Response to comments by Berry and Schneidman regarding Nirenberg et al., *Nature* 411:698-701 (2001)

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Berry and Schneidman's first two comments focus on their view of how our paper will be interpreted; the second two reflect, we believe, misunderstandings that we think can easily be cleared up. Their main criticisms are as follows:

1. "The casual reader might assume that ΔI tests whether pairs of ganglion cells are independent, i.e. that there are no correlations in the two cell's responses."

2. "The more careful reader might assume that ΔI measures whether pairs of ganglion cells are conditionally independent."

3. "... one cannot claim that the problem of decoding the retina can be greatly simplified [if ΔI is zero]."

4. "If [ΔI were an information loss], it would be possible to express ΔI as the difference between the information that the two cells convey about the stimulus, $I(r_1,r_2;s)$ and the information conveyed by the independent decoder", thus "for ΔI>0, one cannot say how important the error is for information transmission."

The following is our response:

1, 2. While we cannot prove it, we feel that most readers would be unlikely to make either of the assumptions stated in points (1) and (2). Our paper opens by saying that the ganglion cells we are studying are correlated (with "correlated" defined in Methods[1]), and that the subject of the paper is to determine if the correlations are important. Moreover, our Fig. 2 shows how correlated each and every pair is. It seems hard to imagine that the reader would think that we would first show that the cells are correlated using cross-correlograms and then test whether the cells are correlated using ΔI.

3. We do not fully understand Berry and Schneidman's third criticism. If $\Delta I = 0$, then the probability of observing stimulus s given responses r_1 and r_2, denoted $P(s| r_1, r_2)$, is proportional to $P(r_1|s)P(r_2|s)$; otherwise, it is proportional to $P(r_1, r_2|s)$. Construction of two one-dimensional distributions, $P(r_1|s)$ and $P(r_2|s)$, takes significantly less data than construction of one two-dimensional distribution, $P(r_1,r_2|s)$. The reduction in the data required to construct a decoder is, to us, a major simplification.

4. Berry and Schneidman's fourth criticism consists of an assertion and a conclusion. While the assertion may *sound* reasonable, it's really only an opinion of what information loss should be (see Chapter 5 of Cover and Thomas[2] for a different opinion, the one we adopt). As to their conclusion -- we disagree, as we can say very clearly how important the error is for information transmission. As we explain in Methods[1], information about a stimulus can be thought of as the average number of yes/no questions it would take to identify a stimulus minus the average number of yes/no questions it would take to identify a stimulus given that responses have been observed. The quantity ΔI is the extra number of yes/no questions it would take to identify the stimulus if one were to treat the cells as independent (i.e., ignore correlations). It is in this sense that we interpret ΔI as an information loss.

Thus, while it is true that the nature of population coding in all retinas for all species remains to be determined, for the mouse, we have shown that little information is lost when pairwise correlations are ignored.

References

1. Nirenberg, S., Carcieri, S.M., Jacobs, A.L.,& Latham, P.E. Retinal ganglion cells act largely as independent encoders. *Nature* **411**, 698-701 (2001).
2. T.M. Cover and J.A. Thomas. *Elements of Information Theory*. John Wiley & Sons, New York, (1991).