of syllables within a certain time window. Females would respond positively if all features cross thresholds. In yellow, we draw the read-out of a computational model of ascending neurons. The AN12 measures pause duration, a tonically responding neuron measures syllable duration (AN6) and a strongly adapting neuron $(\tau = 3$ ms) counts the number of syllables.

6 Conclusions

- Bursts multiplex complex and behaviorally relevant stimulus features into a single spike train: pause duration is encoded by the spike count and period duration is encoded in the interspike interval.
- A plausible read-out neuron can integrate the AN12 spike train over a fixed time (moving average) and, by this, forms a time-warp invariant sequence recognition.
- A computational model calculates the moving averages of 3 different feature detectors and elicits an output similar to behavioral response curves.

References:

1. O. von Helversen and D. von Helversen. Forces driving coevolution of song and song recognition in grasshoppers. *Fortschritte der Zoologie*, 39: 253-284, 1994