Elaine Perry
Matthew Walker
Robert Perry
MRC Neurochemical Pathology Unit,
Newcastle General Hospital,
Newcastle upon Tyne, UK NE4 6BE.

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Estimation of information in neuronal responses

The article by Buračas and Albright[1] provides an excellent review of recent progress concerning the neural representation of sensory stimuli. The authors outline clearly the potential pitfalls of the 'direct'[2,3] and 'reconstruction'[4–6] methods for estimation of mutual information (namely, the need to estimate a probability distribution of spike trains, which are considered as vectors in what could be a very large space), but the naïve reader might be left with the belief that there are no good alternatives.

However, such alternatives do exist. We recently developed an approach to the analysis of information in spike trains that encompasses dynamics, but does not require a vector-space embedding nor the estimate of a multivariate probability distribution[7]. This method has been applied in mammalian visual cortex by us[8–10], and in the insect olfactory system by Laurent and colleagues[11].

Any method for estimation of information in spike trains requires making assumptions about the nature of the code. The accuracy of the information estimate depends on both the correctness and the breadth of the assumptions. Fewer assumptions about the nature of the neural code are made by the metric-space methods than by vector-space methods (such as the direct and reconstruction methods). However, this broader scope necessarily incurs a penalty in terms of the amount of mutual information that can be identified. A rough estimate of this penalty can be determined by comparing information calculations based on model data in which the vector-space assumptions are known to be appropriate. This comparison indicates a penalty of about 25% paid by the metric-space methods in return for their broader scope. Conversely, assumptions concerning the nature of the code that are overly narrow could also lead to underestimates of information, as the aspects of the spike train that carry the information might be overlooked.

As discussed by Buračas and Albright[1], even the most efficient neuronal representations are only about 50% efficient, when efficiency is determined by the reconstruction and direct methods. Residual inefficiency is generally attributed to neuronal noise. However, some of this 'inefficiency' might be only apparent, representing instead a contribution from forms of coding beyond the scope of the analysis method. Moreover, theoretical considerations have raised the possibility that the structure of central neuronal representations has the abstract properties of a metric space, rather than a vector space[12,13]. For these reasons, as information-theoretic analyses are pursued in a wider variety of settings, the neurophysiologist should be prepared to use a wide range of techniques for information analysis, with both narrow and broad prior assumptions.

Jonathan Victor
Keith Purpura
Weill College of Medicine of Cornell
University, New York City,
NY 10021, USA.

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Reply

Victor and Purpura[1] draw attention to an alternative information-theoretic data-processing method, which is complementary to those mentioned in our article[2]. The metric-space method introduced by these authors (see, for example, Ref. 3) is based on the concept that the direct and reconstruction methods of calculating mutual information in spike trains hinge on the assumption that these responses essentially 'live' in a multidimensional vector space. This assumption demands large amounts of data for estimating information content of spike trains. The metric-space method does not use such an assumption, and, as pointed out by Victor and Purpura, is less costly with respect to the amount of data required. Furthermore, despite their abstract appearance, the metric-space measures are in fact motivated by known biophysical properties of synaptic integration (such as coincidence detection, and paired-pulse facilitation or depression). These measures have been instrumental in addressing such pending problems as the role of time in neural coding[3].

A natural extension of these metric measures would be the inclusion of further biophysical details of cortical neurons: the ultimate goal of the stimulus discriminability analyses is to understand neuronal representations as they are seen by the brain. Alternatively, one might proceed with further rejection of assumptions. For example, neuronal biophysics does not always support the assumption, used by both conventional and metric-space approaches, that displacement of a spike in time is time-symmetrical (for example, synaptic plasticity appears to be temporally antisymmetrical). It would be interesting to see how conclusions about neuronal encoding of various parameters of visual stimuli[3] will change as one proceeds with relaxing further tacit assumptions. We hope that the increasingly wider acceptance of these measures will eventually permit cross-species and cross-system comparisons of neural codes.

Giedrius T. Buračas
Thomas D. Albright
Howard Hughes Medical
Institute, Salk Institute for
Biological Studies,
La Jolla,
CA 92037, USA.

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