Response to comment by Meister and Hosoya regarding Nirenberg *et al.*, Nature, 411: 698-701

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Meister and Hosoya assert that our method of analysis[1] is flawed, that it "cannot detect even simple cases where correlated firing is important for decoding". To make their case, they show two examples, claim that the correlations in these examples are important, and state that our method fails to detect this. Their argument rests on the claim that the correlations in these examples are, in fact, important for decoding. We believe this claim is incorrect. Below is our reasoning.

Decoding means, essentially, building a dictionary that translates responses into stimuli. To test whether correlations in responses are important for decoding, one needs to build *two* dictionaries: one where correlations in responses are taken into account and one where correlations in responses are ignored (i.e., the responses are treated as independent). If correlations are important for decoding, then the two dictionaries will translate responses differently; otherwise, they won't.

For Meister and Hosoya's examples, then, one should take each example by itself and compare the "correlated dictionary" with the "independent dictionary". Meister and Hosoya don't do this; instead they compare the two examples with each other.

Here we perform the appropriate comparison. Meister and Hosoya provide the correlated dictionary for each example, which is $P(s=1|r_1,r_2)$, and we provide the independent dictionary, $P_{IND}(s=1|r_1,r_2)$, both listed in the table below. As can be readily seen, each pair of responses in ***a*** and ***b*** is translated exactly the same way whether one uses $P_{IND}(s=1|r_1,r_2)$ or $P(s=1|r_1,r_2)$. (For completeness, we point out that $P_{IND}(s=1|r_1,r_2)$ is a superset, containing more elements than $P(s=1|r_1,r_2)$, but every response pair (r_1,r_2) that occurs is correctly translated by $P_{IND}(s=1|r_1,r_2)$. Only responses that occur are shown.)

Thus, the correlations in these examples are not important for decoding. This lack of importance is just what was predicted by ΔI=0, since ΔI is a measure of the difference between the correlated and independent dictionaries. Meister and Hosoya's comment that "scheme ***b*** conveys twice as much information about the stimulus as scheme ***a*** … yet ΔI=0 in both" is thus irrelevant, as ΔI clearly doesn't measure differences between ***a*** and ***b***. Instead, it measures the information loss associated with using the independent rather than the correlated dictionary -- for ***a***, for ***b*,** or for *any* example.

Table 1. Translation of responses. By definition, $P_{IND}(s|r_1,r_2) \propto P(r_1|s)P(r_2|s)P(s)$.

	r_1	r_2	Correlated dictionary $P(s=1|r_1,r_2)$	Independent dictionary $P_{IND}(s=1|r_1,r_2)$
a	0	0	0	0
	1	1	0.5	0.5
	2	2	1	1
b	0	1	0	0
	1	0	0	0
	1	2	1	1
	2	1	1	1

That correlations can exist and be unimportant for decoding may seem surprising and counterintuitive. For an intuitive feel for why it happens here, examine their Fig.1, left panels. In ***a***, the two cells are perfectly correlated no matter what the stimulus is, so the fact that a given pair of responses is correlated doesn't, by itself, provide information about what the stimulus is. In contrast, the fact that a given pair of responses contains, say, a *2*, *does* provide information, and this information can be obtained even from cells that are treated as independent. The same reasoning applies to ***b***, but responses are all *anti*-correlated. (Note that treating the two cells as independent doesn't mean using one or the other to decode; one still uses two cells. Instead, it means taking their independent responses, pairing them, and then using the paired independent distribution to generate a dictionary.)

In these examples, correlations aren't important and ΔI detected this. For an example where correlations *are* important and ΔI detects it, along with a proof that ΔI always does, see Supplementary Information[2].

Regarding their second comment, we disagree that linear reconstruction can't detect effects of correlations on millisecond timescales, as the error in our filters scaled as $\Delta I/I$. Note, also, that the stimuli used in our paper[1] for the main analysis -- the information theoretic analysis -- were all natural movies (i.e., mice running around). See Supplementary Information[2] for further discussion of these points.

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. Supplementary Information, http://culture.neurobio.ucla.edu/~pel/critics/Meister_SI.pdf