Spike correlation measures that eliminate stimulus effects in response to white noise

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Data from simultaneous recordings of two spike trains in response to a common stimulus are typically analyzed using the correlation between the spike times of the two neurons. Correlations between the spike times could be induced by a number of factors, including (but not limited to) the presence of the common stimulus and the structure of the neural network containing the measured neurons [13, 1, 12, 2]. Thus, before one can make inferences based on spike correlations about the underlying circuitry, one must, at minimum, remove contributions to the correlations due simply to the common stimulus.

The responses of two neurons are independent conditioned on the stimulus $\mathbf{X}$ when

$$\Pr\left(R_1^i = 1 \,\&\, R_2^j = 1 | \mathbf{X}\right) = \Pr\left(R_1^i = 1 | \mathbf{X}\right) \Pr\left(R_2^j = 1 | \mathbf{X}\right), \qquad (1)$$

where $R_p^i = 1$ if neuron p spiked at the discrete time point i and is zero otherwise. If, when Eq. (1) is satisfied, the expected value of a correlation measure converges to zero as the sample size increases, we refer to it as stimulus independent correlation measure (SICM). When spikes are recorded in response to the repetition of an identical stimulus, one can estimate $\Pr\left(R_p^i = 1 | \mathbf{X}\right)$ as well as $\Pr\left(R_1^i = 1 \,\&\, R_2^j = 1 | \mathbf{X}\right)$ by averaging the responses to the stimulus. Then one can subtract the estimates of both sides of Eq. (1) to form the joint peristimulus time histogram (JPSTH) [13, 1]. Thus the JPSTH and its integral, the shuffle-corrected correlogram, are unbiased SICMs [12, 2].

A bigger challenge is to develop SICMs for experiments, such as white noise and related experiments, where one does not repeat a particular realization of the random stimulus. In such experiments, one is sampling a

large stimulus space and would like to avoid repeats that, for an given experiment duration, would reduce the size of the sampled space and increase the noise. However, when the stimulus is not repeated, one cannot estimate the probabilities in Eq. (1) (other than by the value of the one sample recorded) without specifying additional assumptions on how the neurons' responses depend on the stimulus. Thus one cannot derive *model-free* SICMs for such experiments.

When one uses a random sequence of a discrete number of stimuli and makes the realistic assumption that a neuron's response depends only on the previous few stimuli, one could theoretically form a JPSTH for each distinct combination of such stimuli. However, when the stimulus is multidimensional, the number of possible sequences is so large that each combination will rarely occur in a realistically long experiment. For example, even in the subspace experiments designed by Ringach et al. [16], most combinations would not be presented even once.

One can form a correlation measure that looks similar to the shuffle-corrected correlogram, the covariance between the response of one neuron and the (delayed) response of the other,

$$C^j = \langle R_1^i R_2^{i-j} \rangle - \langle R_1^i \rangle \langle R_2^{i-j} \rangle, \tag{2}$$

where $\langle \rangle$ represents averaging over the entire stimulus. However, we show that the covariance can have large stimulus-induced components even when Eq. (1) is satisfied. Alternatively, if one assumed that stimulus dependent effects occur at a different time scale than the pertinent correlations, one could filter out those stimulus effects from $\langle R_1^i R_2^{i-j} \rangle$ with a bandpass filter [14]. But, not only won't the resulting measure necessarily be a SICM, the filtering might also remove stimulus independent correlations.

We derive two SICMs based on a linear-nonlinear model of neural respose to a white noise stimulus. Let the stimulus $\mathbf{X}$ be a vector of independent Gaussian random variables with zero mean and standard deviation $\sigma = 1$. Thus $\mathbf{X}$ is a discrete approximation to temporal or spatio-temporal white noise. Let the probability of a spike of neuron p for $p = 1, 2$ be a linear-nonlinear function of the input and the response of neuron $q \neq p$,

$$\Pr\left(R_p^i = 1 \big| \mathbf{X} = \mathbf{x}, \mathbf{R}_q = \mathbf{r}_q\right) = g_p\left(\mathbf{h}_p^i \cdot \mathbf{x} + \sum_{j \geq 0} \bar{W}_{qp}^j r_q^{i-j}\right) \tag{3}$$

where $\mathbf{h}_p^i$ is the linear kernel of neuron p shifted i units in time, $g_p(\cdot)$ is its output nonlinearity (representing, for example, its spike generating mecha-

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nism), and $\bar{W}_{qp}^j$ is a connectivity term representing how a spike of neuron q at a particular time modifies the response of neuron p after j time steps.

If one assumes that the coupling $\bar{W}$ is small enough to justify retaining only first order terms in the coupling strength, one can express the correlation between the responses of the neurons as a linear function of the the coupling

$$\langle R_1^i R_2^{i-k} \rangle \approx \nu^k + \sum_j A^{kj} \bar{W}^j \tag{4}$$

where $\bar{W}^j = \bar{W}_{12}^{-j}$ for $j < 0$, $\bar{W}^j = \bar{W}_{21}^j$ for $j > 0$, and $\bar{W}^0 = \bar{W}_{12}^0 + \bar{W}_{21}^0$. The $\approx$ indicates equality within $O((\bar{W}_{pq}^j)^2)$ as the sample size increases. If one approximates the nonlinearity $g_p(\cdot)$ as an error function, one can compute the vector ν and matrix A analytically from the mean rates $\langle R_p^i \rangle$ and stimulus-spike correlation $\langle \mathbf{X} R_p^i \rangle$.

We thus propose two SICMs for the linear-nolinear system:

$$\mathcal{S}^k = \langle R_1^i R_2^{i-k} \rangle - \nu^k$$

and

$$\mathcal{W} = A^{-1} \mathcal{S}.$$

We demonstrate through simulations that both measures, unlike the covariance, behave like SICMs not only with linear-nonlinear neurons but also with integrate-and-fire neurons. Moreover, in cases where the stimulus independent correlations were due solely to mutual coupling, the SICM $\mathcal{W}$ accurately reconstructed the coupling.

Although the linear-nonlinear framework limits the strict applicability of this analysis to neurons that can be approximated as such, the linear-nonlinear model is commonly used to analyze neurons in the auditory, visual, and somatosensory systems [14, 11, 5, 6, 9, 10, 3, 4, 15, 16, 8, 7]. The proposed analysis can thus be readily used on simultaneous recordings of these neurons in response to white noise.[1] Moreover, since the proposed SICMs give good results even with simulations of the more realistic integrate-and-fire model, the utility of the SICMs appears broader than required for their derivation.

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[1]Note that somatosensory experiments do typically repeat the stimulus [8, 7] and thus could use the JPSTH as well.

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