The important aspects of visual encoding: relating receptive fields to mutual information rates in visual neurons
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In studying how visual neurons encode stimuli, there is currently a large divide between information theoretic approaches and more traditional receptive field-based analyses. While receptive fields (RFs) are straightforward to measure and are a standard part of almost every visual physiology experiment, traditional RF-based models of neurons are unable to explain the timing precision and the reliability of neural responses. At the same time, mutual information rates – which demonstrate the importance of reliability and precise timing in representing visual stimuli – are both difficult to measure experimentally and, on their own, do little to elucidate how the neuron actually encodes visual stimuli. Using a combination of experimental data and realistic simulations, we directly relate easily measurable elements of neuron encoding to the mutual information between the stimulus and response. We thus demonstrate how differences in visual encoding either across neurons or in the same neuron in different adaptation states relate to the role of the neuron in conveying visual information.

We first develop an RF-based model of encoding that can reproduce the information rate of the neuron. Typical RF-based models of encoding use the receptive field to produce a linear prediction of the neural response, and then a non-linear function (the “non-linearity”) to map the linear prediction to a firing rate. In this way, this LN (linear-non-linear) model conceptually separates how the neuron processes stimuli (L) from the details of how its response is generated (N). We show that the non-linearity – which intuitively corresponds to the neuron’s reliability – is underestimated for real neurons because of their refractory period, and present a robust way to account for the refractory period and recover an accurate estimate of the neuron’s reliability. In doing so, we identify other easily measurable aspects of the neural response (such as the spike-time “jitter”) that are important in determining its information rate. Measuring these elements allows for a “model-based information calculation” (MBIC) that matches the single-spike information rate calculated through conventional approaches. This MBIC can be performed over single experimental trials, and applied to a vast array of conventional visual physiology experiments.

Finally, we describe the dependence of the information rate on each encoding element. We analyze a library of LGN neurons recorded during spatiotemporal white noise experiments, and show how their information rates vary as a function of differences in their measurable properties. For example, an increased time scale of the refractory period corresponds to a decrease in both the information rate and firing rate, such that the amount of information per spike is higher. Similarly, a higher threshold (i.e., how selectively a neuron responds to stimuli) implies lower information and firing rates, but a higher information per spike. On the other hand, neurons with higher gain (i.e., stronger responses to the same stimuli) have a larger information rate but proportionally larger firing rate, such that there is negligible effect on the information per spike. In this way, we can relate the differences in information rates across the population of LGN neurons to different properties of their encoding.

Thus, in developing a model-based information calculation, we describe which features of neuronal encoding are important to the role of visual neurons in representing the visual world. These features are the (1) receptive field, which describes the spatiotemporal integration of the neuron; (2) the non-linearity, which accounts for the reliability of firing; and (3) the recovery function and timing jitter, which account for the neuron’s temporal precision. In addition to providing an intuitive understanding of a neuron’s information rate, these encoding properties can be measured in any visual experiment that maps receptive fields, making an information theoretic approach accessible in a wide variety of experimental contexts.

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