



**Small-correlation expansion to quantify information in noisy sensory systems**Gabriel Mahuas <sup>1,2</sup> Olivier Marre,<sup>1</sup> Thierry Mora,<sup>2,\*</sup> and Ulisse Ferrari <sup>1,\*</sup><sup>1</sup>*Institut de la Vision, Sorbonne Université, CNRS, INSERM, 17 rue Moreau, 75012 Paris, France*<sup>2</sup>*Laboratoire de Physique de École Normale Supérieure, CNRS, PSL University, Sorbonne University, Université Paris-Cité, 24 rue Lhomond, 75005 Paris, France*

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Neural networks encode information through their collective spiking activity in response to external stimuli. This population response is noisy and strongly correlated, with a complex interplay between correlations induced by the stimulus, and correlations caused by shared noise. Understanding how these correlations affect information transmission has so far been limited to pairs or small groups of neurons, because the curse of dimensionality impedes the evaluation of mutual information in larger populations. Here, we develop a small-correlation expansion to compute the stimulus information carried by a large population of neurons, yielding interpretable analytical expressions in terms of the neurons' firing rates and pairwise correlations. We validate the approximation on synthetic data and demonstrate its applicability to electrophysiological recordings in the vertebrate retina, allowing us to quantify the effects of noise correlations between neurons and of memory in single neurons.

DOI: [10.1103/PhysRevE.108.024406](https://doi.org/10.1103/PhysRevE.108.024406)**I. INTRODUCTION**

Networks of neurons from sensory systems are characterized by strong correlations that shape their collective response to stimuli [1–6]. These correlations have two sources [1]: *stimulus correlations*, which originate from shared or correlated stimuli that affect the mean activities of different neurons in a concerted way; and *noise correlations*, which stem from network interactions that couple noise across cells. These two sources of correlations impact how well the population encodes stimulus information, and detailed investigations have explored this effect both experimentally [5–9] and theoretically [10–16], showing a wide variety of scenarios in which noise correlations could either hurt or improve information transmission (see Ref. [17] for a recent review).

While geometric arguments about the structure of stimulus and noise correlations can help interpret and evaluate the impact of their interplay on information transmission for pairs or small groups of cells [16,17], specific challenges arise when dealing with large populations of cells. A common way to quantify these effects is by computing the mutual information between the stimulus and the activity of the whole population. However, attempts at quantifying this information are inherently limited by the curse of dimensionality, whereby the size of the state space to be sampled grows exponentially with the system's size. Models based on the principle of maximum entropy have been proposed to build explicit probabilistic models of the collective activity of many neurons, based on mean spike rates and correlation functions [2,18–22]. These distributions map onto known models of statistical mechanics, and can be used to evaluate entropies as well as mutual information.

In this paper, we leverage these techniques from statistical physics to compute the information of experimental spike trains using a small-correlation expansion [23]. We show on synthetic data that this approach outperforms previous approximations of the mutual information and is computationally efficient. The resulting formulas are expressed as simple functions of the experimental observables, yielding an intuitive picture of how correlations affect information encoding in sensory systems beyond the previously discussed “sign rule” [16], which states that noise correlations are beneficial when of opposite sign to stimulus correlations. We apply our formulas to real electrophysiological recordings from the retina, to illustrate how it can be used to quantify the effect of noise correlations between neurons and across time.

**II. SMALL-CORRELATION EXPANSION OF THE MUTUAL INFORMATION**

The collective response of a neural network of size  $N$  can be described by the neuronal activities  $\mathbf{n} = (n_1, \dots, n_N)$ , taking value 0 or 1 depending on whether or not the neuron spikes within a short time window  $\Delta t$  (typically 10–20 ms). In general, because of processing delays and adaptation, the response is a stochastic function  $P(\mathbf{n}|\mathbf{s})$  of the history of the stimulus  $\mathbf{s}$  up to the response. The mutual information  $I(\mathbf{n}, \mathbf{s})$  quantifies the amount of information conveyed by the neural response about the stimulus [24,25]. Since it is expressed as a difference of entropies  $I = H[\mathbf{n}] - \langle H[\mathbf{n}|\mathbf{s}] \rangle_{\mathbf{s}}$ , where  $H[x] = -\sum_x P(x) \ln P(x)$ , its quantification requires good entropy estimators. Direct estimation methods from data exist, and can be applied for relatively small groups of neurons [26]. However, the estimation problem quickly becomes intractable as the number of neurons increases and the size of the response space grows exponentially. To deal with large networks, we

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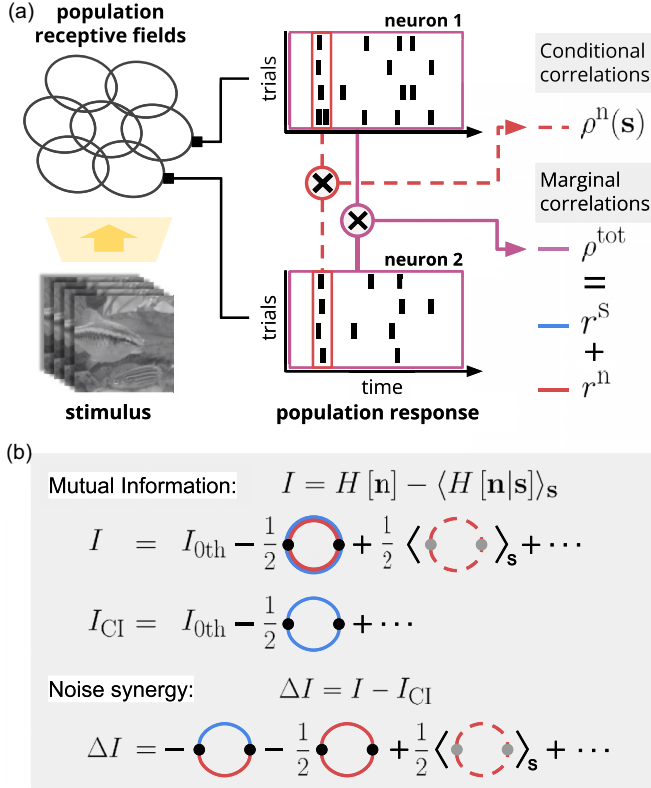


FIG. 1. How correlations affect information. (a) Visual stimuli drive the noisy response of sensory neurons (spikes, represented by vertical ticks).  $\rho_{ij}^N(\mathbf{s})$  is the pairwise Pearson correlation between the activities of cells  $i$  and  $j$  in a short window  $\Delta t$ , conditioned on past stimuli  $\mathbf{s}$ . The total Pearson correlation  $\rho^{\text{tot}}$  can be decomposed into stimulus and noise contributions,  $r^S$  and  $r^N$ . (b) Small-correlation expansion of the mutual information  $I$  and synergy  $\Delta I = I - I_{\text{CI}}$  between stimulus  $\mathbf{s}$  and response  $\mathbf{n}$ , based on Ref. [23].  $I_{\text{CI}}$  is the information in the absence of noise correlations. In the diagrams each line corresponds to a correlation term; double lines are sums of two correlations; multiple lines connecting the same two points are multiplied.

thus developed a method based on a small-correlation expansion of entropies [23], which allows us to express them as analytical functions of the empirical correlations.

We start by assuming that both  $P(\mathbf{n})$  and  $P(\mathbf{n}|\mathbf{s})$  follow the form of maximum entropy models consistent with empirical pairwise covariances and spike rates. Later we will discuss the limitations of this assumption. The total covariance between two cells  $i$  and  $j$  across stimuli,  $C_{ij} \equiv \text{Cov}(n_i, n_j)$ , can be decomposed into two contributions corresponding to the effects of stimulus and noise:  $C_{ij} = C_{ij}^S + \langle C_{ij}^N(\mathbf{s}) \rangle_{\mathbf{s}}$ , with  $C_{ij}^S \equiv \text{Cov}_{\mathbf{s}}(\langle n_i \rangle_{\mathbf{s}}, \langle n_j \rangle_{\mathbf{s}})$ ,  $C_{ij}^N(\mathbf{s}) \equiv \text{Cov}(n_i, n_j | \mathbf{s})$ , which can be computed from the response to repeated presentations of the same stimulus. Likewise, the Pearson correlation coefficient  $\rho_{ij}^{\text{tot}} \equiv C_{ij} / \sqrt{C_{ii} C_{jj}}$  can also be decomposed into stimulus- and noise-induced contributions:  $\rho_{ij}^{\text{tot}} = r_{ij}^S + r_{ij}^N$  [Fig. 1(a)], with  $r_{ij}^S \equiv C_{ij}^S / \sqrt{C_{ii}^S C_{jj}^S}$  and  $r_{ij}^N \equiv C_{ij}^N(\mathbf{s}) / \sqrt{C_{ii}^N(\mathbf{s}) C_{jj}^N(\mathbf{s})}$ . Note however that these two terms are not proper correlation coefficients because of the normalization. Stimulus correlations may instead be quantified by  $\rho_{ij}^S \equiv C_{ij}^S / \sqrt{C_{ii}^S C_{jj}^S}$ , and noise

correlations in a stimulus-dependent manner through  $\rho_{ij}^N(\mathbf{s}) \equiv C_{ij}^N(\mathbf{s}) / \sqrt{C_{ii}^N(\mathbf{s}) C_{jj}^N(\mathbf{s})}$ .

Following Ref. [23], we expand the entropy of the maximum entropy models—and thus the mutual information—at small values of the covariance parameter  $[C_{ij}]$  or  $C_{ij}^N(\mathbf{s})$ ,  $I = I_{0\text{th}} + I_{1\text{st}} + I_{2\text{nd}} + \dots$  [see Supplemental Material (SM) [27]]. The leading order of this expansion is the sum of the information carried by each neuron:  $I_{0\text{th}} = \sum_i [H[n_i] - \langle H[n_i | \mathbf{s}] \rangle_{\mathbf{s}}]$ . The first-order term vanishes, while the second one reads [see Fig. 1(b) and SM [27]]

$$I_{2\text{nd}} = -\frac{1}{2} \sum_{i < j} (\rho_{ij}^{\text{tot}2} - \langle \rho_{ij}^N(\mathbf{s})^2 \rangle_{\mathbf{s}}). \quad (1)$$

We can compute higher-order terms using Feynman diagrams rules [28], but they quickly become unwieldy. However, some of these terms can be resummed to yield a better approximation of the mutual information than (1) in terms of first- and second-order moments [23] (see SM [27]):

$$I \approx I_{0\text{th}} + I_{\text{pairs}} + I_G - I_{\text{dbl}}. \quad (2)$$

$I_{\text{pairs}}$  is the sum of the mutual information gains (with respect to single cells) of each pair  $(i, j)$  calculated one by one, ignoring the rest of the network.  $I_G$  is the mutual information gain computed through a mean-field (or *loop*) approximation [23,29], which is equivalent to assuming that all fluctuations (stimulus and noise) are Gaussian,

$$I_G = \frac{1}{2} \log(|\rho^{\text{tot}}|) - \frac{1}{2} \langle \ln(|\rho^N(\mathbf{s})|) \rangle_{\mathbf{s}}, \quad (3)$$

where  $|\rho|$  denotes the determinant of the correlation matrix. Finally  $I_{\text{dbl}}$  corrects for terms that are double counted in  $I_{\text{pairs}}$  and  $I_G$ .

### III. NOISE SYNERGY

These expansions can be used to investigate the impact of noise correlations on information transmission. We define the *noise synergy*,  $\Delta I \equiv I - I_{\text{CI}}$ , as the gain in information relative to the conditionally independent case [Fig. 1(b), bottom line].  $I_{\text{CI}}$  can be computed in practice by shuffling the response of individual neurons across repetitions of the same stimulus, which preserves stimulus correlations but destroys noise correlations. At second order we obtain (see SM [27])

$$\Delta I \approx \sum_{i < j} \left[ -r_{i,j}^N r_{i,j}^S + \frac{1}{2} (\langle \rho_{i,j}^N(\mathbf{s})^2 \rangle_{\mathbf{s}} - r_{i,j}^N{}^2) \right]. \quad (4)$$

This expression shows how noise synergy depends on noise correlations through  $r^N$  and  $\rho^N$ . The first term is positive when noise and stimulus correlations have opposite signs. This effect is known in the literature as the *sign rule* [16] and can be interpreted in terms of the whitening of the output power spectrum: It is beneficial for the network to “cancel out” input correlations by adding noise correlations of opposite sign, in order to approach a uniformly distributed output, thereby increasing output entropy and information. The second term of (4), which is of second order in the noise correlation parameter, can be either positive or negative in general. However, in the particular case of noise correlations independent of the

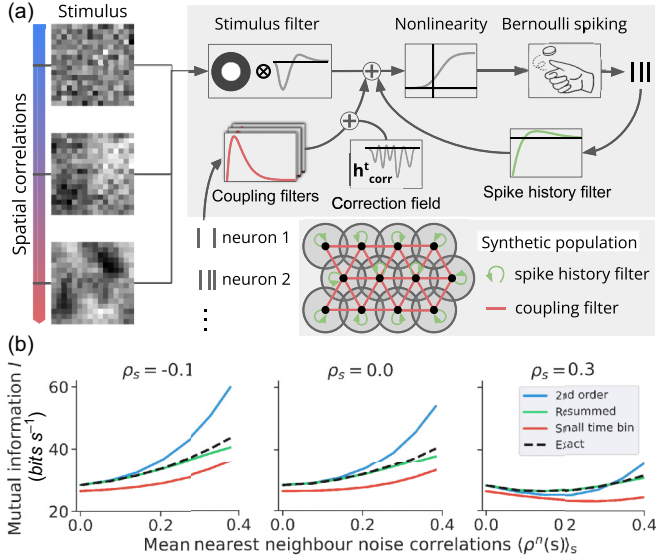


FIG. 2. (a) A spatially correlated random stimulus activates a network of 12 neurons according to a generalized linear model defined by stimulus, coupling, and spike-history filters. (b) Exact, second order (1), resummed (2), and small time bin expansion [12] of the mutual information for various strengths of the noise and stimulus correlations (averaged over all pairs of neighbors). Note that since mutual information is a difference of entropies, the error may be a nonmonotonic function of  $\rho^n$  and  $\rho^s$ .

stimulus,  $\rho^n(\mathbf{s}) = \rho^n$ , the Cauchy-Schwarz inequality guarantees its non-negativity (see SM [27] for a proof). This implies that noise correlations may be beneficial even when the sign rule is violated and the noise correlations are constant (see the last section the SM [27]). Noise synergy can also be computed using the resummed entropies of (2). The formulas are slightly more involved and are reported in the SM [27].

#### IV. NUMERICAL TEST ON SYNTHETIC DATA

To test our approximations (1) and (2), we built a generalized linear model to mimic the response of a small population of 12 retinal neurons with nearest-neighbor interactions [Fig. 2(a)] for which mutual information could be estimated exactly. The stimulus is modeled as a random Gaussian field sampled at 100 Hz, with varying spatial correlations, allowing us to tune the strength of stimulus correlations (see SM [27]). The stimulus is convolved with a linear filter consisting of a difference-of-Gaussians receptive field with a biphasic temporal kernel [30] (see SM [27]). The mean spike rate is controlled by the result of this convolution, to which the effect of its own spiking history is added, through a nonlinear function. In addition, the past activities of its neighbors control the stochastic part of firing, through coupling filters (the mean effect of which is subtracted from the average rate—see SM [27]). This strategy allows us to tune noise correlations while keeping the stimulus correlation constant. Importantly, this model is mathematically inconsistent with the maximum entropy assumption. It thus allows us to test for both the appropriateness of the maximum entropy approximation in

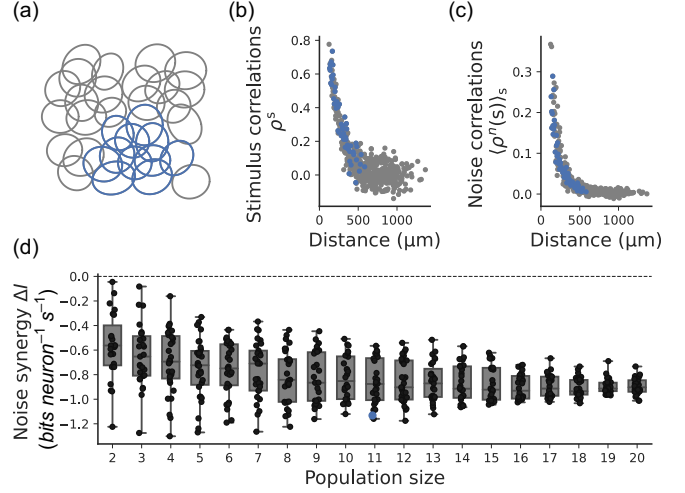


FIG. 3. Application on retinal population response to visual stimulation. (a) A mosaic of a population of off alpha cells in the rat retina. (b) Stimulus correlation ( $\rho_{ij}^s$ ) plotted against the distance between pair of cells stimulated with a white-noise movie. (c) Same as (b) but for noise correlations ( $\rho_{ij}^n(\mathbf{s})_s$ ). (d) Noise synergy for subset populations of nearby cells. Each box plot corresponds to the noise synergy of many subgroups of ganglion cells. Only nearby cells are considered.

the context of a realistic spiking model, and the accuracy of the small-correlation expansion.

After binning at 15 ms, we computed the exact mutual information between the stimulus and response using exhaustive numerical simulations, and compared it with the predictions of our approximations, as well as the state-of-the-art small time bin expansion of Ref. [12] [Fig. 2(b)]. We observed an excellent agreement between numerical calculations and analytical expressions, in particular for the resummed mutual information (2), in contrast to the small time bin approximation, which yields inaccurate results even in the absence of noise correlations. Although less accurate, the second-order approximation (1) still provided fair estimates for a wide range of correlation strengths. We further checked that the error did not blow up with the system's size, by analyzing networks subsampled from the full population with sizes 3–12 for various values of the stimulus and noise correlations (Fig. S1 [27]).

#### V. APPLICATION TO RETINAL DATA

We applied our formulas to *ex vivo* multielectrode array recordings of rat retinal ganglion cells in response to black and white checkerboard stimulation [31,32]. The receptive fields of the cells have a mosaic structure [Fig. 3(a)], so that neuronal responses show strong stimulus correlations between neighbors, which decay with the distance between the receptive field centers [Fig. 3(b)]. Due to network effects [1], nearby cells also show strong noise correlations that decay with distance on a similar length scale [Fig. 3(c)].

We computed the noise synergy using our resummed approximation (2) for many subgroups of nearby cells of different sizes [Fig. 3(d)]. In this case it is not possible to estimate mutual information exactly because of limited data,

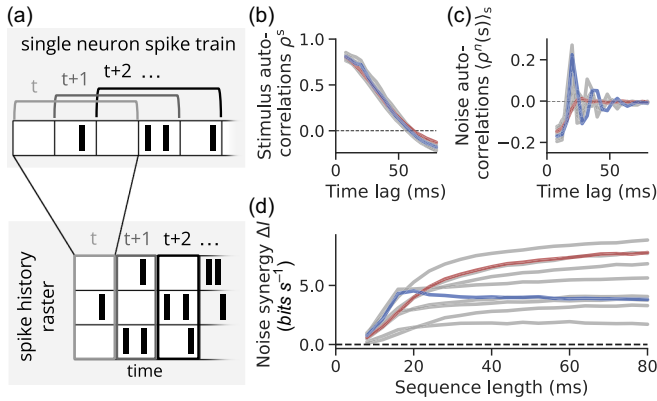


FIG. 4. Application on retinal temporal response to visual stimulation. (a) We build a pseudopopulation of neurons to describe the spiking history of single neurons. (b) Stimulus autocorrelations for different cells responding to a white-noise stimulation. Highlighted lines correspond to two example cells. (c) Same as (b) but for noise autocorrelations. (d) Noise synergy for different cells plotted against increasing temporal integration length.

making it a good test case for the usefulness of our analytical formulas. Spike trains were binned at 15 ms and, to correct for the bias stemming from noise in estimating correlations, we subtracted the value obtained after shuffling individual cell activities across repetitions. We observe that noise correlations impede information transmission, by the order of 1 bit per neuron per second, for a total information of around 10 bits per neuron per second. It should be stressed however that this result is specific to the white-noise stimulus statistics considered here, and may not be a general feature of retinal processing, as other stimulus statistics would change both the nature of stimulus correlations and the input-output relationship as the network adapts.

We also used our method to study the effect of spiking memory in single neurons, by treating the spike activity of the same neuron in  $N$  consecutive 4-ms time bins as our activity vector  $(n_1, \dots, n_N)$  [treating time bins as we treated individual neurons previously—see Fig. 4(a)]. Stimulus temporal autocorrelations are positive for about 50 ms [Fig. 4(b)], then become negative and go to zero for longer times (not shown). Noise temporal correlations are driven by refractoriness, which suppresses activity immediately following a spike, and by burstiness, which induces rippling effects up to 50 ms [Fig. 4(c)]. We find that these correlations improve information transmission by up to 8 bits per second [Fig. 4(d)], almost doubling it for some cells. This suggests that information is encoded not just in the average spike rate, but also through the control of interspike timing, consistent with previous findings [33–36].

## VI. DISCUSSION

Despite being based on a small-correlation expansion, our analytical predictions, especially (2), work well even in the presence of strong correlations, which are ubiquitous in neuroscience [1,2,37]. We showed how our results can be applied to same-time correlations between neurons, or to neu-

ron autocorrelations, and they can readily be used on general spatial-temporal correlations.

Our work shares some connections with previous efforts to estimate or interpret information in population codes [12–14,16,17,38,39]. Reference [13] proposes decompositions of the mutual information with different interpretations, but does not provide ways to estimate it. References [16,38,39] are mostly based on the Fisher information, which in some limit can be related to the mutual information. While the first term of our simpler expression (4) recovers one of their main results—the so-called sign rule—second- and higher-order terms in the noise correlation parameter provide important corrections when correlations are high, as can be seen from deviations from the initial slope in Fig. 2(b). In Ref. [12] the authors developed a small time bin expansion of the mutual information. Expanding their results for small correlations (and further assuming Poisson distributed spike counts—see SM [27]) gives back our second-order expression (1). Our method however does not need to assume small time bins, and still works well for large correlations. Reference [14] provides an estimate of the mutual information when the neuronal responses are correlated but have only small fluctuations around a large mean activity, which is not appropriate for small time bins or for low spike rates as in the retina.

Our results are based on the small-correlation expansion developed in Ref. [23]. In order to apply this theoretical tool, we assumed that both the stimulus-conditioned and the marginal responses follow a pairwise maximum entropy distribution. These models are characterized by many unknown parameters that in principle need to be inferred from data. However, the final expressions for the mutual information contain only quantities that can be directly estimated from data, without needing any inference. This makes our approximations ready and easy to use, without requiring much computational effort. We showed that it works well even when the data were generated with a very different model. Maximum entropy distributions are actually a series of approximations which, just as Taylor expansions, can be refined by adding higher-order correlations. A future direction could be to compute corrective terms to the mutual information corresponding to third- and higher-order correlation functions, rather than just pairwise correlations as we did in this work. At the same time, the pairwise approximation has proven very accurate for both marginal [2,19,22,40,41] and conditional [42–45] responses of populations of neurons, and is only expected to break down for very large densely correlated populations [46]. We thus expect our results to be applicable to a wide array of neuronal contexts.

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