Influence of Adaptation on Information Transfer by Sensory Afferents

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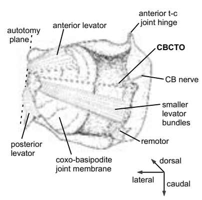
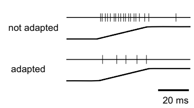
Introduction

Most sensory organs adapt and decrease their response to sustained stimulation. This reduces the amount of redundant information transmitted to the central nervous system. But adaptation also limits overall information transmission. We studied to what extent and how adaptation effects the information transmitted by the CBCTO chordotonal organ, spanning the CB-leg joint of the crab *Carcinus maenas*. Using a stimulus protocol with inserted pauses, we achieved different levels of adaptation, reflected in different mean spike rates. Through presentation of random as well as repeated noise sequences, we determined information transfer rates at different levels of adaptation and studied the effect on precision and reliability of individual spikes.

We used an isolated ganglion-receptor preparation of the fifth thoracic segment of the green shore crab, *Carcinus maenas*. The CBCTO was attached to an electromechanical puller (Aurora Scientific model 322C). The signal used for stimulation was Gaussian white noise, low-pass filtered at a corner frequency of 140Hz (custom built generator; Wavetek 8th-order low-pass filter). It was either recorded and played back, or gated by a CED power 1401 AD/DA interface. Typically a total of 300 seconds of noise was recorded, in some experiments 500 seconds to validate the sufficiency of data for entropy calculations. The peak to peak amplitude of movements corresponded to an overall joint angle of ~30°. Intracellular recordings were made from 32 receptor axons with a WPI 767 or NPI SEC-05 electrometer. The data was evaluated using custom written programs (SPIKE II script language and Borland Delphi). The algorithm used to directly estimate the information transfer rate was described by Strong et al. 1998.



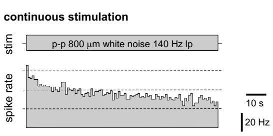


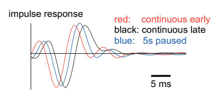
Results

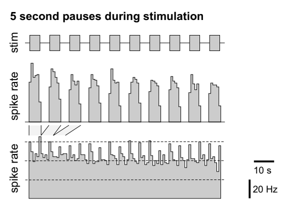
Paused stimulation gives higher mean spike rates and less adaptation

During continuous stimulation, CBCTO afferents firing rates typically fall from an initial 64 Hz (SD 28, N=31) by 64% to 23 Hz (SD 9, N=31) within 60 seconds after stimulation onset. Our paused stimulus protocol consists of 5 second blocks of white noise that are interrupted by pauses of 0, 5, 10, 20, or 40 second length. After the experiment the pauses are removed from the recording and entropy rates calculated.

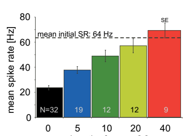
Paused stimulation does not influence the general response characteristics of the CBCTO afferents. The impulse response functions are identical for unpaused and paused stimulation. Steady state firing rates are higher than during continuous stimulation: e.g. on average 39 Hz SD 10 (N=15) with 5 second pauses.

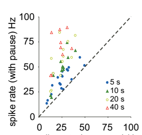




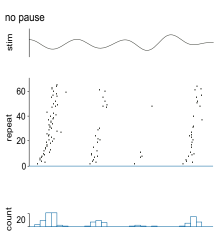


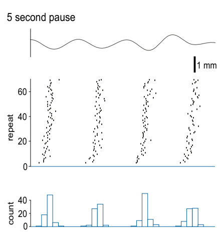
Increasing the length of the pause results in higher average firing rates of afferents and reflects reduced adaptation.

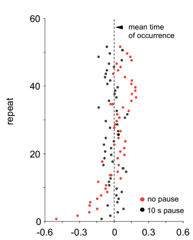




To study the effect of paused stimulation on the individual spike, an identical five second block of random noise is played back repeatedly. Regarding the time a spike occurs with respect to the triggering stimulus feature, it occurs slightly sooner during early noise blocks than during later repetitions of the noise block. This *treshold change* reflects the initial spike rate drop after onset of stimulation. To avoid a bias from this change, we use only repetitions 21 and later for any timing analysis.

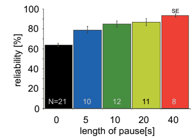


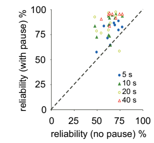




Reliability of individual spikes

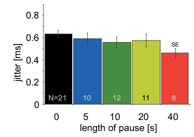
Comparing afferent responses to **repeatedly presented noise blocks**, insertion of pauses increased the likelihood that a particular stimulus feature triggers a spike. Comparing spikes with a reliability >40%, reliability correlates with pause length and increases with less adaptation.

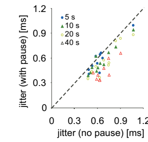




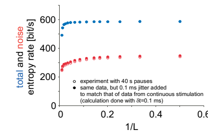
Timing precision (jitter) of individual spikes

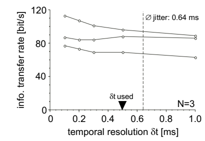
The insertion of pauses during stimulation with **repeated noise blocks** resulted in less timing jitter (standard deviation) of individual spikes. For individual experiments, this decrease was significant in 5 out of 9 afferents tested (p<0.04; t-test). Reduced adaptation means better timing precision.

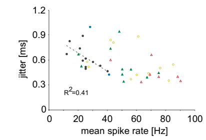




However, the reduced timing jitter has little effect on information transfer rate as shown by artificially adding jitter to a recording. The temporal resolution δt = 0.5 ms used for the calculations is adequate. Furthermore jitter appears independent of afferent firing rate.

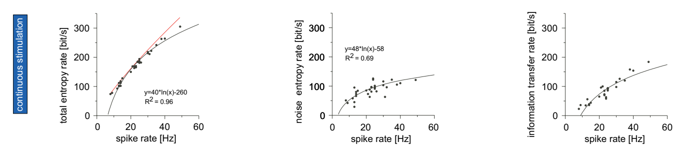




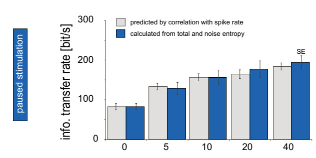


Information transfer

Total entropy increases with mean spike rate and stays close to the upper bound limit[1] for a binary modulation system (red trace). Noise entropy increases with a shallower slope with spike rate, which results in a correlation of information transfer rate[2] and mean spike rate.



Inserting pauses during the stimulation leads to higher information transfer rates. An assumed logarithmic correlation between spike rate and total or noise entropy rate allows to predict and explain the information transfer rate in a less adapted state. The predictions results closely resemble the actual rates.



[1] the upper bound limit of the entropy rate of a binary modulation system is approximated by $H \approx \bar{r}\log_2\left[\frac{e}{\bar{r}\Delta t}\right]$ with $\bar{r}$ being the mean rate and Δt bin with of a spike train (MacKay and McCulloch 1952, Rieke et al. 1997).

[2] $I = H_{total} - H_{noise}$, with entropies calculated as $H(L,\Delta t) = -\frac{1}{L\Delta t}\sum_{w \in W} P(w)\log_2 P(w)$ with w being a spike pattern, W(L,Δt) a set of all possible spike patterns comprised of L bins of width Δt, and P(w) being the probability of observing pattern w (Strong et al. 1998).

Conclusions

- A paused stimulus protocol decreases adaptation, reflected by increased mean spike rate and improved timing precision of individual spikes.
- Information transfer rate is positively correlated with the afferent mean spike rate. This is due to total entropy rising faster than noise entropy as spike rate increases.
- Reduced adaptation leads to higher information transfer rates. These higher rates can be completely explained by the higher mean spike rates.