Analyzing mechanosensory transduction by identifying invariant directions in stimulus space

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Abstract

Auditory receptor neurons, such as hair cells and chordotonal sensilla, transduce vibrations of the basilar or tympanal membrane into deflections of the membrane potential and, possibly, spikes. In doing so, the neuron performs an integration in the frequency domain as well as over a certain temporal window. We show how the nature of these integration processes can be investigated by identifying those regions in stimulus space that result in a given neuronal activity. For locust auditory receptors, we find good agreement of the experimental data with a description based on an energy–integration mechanism.

Summary

Responses of receptor neurons can often be effectively described by a mean activity. As the space of possible stimuli is usually very high dimensional, this corresponds to a drastic dimensional reduction from stimulus space to response space. For the auditory receptors of locusts, which are spiking neurons, the responses to stationary stimuli are well characterized by a mean firing rate. On the other hand, the neuron is sensitive to sound frequencies spanning a range of several kilohertz thus collapsing a high dimensional input space, given by the contents of the stimulus power spectrum, into a single output dimension. Equivalently for non–stationary sound stimuli, the probability of occurrence of a spike is influenced by the stimulus intensities during an extended temporal window. As a consequence of this dimensional reduction, there must be a class of stimuli, which leave the mean response of a single receptor invariant. The composition of these invariance classes depend on the cellular properties of the receptor, especially on the characteristics of the transduction process. Identifying regions of constant receptor response while systematically varying stimulus attributes can therefore give valuable insight into the biophysics of sensory transduction.

We demonstrate how this idea can be applied to a specific mechanosensory system and use the auditory receptors of the migratory locust as a model system. The auditory organ of locusts contains a tympanal membrane with the receptor cells directly attached to it. It therefore lacks a complicated mechanical signal transduction and amplification machinery as, e.g., the vertebrate cochlea, which would need special attention in modeling the signal pathway from sound to spikes. We performed intracellular recordings from the receptor axons while playing the sounds over loud–speakers. Stimuli were either 100–msec sounds of varying spectral composition, mainly superpositions of two or three pure tones with varying relative amplitudes, or short clicks with varying relative amplitudes separated by different time intervals. In the first case, we determined those stimuli that lead to the same mean firing rate, while in the latter case, combinations of clicks were determined yielding the same probability that at least one spike was elicited. An effective measurement of invariance classes is assured by implementing a feedback loop that takes the previously gathered data into account for an online determination of subsequent stimuli.

The results can be used to test different hypotheses about the nature of the transduction process and yield a complete phenomenological description of the relationship between the input and the mean output of the receptor cell. We explicitly investigate three descriptions, which use (a) the maximum signal amplitude, (b) the signal energy, or (c) the integrated pressure as a measure for the receptors' responses. Each hypothesis results in quantitative predictions about the invariance classes in the respective experiments, which are compared to the experimental findings. We conclude that the maximum signal amplitude as well as the integrated pressure have to be rejected as the crucial quantities of the transduction, while the signal energy is an excellent indicator of the mean activity. This allows us to construct a simple and effective model of the encoding by the receptor cells, which takes the frequency–resolved sensitivity (i.e. the threshold curve), the relationship between the signal energy and the firing rate, and the integration time constant as parameters. While the first two sets of parameters can be obtained from simple standard measurements with pure–tone stimulation, the time constant can be determined from the invariance class in the double–click experiments directly.

Our specific findings set quantitative constraints on any future biophysical model of this mechanosensory transduction process; the general approach will also be useful to study other (mechano)sensory systems.