An Ecological Approach to the Neural Code

Akaysha C. Tang[1,2] & Terrence J. Sejnowski[1,2]

Howard Hughes Medical Institute[1]
Computational Neurobiology Lab, The Salk Institute
La Jolla, CA 92037
and
Department of Biology[2]
University of California, San Diego
La Jolla, CA 92093
{tang, terry}@salk.edu

Introduction

The primary mode of neural signaling involves the generation, transmission and transformation of spike trains by neurons in the central nervous system. The debate concerning spike timing versus rate coding has received increasing attention among neuroscientists, particularly within computational neuroscience (Shadlen & Newsome, 1994; Softky, 1995; Theunissen & Miller, 1995). It is widely believed that neurons in the nervous system are noisy, and that therefore only the rate or frequency of firing could reliably serve as a neural code. Recently this long held view has been directly challenged by a number of studies. Under tightly controlled input conditions, cortical neurons in the mammalian brain are capable of generating rather precisely timed spike trains, in both rat brain slices and behaving monkeys (Mainen & Sejnowski, 1994; Gallant, 1996). Information theoretic analysis has been successfully applied to this coding problem, and provides answers to the question of how much information is contained in a spike train (Bialek, Rieke, de Ruyter van Stevenick, & Warland, 1991). Although powerful, information theory has not yet answered the crucial question of whether the information measured is relevant to the neural system in the generation of behavioral output.

The specificity hypotheses

From an ecological point of view, the relevance of the information coded in a spike train, be it in a rate code or a spike timing code, depends heavily on the "what" aspect of the information and the survival value of its appropriate processing. Depending on what is to be encoded in the organism's environment, one type of code may serve as a better candidate than another. The onset of a stimulus, *e.g.* the appearance of a tiger, has to be coded with greater temporal precision, and with greater reliability, than the exact pattern of the tiger's fur coat. This proposed dependency of an optimal code on the type of information to be encoded implies at least three classes of testable hypotheses: modality specificity, property specificity, and domain specificity.

First, the optimal coding scheme should depend on the sensory modality under discussion, because different sensory modalities may be of different importance to a given organism in a given environment. Secondly, the optimal coding scheme should show property specificity within a given modality, because different sensory properties, such as color, form, onset/offset, or motion of a stimulus, may be of different predictive values for an organism exploring its environment. Finally, the optimal coding scheme, and in particular whether a spike timing code is required, should depend on whether the physical variables defining the stimulus are rapidly varying in the time domain.

Implications

We investigate these three classes of hypotheses by reviewing and reexamining the single and multicellular recording literature involving multiple sensory modalities and multiple sensory properties within a given modality. The final implication of the specificity hypotheses is that it would be hard, or perhaps even impossible, to find a general coding scheme applicable to all types of information present in the sensory environment. Therefore, conclusions concerning the coding problem without reference to the "what" aspect of the information would be difficult to interpret. Perhaps it is the modality, property, and domain specificity of the neural code that accounts for the heterogeneity of experimental results supporting both rate codes and spike time codes.

References

Bialek, W., Rieke, F., de Ruyter van Stevenick, R. R., & Warland, D. (1991). Reading a neural code. *Science*, *252*, 1854–7.

Gallant, J. L. (1996). Neural codes for natural vision. Jackson Hole Workshop on Neural Information and Coding. Invited talk.

Mainen, Z. F., & Sejnowski, T. J. (1994). Reliability of spike timing in neocortical neurons. *Science*, *268*, 1503–6.

Shadlen, M. N., & Newsome, W. T. (1994). Noise, neural codes and cortical organization. *Current Opinion in Neurobiology*, *4*, 569–579.

Softky, W. R. (1995). Simple codes versus efficient codes. *Current Opinion in Neurobiology*, 239–247.

Theunissen, F., & Miller, J. P. (1995). Temporal encoding in nervous systems: a rigorous definition. *J. Computational. Neurosci.*, 2, 149–162.