FREQUENCY RESPONSE FUNCTIONS AND INFORMATION CAPACITIES OF PAIRED SPIDER MECHANORECEPTOR NEURONS

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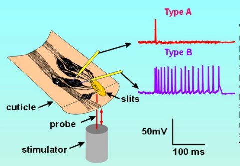
INTRODUCTION

Action potentials allow nervoussystems to transmit information reliably over longer distances than would be possible with graded membrane potentials, but the additional encoding and decoding mechanisms create other problems because encoding is a strongly nonlinear dynamic process. These problems also limit the measurement of how efficiently neurons transmit information, but it has been possible to estimate the information capacities of some neurons by the application of ideas from communications theory and systems analysis. Here, we address several aspects of the encoding problem, using paired mechanoreceptors from the spider *Cupiennius salei* that display very different dynamic properties during simple step stimuli. **The questions we ask are: Does the strong difference in dynamic behavior seen with step stimuli persist with wide-band stimuli? How does the mean rate of action potential production affect dynamic behavior? What are the information capacities of these neurons? Are total information capacities and information per action potential affected by firing rate?**

PREPARATION



VS-3 slit-sense organ preparation for mechanical stimulation. A section of the patellar cuticle was dissected to reveal the neurons innervating the slits, which were stimulated from below by a piezoelectric pusher. Sharp electrodes penetrated the cell bodies from above. One neuron of each pair fired 1-2 action potentials following a step stimulus (Type A). The other fired a burst (Type B). Recordings are from two neurons used in this study, but not in the same preparation. The stimulus was 1.6 μm for 200 ms.

METHODS

For mechanical stimulation a concave piece of cuticle containing the intact VS-3 lyriform organ, was dissected from the patella of an autotomized leg and mounted on a custom designed metal holder. The neurons were penetrated with microelectrodes from above. For electrical stimulation we detached the patellar hypodermis containing the neurons from the cuticle and placed it on a glass coverslip fixed to the bottom of a 35mm culture dish. Experiments were performed in spider saline: (in mM)(223 NaCl, 6.8 KCl, 8 CaCl, 5.1 MgCl, 10 HEPES, pH 7.8).

We used the discontinuous single electrode current-clamp technique to record membrane potentials with an SEC-10L amplifier. Microelectrodes were filled with 3M KCl, and coated with petroleum jelly to decrease stray capacitance. Electrode resistances were 45-70 MΩ with time constants of 1-3 μs. Switching frequencies were 20-23 kHz and duty cycle 1:8 for current passing:voltage recording.

Pseudorandom Gaussian white noise was generated by a 33-bit binary sequence algorithm and filtered by a nine-pole active filter so that the power spectrum was below 1% of the low frequency asymptote by 300 Hz. Each signal was sampled at 50 kHz by an independent 12-bit analog-to-digital convertor to avoid sampling delays between channels. All recordings were of at least 60 s duration.

Action potentials were separated from the continuous membrane potentials by an algorithm that identified action potentials as the potential increasing and then decreasing by a fixed amplitude within less than 2 ms. Action potential signals were digitally filtered by convolution with the sin(x)/x function to band-limit them to the range 0-500 Hz and produce a regularly sampled (1 ms interval) signal. Sampled analog signals (mechanical displacement or membrane potential) were digitally re-sampled by averaging to give a 1 ms sample interval.

Frequency response functions (gain and phase) between the input (mechanical displacement or membrane potential) and the output (action potentials) were calculated via the fast Fourier transform and plotted as Bode plots of phase and log gain versus log frequency. Coherence functions were calculated from the same spectra and plotted versus log frequency.

THEORY

All frequency responses could be well-fitted by a linear relationship between log gain and log frequency, corresponding to a fractional differentiator, or power-law model:

$$G(f) = Af^{k} \qquad (1)$$

The fractional exponent, k, was used to predict the phase relationship:

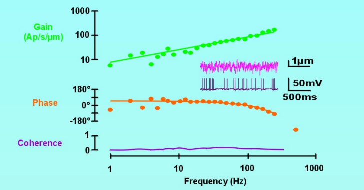
$$P(f) = k \cdot 90° \qquad (2)$$

where $P(f)$ is the phase lag as a function of frequency. Increasing phase lag at high frequencies was fitted by the addition of a time delay, Δt, using linear regression between phase and frequency.

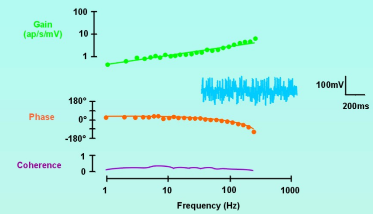
Information capacity, R, was calculated from the coherence function, $\gamma(f)$:

$$R = \int \log_2 \{1/(1-\gamma^2(f))\}\, df \qquad (3)$$

Frequency response functions were always well-fitted by a power-law model



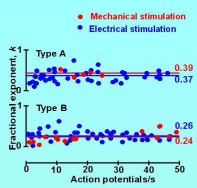
Frequency response and coherence functions for mechanical stimulation of a Type A neuron. Inset is a portion of the raw data, showing random noise mechanical stimulation and the resulting action potentials. Solid lines show Equations (1) and (2) fitted to the gain and phase with k=0.52 and Δt=1.50 ms. Maximum coherence was 0.18, and the information capacity, R, from Equation (3) was 38.7 bits/s.



Frequency response and coherence functions for electrical stimulation of a Type A neuron. Inset is a portion of the raw data, showing action potentials superimposed on the randomly fluctuating membrane potential. Solid lines show Equations (1) and (2) fitted to the gain and phase with k=0.39 and Δt=1.41 ms. Maximum coherence was 0.37, and the information capacity, R, from Equation (3) was 136.8 bits/s.

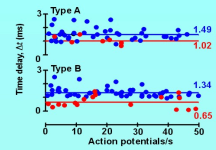
RESULTS

Adaptation rate depends on cell type for both mechanical and electrical stimulation



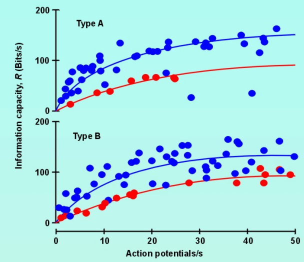
Fractional exponent values, k, for Type A and Type B neurons during mechanical and electrical stimulation, as a function of mean action potential firing rate. Horizontal lines and adjacent numbers indicate the mean values of k from the different data sets over the range 10-50 action potentials/s.

Time delay depends on type of stimulation - not on cell type



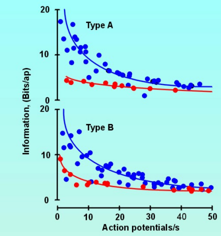
Time delay values, Δt, for Type A and Type B neurons during mechanical and electrical stimulation, as a function of mean action potential firing rate. Horizontal lines and adjacent numbers indicate the mean values of Δt from the different data sets over the range 10-50 action potentials/s.

Information capacity varies strongly with firing rate



Information capacity values, R, for Type A and Type B neurons during mechanical and electrical stimulation, as a function of mean action potential firing rate. Lines through the data were drawn by eye.

Information per action potential decreases to an asymptotic value as firing rate increases



Information per action potential, for Type A and Type B neurons during mechanical and electrical stimulation, as a function of mean action potential firing rate. Lines through the data were drawn by eye.

CONCLUSIONS

- The frequency responses of both Type A and Type B neurons could be well fitted by the power-law (fractional differentiator) relationship that has been used previously to model the step and frequency responses of other sensory receptors.
- The fractional exponent for Type A neurons was higher than for Type B neurons, consistent with the more rapid adaptation seen in the neurons' step responses.
- Information capacity estimates were much higher for electrical than for mechanical stimulation. This was due to the limited bandwidth available for mechanical stimulation and emphasizes the general problem of providing an adequate bandwidth stimulus to investigate rapidly adapting sensory neurons.
- Information capacity in both neuron types was strongly dependent on mean action potential firing rate. This is a new observation that probably reflects the range of firing rates that are available with higher mean rates.
- The maximum information capacities of approximately 200 bits/sec are in good agreement with the small number of other measurements from neurons that use action potentials.
- Information rates of 2-4 bits/action potential at high firing rates are also in good agreement with the few estimates available from other systems that use action potentials.
- Information per action potential increased sharply at low firing rates, which has not been reported before. This presumably reflects the increasing significance of the timing of each individual action potential as the number of available action potentials decreases.

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