Information Transmission is Limited by Entropy in Spider Mechanoreceptors

Keram Pfeiffer, Päivi H. Torkkeli and Andrew S. French
Department of Physiology and Biophysics, Dalhousie University, Halifax, Nova Scotia, B3H 1X5, Canada

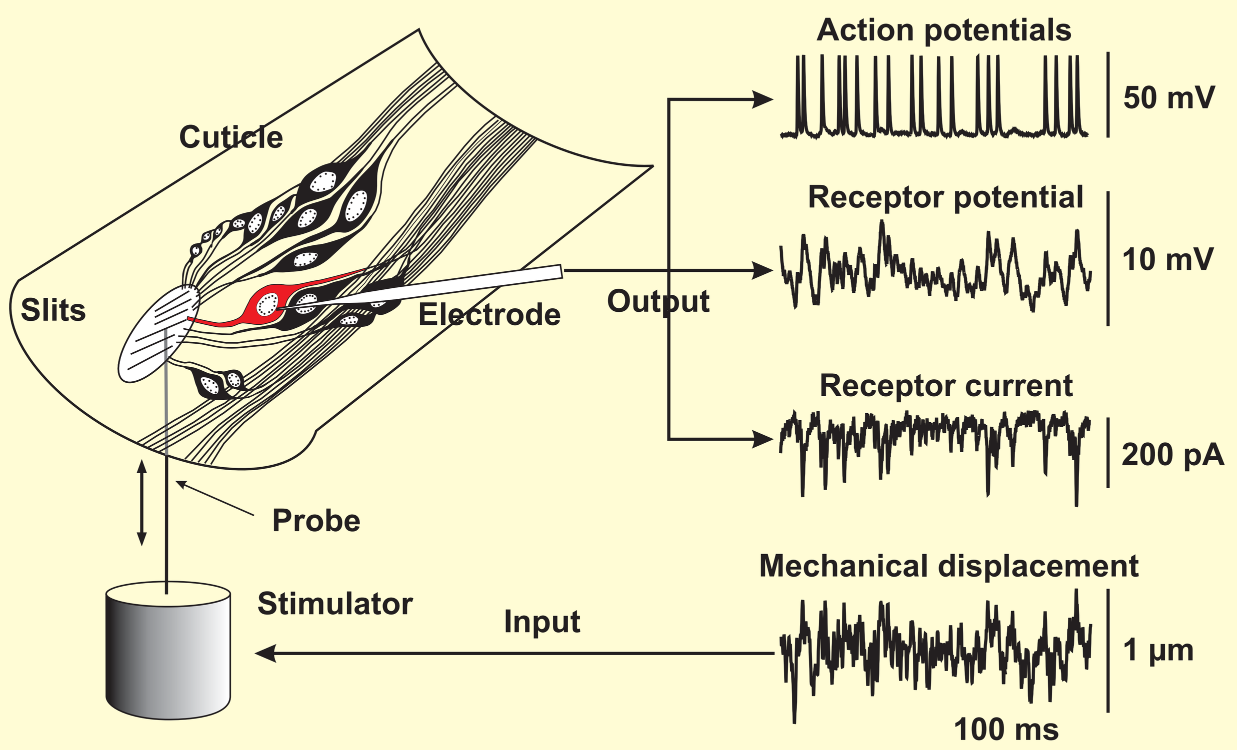
1. Introduction

Most neurons propagate information encoded in action potentials. While the binary nature of action potentials allows for robust information transmission over large distances, it also creates a cost, because the durations and refractory periods of action potentials set an upper limit to the amount of information that can be encoded per unit time (Entropy). A second factor that can limit information rate, is the inherent noise of the system.

In this study we asked whether noise or entropy limits information transmission during sensory transduction and encoding in mechanosensory neurons of the lyriform organ VS-3 of the spider *Cupiennius salei*. To this end we compared the information capacity, i.e. the maximum information rate that can be transmitted by a system to the entropy, i.e. the actual information that is being transmitted at each stage of sensory processing.

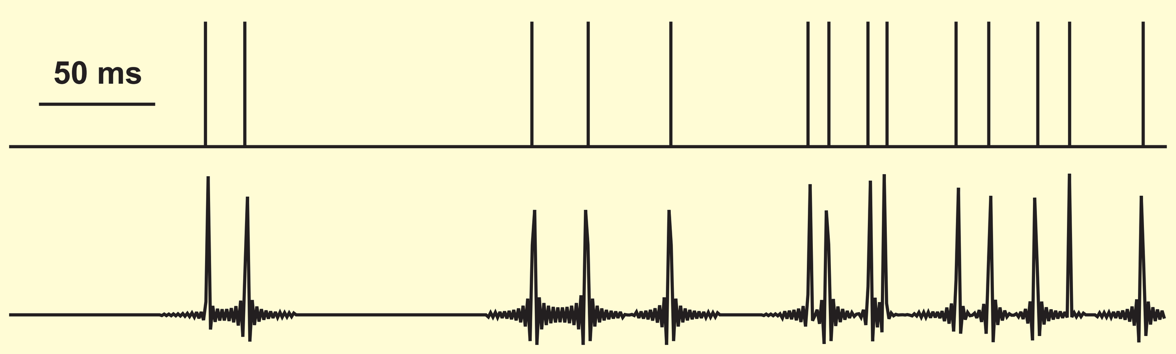
To facilitate these comparisons we developed a new method of estimating the entropy of continuous signals, based on data compression. This method is not based on probability density functions and can be applied to both random and deterministic signals.

2. Methods



A small piece of patellar cuticle containing the VS-3 slit sense organ was dissected and placed on a plexiglass holder that allowed the slits to be stimulated mechanically. The preparation was superfused continuously with spider saline (in mM: 223 NaCl, 6.8 KCl, 8 $CaCl_2$, 5.1 $MgCl_2$, 17 glucose, and 10 HEPES, pH 7.8).

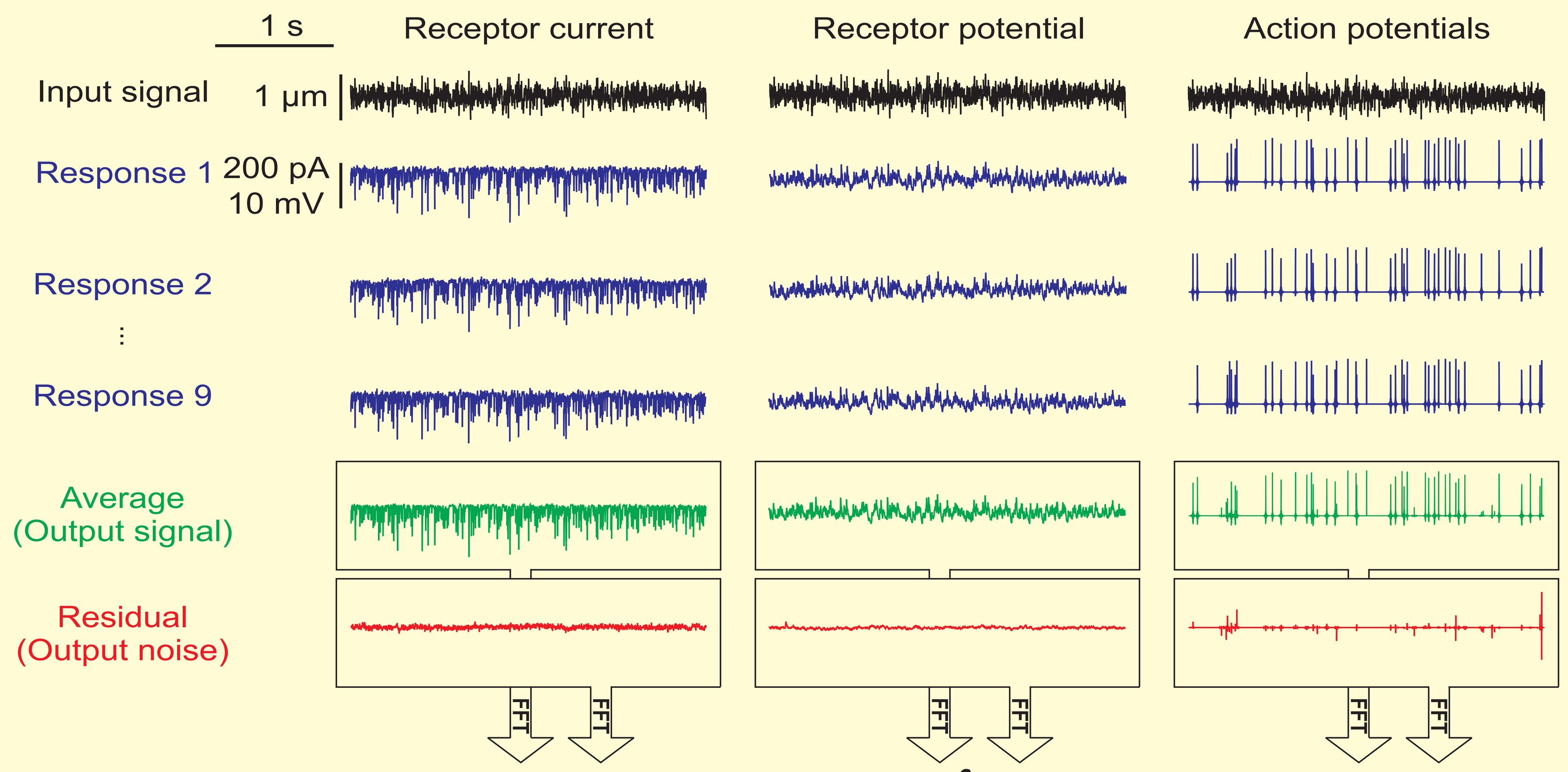
Intracellular recordings were performed using a SEC-10LX amplifier (NPI Electronic) in discontinuous single-electrode current- and voltage-clamp modes. Recording electrodes were filled with 2.5 M KCl and their resistances were 40-80 MΩ in solution. Mechanical stimulation was performed using a piezoelectric stimulator (P-841.10 translator and a PZT controller - Physik Instrumente) that pushed a glass probe against the slits. The stimulator was driven by repeated sequences of pseudorandom gaussian white noise.



Times of action potentials were found by threshold-detection and stored as time of occurrence (upper trace). They were then digitally filtered by convolution with a sin(x)/x function and re-sampled at 1 kHz, to obtain a signal, band-limited to a frequency range of 0-500 Hz (lower trace). All other signals were also resampled at 1 kHz by averaging. The resolution for all signals was 10 bits, i.e. 1024 levels.

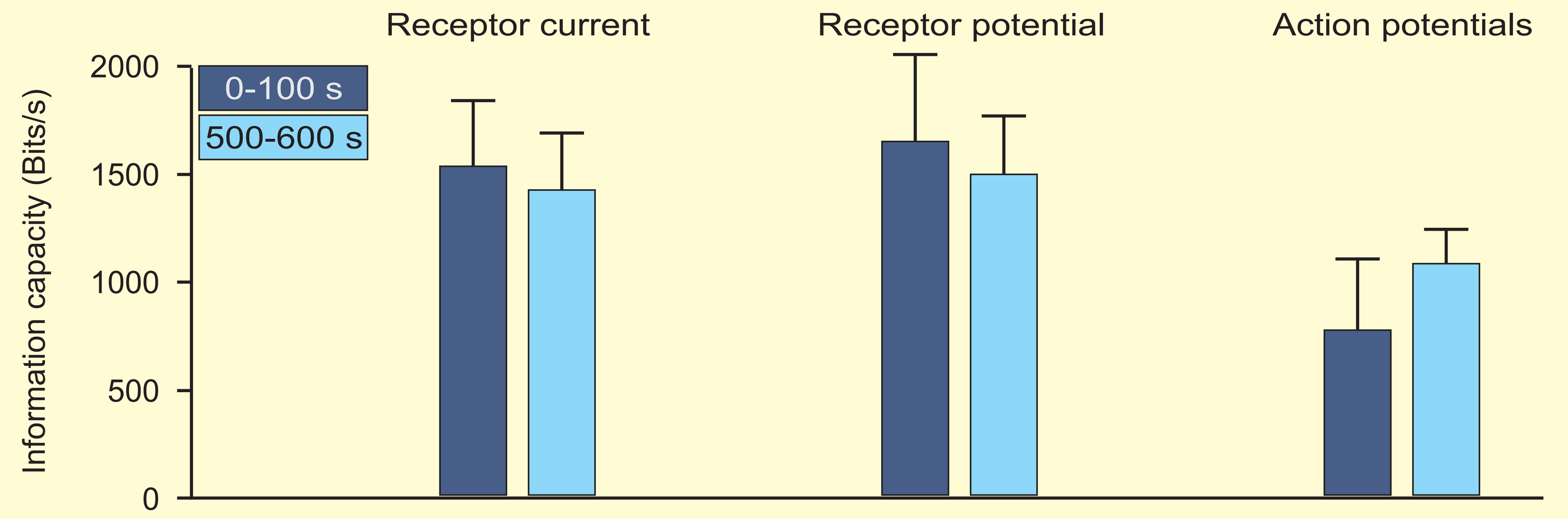
3. Estimation of Entropy and Information Capacity

Information Capacity



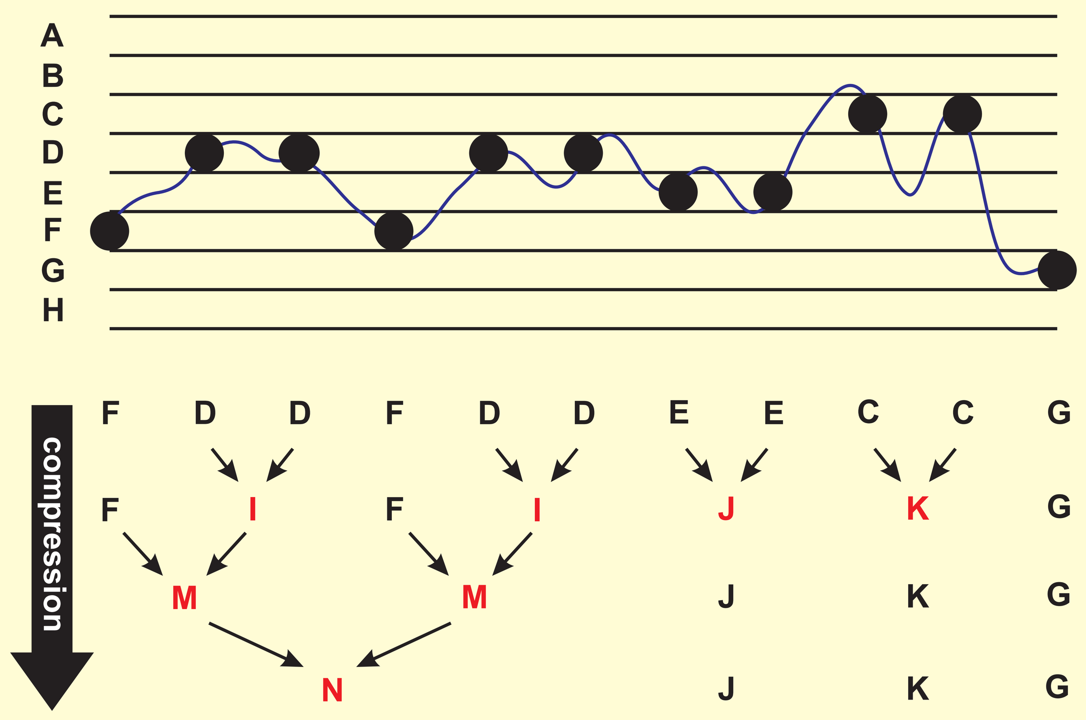
$$\text{Information Capacity } R_{AV} = \int \log_2 (1 + SNR(f))\, df, \text{ with}$$
$$SNR(f) = FFT_{signal}(f) / FFT_{noise}(f)$$

The average of ten successive responses to the same random stimulus sequence were regarded as the noise free signal. Each of the ten individual responses was substracted from this average to obtain the noise. Signal and noise were converted to the frequency domain using the fast Fourier transform. Information Capacity R_{av} was then calculated using the Shannon formula (Shannon & Weaver 1949).



Information capacity of receptor current, receptor potential, and action potentials. Information capacity of receptor current and receptor potential were both around 1500 Bits/s. At the stage of action potentials, information capacity dropped to about 1000 Bits/s. The capacity of the neurons to transfer information at each stage is higher than the actual information rate that was being transmitted (green bar graph to the right).
Dark/light blue: beginning/end of recording, respectively.

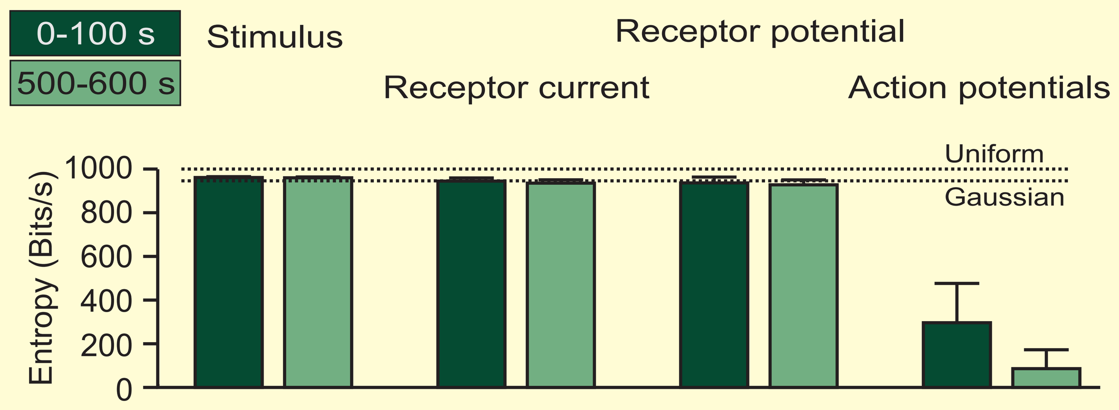
Entropy



Signals were normalized to cover the entire range of 1024 levels. Each level was treated as a symbol in a linear sequence. Pairs of symbols occurring with greatest frequency were repeatedly replaced until maximum compression was achieved. The compression entropy E_c was then calculated as:

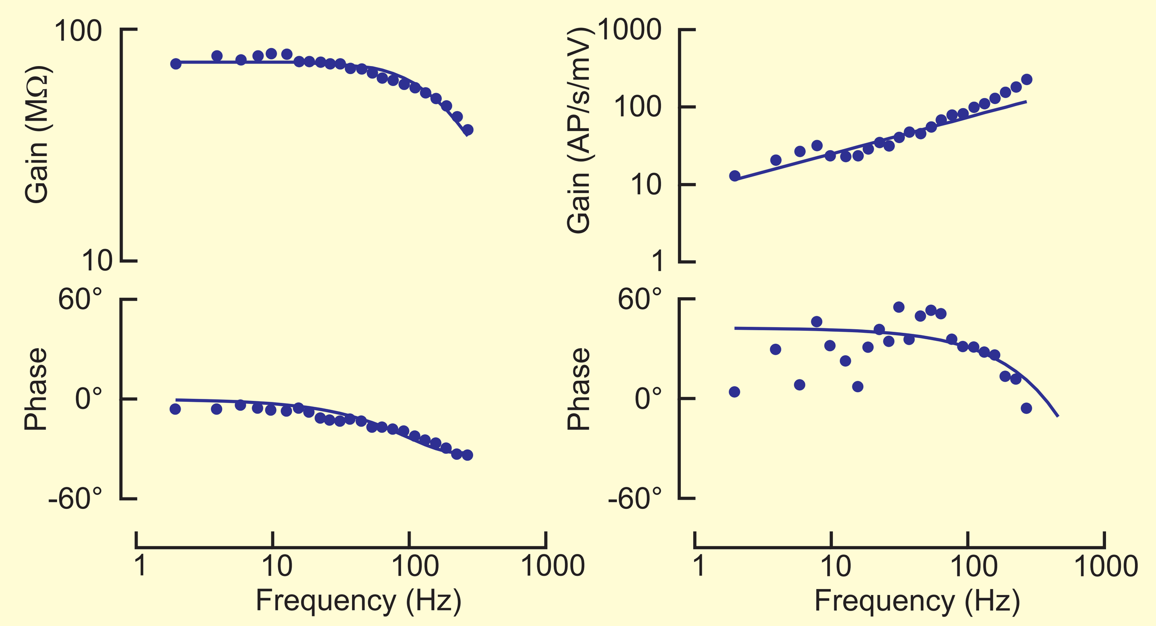
$$E_C = N \log_2 M, \text{ with}$$

N = number of symbols in the compressed message, and
M = number of different symbols in the message.



Entropy of stimulus, receptor current, receptor potential, and action potentials. While entropy of receptor current and receptor potential remain close to that of the input signal, only a fraction of the initial information is transformed into action potentials. Dotted lines show entropy of gaussian and uniformly distributed noise.
Dark/light green: beginning/end of recording, respectively.

4. Information Transfer



Coherence-based information capacities:

Receptor current → (2012 Bits/s) → Receptor potential → (106 Bits/s) → Action potentials

Three average responses of 20 different repetitions each were concatenated to give records of 30.72 s. These were used as input/output pairs to calculate frequency response functions and coherence functions for receptor current to receptor potential and receptor potential to action potential. The coherence function was used to calculate the information capacity R_{CO}:

$$R_{CO} = \int \log_2 (1/(1-\gamma^2(f)))\, df$$

5. Summary and Conclusion

- We developed a new method to estimate entropy in both binary and continuous signals, based on data compression.
- The method makes no assumptions about the content of the data and does not rely on its probability density function.
- The Entropy rate of action potentials was dramatically smaller than that of the receptor current and receptor potential.
- Entropy at each stage of encoding in spider mechanosensory neurons was much smaller, than the information capacity.

The limiting factor of information transmission in these neurons is not noise, but the amount of information that can be encoded into action potentials.

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