A Comment on Data Shuffling

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Abstract

In the analysis of neuronal spike trains in response to experimental stimuli, the question of whether there is 'cooperativity' in the coding of information in the spike trains has been widely addressed by the practice of data shuffling: a measure of mutual information between stimulus and the spike trains is computed using the real data, then the data is shuffled so as to destroy cooperative coding, if it is there, and the same mutual information measure is computed for the shuffled data.

In this note we apply this procedure to a simple model in which it is questionable whether the encoding should be termed 'cooperative', and show that the test nevertheless gives a positive result.

Stimulus S. Cell responses A and B. Cells might also be responding to other stimuli not part of the experiment, N. The question is whether the cells's encoding of the stimulus is 'cooperative' or not.

1 First, describe the method:

Assuming that we can gather plenty of data so as to estimate $P(a, b|s)$ for all values of a, b, and s, we compute the mutual information between [A and B] and [S].

$$I_P(A, B; S) \equiv H_P(A, B) - H_P(A, B|S). \tag{1}$$

Here,

$$H_P(A, B) \equiv \sum_{a,b} P(a, b) \log \frac{1}{P(a, b)} \tag{2}$$

and

$$H_P(A, B|S) \equiv \sum_s P(s) \sum_{a,b} P(a, b|s) \log \frac{1}{P(a, b|s)}. \tag{3}$$

The data–shuffling procedure is equivalent to defining a distribution Q as follows: we compute the marginal probabilities $P(a|s)$ and $P(b|s)$ for all a and b and define:

$$Q(a, b|s) = P(a|s)P(b|s) \tag{4}$$

and

$$Q(a,b) = \sum_s P(s) Q(a,b|s). \tag{5}$$

We then compute the mutual information between [A and B] and S using the shuffled distribution:

$$I_Q(A,B;S) \equiv H_Q(A,B) - H_Q(A,B|S). \tag{6}$$

Here,

$$H_Q(A,B) \equiv \sum_{a,b} Q(a,b) \log \frac{1}{Q(a,b)} \tag{7}$$

and

$$H_Q(A,B|S) \equiv \sum_s P(s) \sum_{a,b} Q(a,b|s) \log \frac{1}{Q(a,b|s)}. \tag{8}$$

We compare the quantities $I_P(A,B;S)$ and $I_Q(A,B;S)$. If they are equal, or differ negligibly (compared to $I_P(A,B;S)$), the encoding is declared to be 'not cooperative'; if $I_P(A,B;S)$ is significantly greater than $I_Q(A,B;S)$ then the encoding is declared to be 'cooperative'.

2 Second, show a case where the method gives a sensible result:

If there are no other stimuli driving the cell and S has independent influences on A and B then $P(a,b|s)$ is separable, so P and Q are identical, and the estimator

$$I_P(A,B;S) - I_Q(A,B;S) \tag{9}$$

is zero.

3 Third, make a simple case where one might hope it is zero

The method is still meant to be useful even if the cells are occasionally driven by other stimuli unrelated to S, so that the distribution $P(a,b|s)$ is not separable. Let's make a simple example and see if this is so.

Let S and N be independent stimuli for the cells. Let the cells respond independently to S and N, with a 'noisy-or' dependence. [There are other ways of defining independent responses of A and B to S and N. We believe that the present example is representative of all of them.]

For cell A,

$$\begin{array}{rcl} P(a{=}1|s=0,n=0) & = & 0 \\ P(a{=}1|s=1,n=0) & \equiv & p_{a|s} \\ P(a{=}1|s=0,n=1) & \equiv & p_{a|n} \\ P(a{=}1|s=1,n=1) & \equiv & 1-(1-p_{a|s})(1-p_{a|n}) \end{array} \tag{10}$$

$$\begin{array}{rcl} P(a{=}0|s=0,n=0) &=& 1 \\ P(a{=}0|s=1,n=0) &=& 1-p_{a|s} \\ P(a{=}0|s=0,n=1) &=& 1-p_{a|n} \\ P(a{=}0|s=1,n=1) &=& (1-p_{a|s})(1-p_{a|n}) \end{array}, \tag{11}$$

and similarly for cell B. Let the probability of n, which is not observed, be

$$P(n=1)=p_n \qquad P(n=0)=1-p_n, \tag{12}$$

and let the probability of s, which the experimenter controls, be

$$P(s=1)=p_s \qquad P(s=0)=1-p_s. \tag{13}$$

3.1 Example 1

We give values to these parameters: Let

$$p_n = 0.01 \tag{14}$$
$$p_s = 0.5 \tag{15}$$
$$p_{a|s} = 0.01 \tag{16}$$
$$p_{b|s} = 0.01 \tag{17}$$
$$p_{a|n} = 1 \tag{18}$$
$$p_{b|n} = 1. \tag{19}$$

Then

$$P(AB|S=0) = \boxed{\begin{array}{cc} 0.99 & 0 \\ 0 & 0.01 \end{array}} \qquad P(AB|S=1) = \boxed{\begin{array}{cc} 0.9703 & 0.0098 \\ 0.0098 & 0.0101 \end{array}} \tag{20}$$

and

$$I_P(AB;S) = 0.0099\,\text{bits} \tag{21}$$
$$I_Q(AB;S) = 0.0024\,\text{bits}. \tag{22}$$

In bits per spike, these numbers are:

$$I_P(AB;S)/\text{firing rate} = 0.33 \tag{23}$$
$$I_Q(AB;S)/\text{firing rate} = 0.082. \tag{24}$$

Here, the data shuffling has reduced the mutual information by a factor of four.

It is easy to understand why the information conveyed by A and B about the stimulus is in this case reduced by shuffling. Before shuffling, any $a=1$ accompanied by a $b=1$ was most likely caused by the other stimuli $n=1$, and any lone $a=1$ or $b=1$ was certainly caused by $s=1$; so the lone events convey concrete information about S and the coincident events can be ignored. After shuffling, most of the events that were coincident events are turned into lone events; there are very few coincident events. Any lone event now gives only weak information about S because lone events could have been caused by $s=1$ or $n=1$.

3.2 Example 2

We give values to the parameters corresponding to a pair of cells both of which are very reliably driven by a moderately rare stimulus S and another stimulus N: Let

$$\begin{aligned} p_n &= 0.1 & (25)\\ p_s &= 0.1 & (26)\\ p_{a|s} &= 0.9 & (27)\\ p_{b|s} &= 0.9 & (28)\\ p_{a|n} &= 0.9 & (29)\\ p_{b|n} &= 0.9. & (30) \end{aligned}$$

Then

$$P(AB|S=0) = \boxed{\begin{array}{cc} 0.901 & 0.009 \\ 0.009 & 0.081 \end{array}} \qquad P(AB|S=1) = \boxed{\begin{array}{cc} 0.00901 & 0.082 \\ 0.082 & 0.827 \end{array}} \tag{31}$$

and

$$\begin{aligned} I_P(AB;S) &= 0.27\,\text{bits} & (32)\\ I_Q(AB;S) &= 0.35\,\text{bits}. & (33) \end{aligned}$$

In bits per spike, these numbers are:

$$\begin{aligned} I_P(AB;S)/\text{firing rate} &= 0.79 & (34)\\ I_Q(AB;S)/\text{firing rate} &= 1.0. & (35) \end{aligned}$$

Here, the data shuffling has *increased* the mutual information by 28%.

Again, this result has an intuitive explanation. In the raw data, neurons A and B fire rarely, and, when they do fire, they fire together reliably in response to the events $s = 1$ and $n = 1$, making it hard to distinguish which of the two stimuli caused the firing events. When the data has been shuffled, however, the correlated events ($a = 1$, $b = 1$) produced by the noise become separated from each other, while the corresponding events caused by the stimulus remain aligned. We can now detect the stimulus events with higher reliability.

4 Conclusion

The results of data shuffling should be treated with caution. Would one really call an system in which A and B respond completely independently to the stimuli a cooperative coding? True, the optimal *decoder* for inferring s from a and b in the above problem is a decoder that looks jointly at a and b, so the optimal decoder might be termed cooperative. But does that mean that we should call the spikes' code cooperative?

Perhaps a better approach to the task of inferring how spike trains encode information about stimuli might be to make Bayesian models and compare them.

4.1 Other information measures

For these two examples we can also evaluate another entropy–based statistic that is sometimes used to measure the supposed 'synergy' or 'redundancy' between the spike trains A and B. We define

$$D = I(AB; S) - (I(A; S) + I(B; S)). \tag{36}$$

For example 1, in which the joint events $a = 1$, $b = 1$ could be filtered out as being caused by $n = 1$, $I(A; S) + I(B; S) = 0.0024$ so $D = 0.0074$.

For example 2, $I(A; S) + I(B; S) = 0.45$ so $D = -0.18$.

These two examples thus show that the meaning of the statistic D is not straightforward. A conventional interpretation of these two results would be that in the first case, the two neurons encode information about S 'synergistically', and in the second case they encode information about S 'redundantly'. Yet in both cases the responses of the neurons to S are causally independent.