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The neuronal encoding of information in the brain

Edmund T. Rolls [a,*], Alessandro Treves [b,c]

[a] Oxford Centre for Computational Neuroscience, Oxford, UK
[b] SISSA, Cognitive Neuroscience, via Bonomea 265, 34136 Trieste, Italy
[c] NTNU, Centre for the Biology of Memory, Trondheim, Norway

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ABSTRACT

We describe the results of quantitative information theoretic analyses of neural encoding, particularly in the primate visual, olfactory, taste, hippocampal, and orbitofrontal cortex. Most of the information turns out to be encoded by the firing rates of the neurons, that is by the number of spikes in a short time window. This has been shown to be a robust code, for the firing rate representations of different neurons are close to independent for small populations of neurons. Moreover, the information can be read fast from such encoding, in as little as 20 ms. In quantitative information theoretic studies, only a little additional information is available in temporal encoding involving stimulus-dependent synchronization of different neurons, or the timing of spikes within the spike train of a single neuron. Feature binding appears to be solved by feature combination neurons rather than by temporal synchrony. The code is sparse distributed, with the spike firing rate distributions close to exponential or gamma. A feature of the code is that it can be read by neurons that take a synaptically weighted sum of their inputs. This dot product decoding is biologically plausible. Understanding the neural code is fundamental to understanding not only how the cortex represents, but also processes, information.
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Abbreviation: IT, inferior temporal visual cortex.
* Corresponding author.

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1. Introduction

Because single neurons are the computing elements of the brain and send the results of their processing by spiking activity to other neurons, we can analyze brain processing by understanding what is encoded by the neuronal firing at each stage of the brain (e.g. each cortical area), and determining how what is encoded changes from stage to stage. Each neuron responds differently to a set of stimuli (with each neuron tuned differently to the members of the set of stimuli), and it is this that allows different stimuli to be represented. We can only address the richness of the representation therefore by understanding the differences in the responses of different neurons, and the impact that this has on the amount of information that is encoded. These issues can only be adequately and directly addressed at the level of the activity of single neurons and of populations of single neurons, and understanding at this neuronal level (rather than at the level of thousands or millions of neurons as revealed by functional neuroimaging) is essential for understanding brain computation.

Information theory provides the means for quantifying how much neurons communicate to other neurons, and thus provides a quantitative approach to fundamental questions about information processing in the brain. To investigate what in neuronal activity carries information, one must compare the amounts of information carried by different codes, that is different descriptions of the same activity, to provide the answer. To investigate the speed of information transmission, one must define and measure information rates from neuronal responses. To investigate to what extent the information provided by different cells is redundant or instead independent, again one must measure amounts of information in order to provide quantitative evidence. To compare the information carried by the number of spikes, by the timing of the spikes within the response of a single neuron, and by the relative time of firing of different neurons reflecting for example stimulus-dependent neuronal synchronization, information theory again provides a quantitative and well-founded basis for the necessary comparisons. To compare the information carried by a single neuron or a group of neurons with that reflected in the behaviour of the human or animal, one must again use information theory, as it provides a single measure which can be applied to the measurement of the performance of all these different cases. In all these situations, there is no quantitative and well-founded alternative to information theory.

The overall aim of this paper is to describe the methods used for the analysis of neuronal activity in primates and other mammals, and to describe the main principles that have been discovered to date about the representation of information in the primate brain. Although there have been descriptions of some of the methods used to analyze cortical population encoding (Rolls et al., 1997b; Franco et al., 2004; Quian Quiroga and Panzeri, 2009), this is the first paper we know that provides a comprehensive account of the principles of information encoding by single neurons and populations of neurons in the mammalian and particularly primate cortex, together with the methods used to make these discoveries. We focus on work on the primate to make the findings very relevant to understanding neuronal encoding in the human brain; because primates can be trained to maintain visual fixation and attention in a way that allows reliable and repeated presentation of

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