RANK ORDER CODING

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INTRODUCTION

The idea that neurones transmit information using a rate code is extremely entrenched in the neuroscience community. The vast majority of neurophysiological studies simply describe neural responses in terms of firing rate, and while studies using Peri-Stimulus Time Histograms (PSTHs) are fairly common, only rarely does one get to see the underlying spikes in the form of a raster display. Even rarer are studies that provide information about how spikes are generated across a population of neurones.

One consequence of this strong bias is that many alternative coding schemes, and particularly those involving patterns of activity distributed across populations of neurones, have simply not been considered seriously. It is now virtually 30 years since the publication of Perkel and Bullocks' review of Neural Coding in which a whole range of candidate coding schemes were discussed[1]. Few of these various candidate codes have been disproved experimentally. Even today, when increasing numbers of researchers are interested in the potential of temporal coding schemes and in particular the role played by synchrony[2,3], few question the underlying assumption that this synchrony is imposed on an underlying rate code.

PROBLEMS WITH RATE CODING

Although using rate coding to encode analog values seems reasonable, problems arise when one tries to implement such coding in networks of biologically realistic neurons, because one is forced to deal with the fact that real neurons generate spikes, not floating point numbers! As we have argued in more detail elsewhere[4,5], the assumption that rate coding involves a pseudo-Poisson spike generation mechanism (as is often the case), is difficult to reconcile with the extreme rapidity of processing in sensory pathways, where it appears that sophisticated processing can be performed on the basis of only 10 ms of activity at each stage [6-8]. To take a simple example, suppose that the retina contains two pools of neurones, A and B, firing at rates of 100 spikes.s^{-1} and 75 spikes.s^{-1}, and that we need to know which is which. Suppose that spike generation is Poisson and that we need to make a decision on the basis of 10 ms of activity with an error rate of no more than 5%. How many cells would we need in each pool? A simple calculation[5] reveals that we would need no less than 76 neurones in each pool. Note that this is a situation where we are not even able to recover 1 bit of information about the stimulus.

TEMPORAL CODING

Recent data indicates that the initial transient response of a neuron may in fact be temporally quite precise and reliable [9]. This opens up possibilities for alternative coding schemes that depend on the timing of spikes [10-12]. One such alternative considers a neuron not so much as an *analog-to-frequency* converter, but rather as an *analog-to-delay* converter. The idea is very simple and is based on the fact that the time taken for an integrate-and-fire neuron to reach threshold depends on the strength of the input (see figure 1A). This would lead to the sort of latency-intensity function illustrated in figure 1B. Consider now what would happen with several receptor cells and an intensity profile as illustrated in figure 1C. Because of the intensity-delay transformation, the neurons will tend to generate spikes in an order which reflects the input distribution.

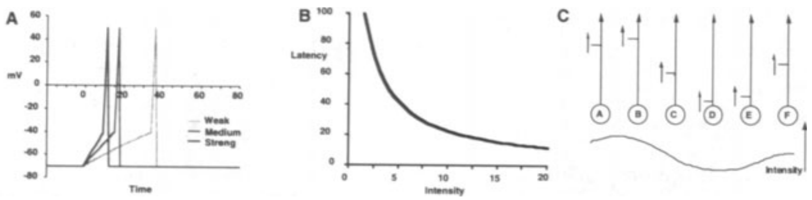

Figure 1. A. The response of a leaky integrate-and-fire neuron to inputs of different strengths. B. A typical intensity-latency response function. C. Generation of an asynchronous spike wave in a population of receptors.

Given this asynchrony in spike generation, there are actually various ways that one could develop a coding scheme. One would be to use the relative timings of spikes across the different cells [13]. This certainly allows a large amount of information to be transmitted within a very short time. Suppose that we have N neurons, and that precise arrival times of spikes can be measured to the nearest millisecond. Within a time window of T milliseconds one can transmit a maximum of $\log_2(T^N)$ bits of information. Thus with 6 neurons, one can transmit up to $\log_2(10^6) \approx 20$ bits of information. Of course, in order to be useable, this information has to be decoded, and although it is possible to conceive of biological circuits capable of responding selectively to particular temporal patterns across a set of inputs, it is likely that this would require a great deal of specialized hardware. Although sensory systems often rely on timing differences between spikes coming from different sources[14], in general, these tend to involve only two sources as in the case of calculating interaural delay times or the timing differences between electrical signals arriving on the left and right hand sides of the body in electric fish [15]. Even these require very large amounts of specialized neural hardware. As far as we are aware, there is little or no direct evidence for neural circuits sensitive to delays arising from several sources at once.

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However, it appears that a simpler coding scheme can be used which also uses the relative timing of spikes across a population of cells, but which is considerably easier to compute. The idea is to throw away the precise timing information, and use a code that depends only on the order in which the spikes arrive. Returning to the six neurons in figure 2, we can now code the stimulus by the ordering B > A > F > C > E > D. Since there are factorial N possible orderings, a rank order code can transmit up to $\log_2(N!)$ bits of information under conditions where each input neuron can only emit one spike.