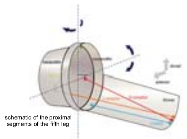

ADAPTATION AND INFORMATION TRANSFER RATE IN PROPRIOCEPTIVE AFFERENTS

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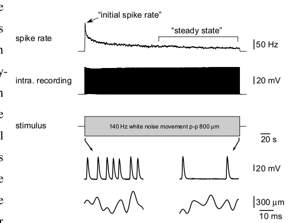
Question

In response to continous stimulation, the firing rate of a spiking sensory receptor decreases: the receptor adapts to the stimulus. Measurement of the information transfer rate relies on data from several hundred seconds of random stimulation and is normally done in fully adapted conditions. This steady-state measurement likely underestimates the maximum information transfer rate of the receptor. To estimate the extent of this error, we stimulated the crab coxo-basal chordotonal organ (CBCTO) with different duration pauses inserted between stimuli. We found that these pauses reduce adaptation and increase precision and reliability of spike timing. This allowed us to estimate the information transfer rate of unadapted CBCTO afferents.

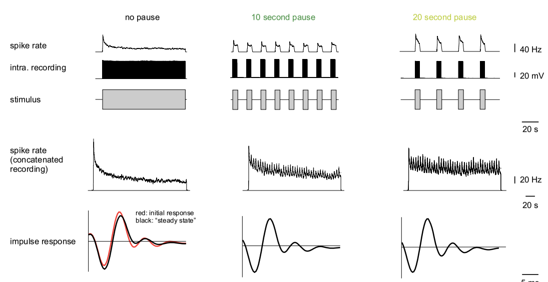


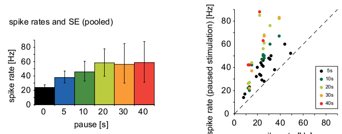
Preparation

The CBCTO in the green shore crab *Carcinus maenas* is a typical arthropod chordotonal organ, signaling the position and movement of the coxo-basal joint. It consists of an elastic connective tissue strand with 70-80 embedded bipolar neurons. These neurons spike in response to either stretch or relaxation, and fall into functional groups responding to position, velocity, or acceleration of the joint. We isolated the CBCTO of the fifth thoracic segment and connected its strand to an electro-mechanical puller. While stimulating it with 140Hz bandpass filtered white noise, we recorded intracellularly from single afferents of the CB nerve (Gamble & DiCaprio 2003). We inserted pauses (5, 10, 20, 30, or 40 seconds) in the stimulus, which were later removed from the recordings by data processing. This allowed us to calculate total and noise entropies and directly estimate the information transfer rate (Strong et al. 1998).

Results: Paused stimulation reduces adaptation and increases spike rates

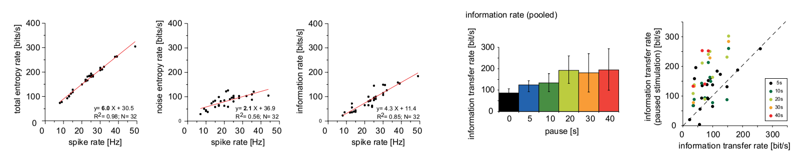
Fully adapted CBCTO afferents respond to continous stimulation with mean spike rates between 8 and 49Hz (N=32, mean: 24±9Hz). If the stimulation is paused every 5 seconds for 5 seconds, the spike rate increases by 169±42% (N=19). The spike rate increases further with increasing pause duration: 10s pause 188±38 % (N=7), 20s pauses 259±58% (N=6), 30s pause 262±101% (N=4), 40s pauses 331±62% (N=4).





Information transfer rate is directly correlated with spike rate

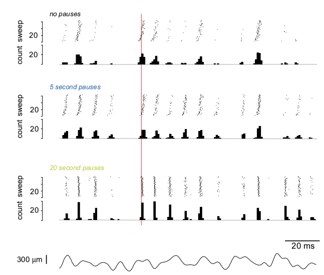
The information transfer rate for a CBCTO afferent is directly correlated with its mean spike rate. It is calculated from the difference of total entropy and noise entropy, both of which are also directly correlated with mean spike rate. However, the total entropy increases faster with mean spike rate than noise entropy.

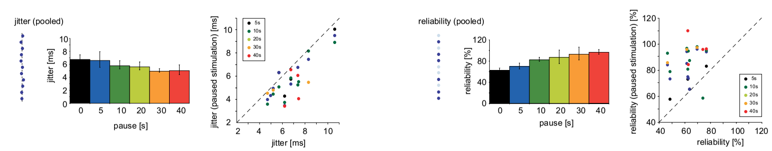


Adaptation does have an influence on the precision of spike timing

The precision of individual spike timing can be determined from repeated presentation of identical stimuli.

- The response of about half of the recorded afferents exhibit a timing "drift" during the first 5-20 repetitions of the stimulation: spikes occur later with each consecutive stimulation, most likely due to an increasing spike threshold. Pauses inserted between stimulation repeats decrease or eliminate this drift.
- Jitter (standard deviation of the time of an individual spike) decreases with increasing duration of a pause. For the individual afferents a 5 second pause decreases jitter on average by 10% (N=4; paired-sample t test all; P<0.01).
  (10s pause 13% N=9; 20s pause 20% N=9; 30s pause 15% N=3; 40s pause 28% N=4).
- Reliability (how often an individual spike is triggered in consecutive trials) increases with increasing length of pause. For the individual afferents a 5 second pause increases reliability on average by 12% (N=4; paired-sample t test; all P<0.01).
  (10s pause 36% N=9; 20s pause 42% N=9; 30s pause 60% N=3; 40s pause 41% N=4).

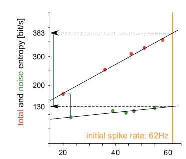




How much does the "steady state" measurement underestimate the information transfer rate?

The spike rate/entropy relation obtained from experiments with pauses of different length allows to estimate the entropy for the initial spike rate (the spike rate during the first three seconds of the stimulation when the afferent was least adapted).

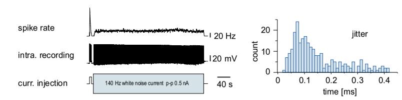
In "steady state" the afferent shown has a spike rate of 25Hz and an estimated information transfer rate of 181-95 = 86 bit/s. The estimated information transfer rate at the initial spike rate of 62Hz would be 383-130 = 253 bits/s. On average the extrapolated transfer rates for the initial spike rate are 220% higher (N=9, range: 139-429%) than those for the "steady state" (no pause) calculation.



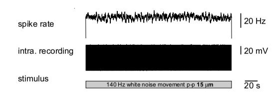
Stimulation of an afferent with 0, 5, 10, 20, and 40 second pauses inserted between stimuli gives the spike rate / entropy relations shown above. The estimated information transfer rate for unadapted conditions is the difference between the extrapolated total and noise entropy at the initial spike rate (62Hz for this afferent).

What are the mechanisms of adaptation?

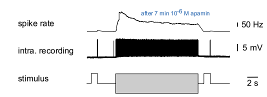
Adaptation of sensory neurons often is based on inactivation or activation of ion channels. The following preliminary data suggest that changes in mechanical properties might also be an important mechanism for adaptation in the CBCTO :



Injection of current close to the transduction region of a sensory neuron evokes spikes. While the neuron quickly adapts to constant current, it does not adapt to white noise current.



Responses to mechanical stimulation with very low movement amplitudes do not show adaptation while other characteristics remain unchanged.



In many systems Ca^{2+} dependent K^{+} currents underlie adaptation. Apamin is a blocker for K(Ca) channels. However, application of 10^{-7} - 10^{-6} M apamin appears to have no effect on CBCTO adaptation.

Conclusions

- Insertion of pauses in the white noise stimulus increases mean spike rates and reduces adaptation of the CBCTO
- Information transfer rate is directly correlated with the spike rate of an afferent. The information transfer rates for the initial spike rates (reflecting unadapted conditions) are 1.4 to 4.3 times higher than those calculated for the "steady state"
- Reduced adaptation leads to a decrease in timing jitter and an increase in reliability of individual spikes.
- Changes in mechanical properties might be an important mechanism for CBCTO adaptation.

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