From Burst Encoding to Time-Warp Invariance

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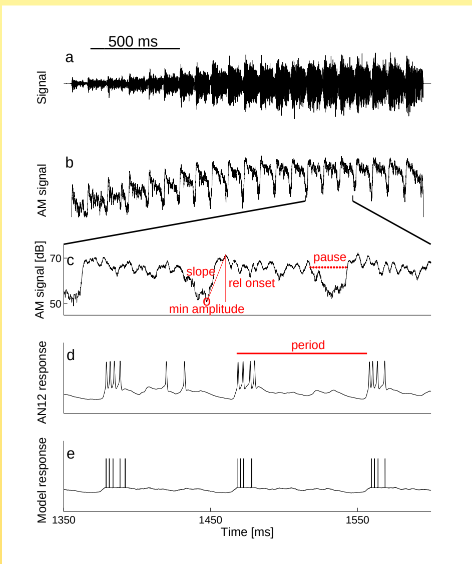
1 Introduction

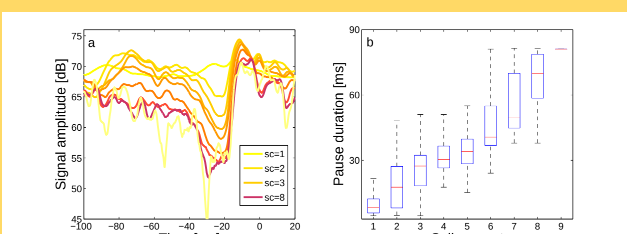
Time-warp invariant pattern recognition is a general task of auditory systems: Temporal sequences, that are stretched or compressed versions of each other, such as "DADADADAMM" and "DDAAD-DAADDAADDAAMMMM" have to be classified as equal. We investigate a possible neuronal realization of this task in grasshoppers of the species *Chorthippus biguttulus*. Female grasshopper respond to male mating songs that consist of specific repetitive syllable-pause sequences. Behavioral experiments with artificial stimuli showed that the female reaction is not determined by the absolute syllable duration but rather by the ratio between syllable and pause duration, indicating time warp invariant pattern recognition. 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-warp invariant decoding mechanism and relate this to the behavioral response of grasshoppers.

2 Stimulus and neuronal response



Grasshopper males communicate with calling songs. An example is depicted as sound-pressure wave (a) and amplitude-modulation (AM) signal (b). The song is composed of 20-40 repetitions of a basic pattern: a period consisting of syllable plus subsequent pause. Typical song features such as pause, minimal pause amplitude, relative onset amplitude and slope are marked in a 250ms extract of the song (c). The AN12 neuron responds with a burst at syllable onset (d). The period is defined as the interburst interval. We explained the AN12 response with a model circuit (see section 4). The model neuron responds in a similar manner with respect to the same stimulus (e).

3 Spike count encodes pause duration



The spike count within bursts is related to parameters in the mating songs: (55 ± 14)% of the variance of the spike-count distribution can be explained by song features. 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 ($sc = 1-9$), 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 ($52\pm25\%$, $p<10^{-5}$). Additionally, only the preceding minimal amplitude adds significantly to the explained variance in each cell, $17\pm7\%$ ($p<10^{-5}$).

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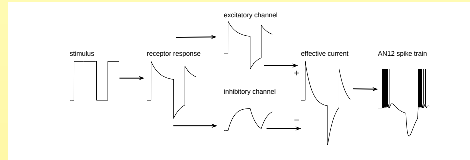
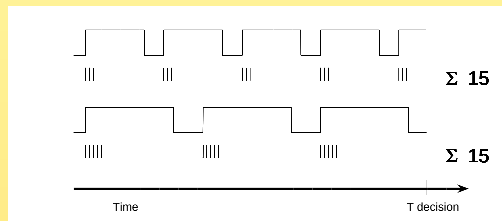
4 AN12 model: fast excitatory and slow inhibitory input



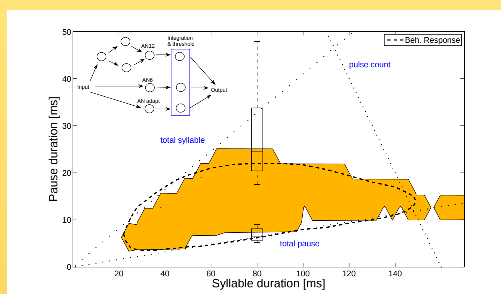
A model simulates the AN12 neuron response. In this figure, we used a block stimulus as input. Receptor neurons are adapting ($\tau_{rec} = 30ms$), emphasizing the first part of the syllable. The excitatory channels forwards this signal to the AN12, whereas the inhibitory channel convolves the signal with an exponential function. Both channels are integrated to form the effective current which drives the neuron. The model has 5 free parameters, 3 for the integrate & fire neuron, the time constant of the inhibitory input channel and the relative amplitude of inhibitory and excitatory channel. Natural songs were taken as the input, and parameters were fitted to the original spike trains.

5 A time-warp invariant read-out



Can this encoding mechanism be related to time-warp invariance? Time-warp invariance in this context means that the ratio between pause duration and period duration is kept constant. Does the grasshopper performs a complicated division? Not necessarily: Integration of the AN12 spike train over a given time is independent of spike count within a burst = pause duration. Such a neuronal mechanism, constituting a moving average, measures the syllable-pause ratio and is time-warp invariant.

6 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. The oval curve depicts the area of syllable and pause values in artificial model songs which elicit positive female response (adapted from Helversen et al., 1994). The boxes show the response variability across 17 females at a given syllable duration of 80 ms. We suggest a possible neuronal read-out mechanism that 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.

7 Conclusions

- Bursts multiplex complex and behaviorally relevant stimulus features into a single spike train: pause duration in encoded by the spike count and period duration is encoded in the interspike interval.
- A fast excitatory and a slow inhibitory input channel can explain AN12 response behavior.
- 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