Are Retinal Ganglion Cells Independent Encoders?

Markus Meister and Toshihiko Hosoya
MCB Department, Harvard University, Cambridge, MA 02138
meister@biosun.harvard.edu

July 14, 2001

In their recent paper "Retinal ganglion cells act largely as independent encoders", Nirenberg et al[1] analyze how pairs of retinal ganglion cells encode the visual stimulus by their firing patterns. Prior work had shown that nearby ganglion cells have a strong tendency to fire in near synchrony[2,3]. The authors claim that these correlations are irrelevant to visual coding by ganglion cells, because "more than 90% of the information about the stimuli can be obtained from the cells when their correlated firing is ignored." They conclude that "ganglion cells act largely independently to encode information, which greatly simplifies the problem of decoding their activity" because "the activity of any given cell can be evaluated separately from other cells." Unfortunately, the article contains no evidence for these propositions. The claims rely on two methods of analysis, both of which are flawed. They would fail to detect even simple cases where correlated firing is important for decoding the activity of two neurons.

The first analysis computes a quantity ΔI, described as the "information loss" if one ignores the correlations in firing between two cells (Eqn 2 in ref. 1). The implication is that when $\Delta I = 0$, then correlations are not important for the neural code (Fig 3 in ref. 1). This can be refuted most easily by example (Figure 1). In each of the coding schemes **a** and **b**, the two neurons encode information in a concerted manner: They have correlations both in their signal (both are excited by stimulus) and their noise (positive covariance in **a**, negative in **b**). If the neurons are evaluated separately from each other – as advocated by the authors – the two schemes yield the exact same single-cell responses. The difference lies in the correlations between the two neurons, and one needs to take these into account to interpret their responses. In doing that, one finds that scheme **b** conveys twice as much information about the stimulus as scheme **a**. Yet, $\Delta I = 0$ for both of these schemes, and thus the authors would characterize these populations as "independent encoders". Clearly, the analysis of ΔI cannot even detect interesting examples of concerted coding, let alone distinguish between such codes that have very different performance.

The second analysis is an attempt to explicitly decode the ganglion cell responses – that is, estimate the stimulus from the spike trains – while either taking correlations into account or not (Fig 4 of ref. 1). To test whether spike pairs that are synchronous on the millisecond scale carry special visual messages, one should use a decoder that can recognize such spike pairs. The method used by the authors, namely linear filtering of the individual spike trains[4], cannot do that. The filter functions are necessarily broad (probably 0.1 s) such that millisecond shifts of individual spikes cannot be interpreted. Instead, one should identify synchronous spike pairs first, and then assign separate messages to them. Also, the current best guess is that synchronous spike pairs originate in retinal interneurons and thus have different spatial receptive fields from those of the participating ganglion cells[3,5]. If so, then the information they convey is about spatial detail, which cannot possibly be tested with the spatially uniform stimulus used by the authors. Both these concerns – detection of synchronous spikes and spatial analysis – were addressed by Dan et al[6], who concluded that synchronous firing of cat LGN neurons does contribute significantly to their encoding of visual information. Ideally, one would carry such an analysis beyond mere pairwise correlations. Any given pair of cells may have only few synchronous spikes in common, but once all the nearby partners are considered, the fraction of spikes in such firing patterns may exceed 80%[7]. Thus, the degree to which concerted firing contributes to coding by retinal ganglion cells remains an open issue.

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a

s	r_1	r_2	$P(r_1, r_2 \mid s)$
0	0	0	0.5
	1	1	0.5
1	1	1	0.5
	2	2	0.5

$P(s=1 \mid r_1, r_2)$

	r_1=0	1	2
r_2=0	0		
1		0.5	
2			1

b

0	0	1	0.5
	1	0	0.5
1	1	2	0.5
	2	1	0.5

	r_1=0	1	2
r_2=0		0	
1	0		1
2		1	

Figure 1: Two examples (**a, b**) of different coding schemes by which the responses of two neurons, r_1 and r_2, encode one stimulus, s. Each neuron fires 0, 1, or 2 spikes, and the stimulus can take on value 0 or 1 with equal probability. **a,** The left table illustrates the probability of getting different response pairs (r_1, r_2) given the stimulus. Both neurons are excited by the stimulus (they fire more on average when $s=1$), have some noise variation in their activity, but are perfectly correlated with each other. The right panel illustrates how these responses are decoded, by giving the probability of the stimulus being 1 as a function of the observed response pair. On half of the trials, namely when the response is (1,1), these neurons leave complete ambiguity about what stimulus was delivered. **b,** A different coding scheme illustrated in the same format. Note that each individual cell analyzed by itself responds in the same way as in **a**. However, their noise correlations are different, and as a result, the response pair uniquely identifies the stimulus on all trials.