

Synchronisation, binding and the role of correlated firing in fast information transmission

Simon R. Schultz¹, Huw D. R. Golledge², and Stefano Panzeri²

¹ Howard Hughes Medical Institute & Center for Neural Science, New York University, New York, NY 10003, USA

² Department of Psychology, Ridley Building,
University of Newcastle upon Tyne, Newcastle NE1 7RU, UK
stefano.panzeri@ncl.ac.uk
<http://www.staff.ncl.ac.uk/stefano.panzeri/>

Abstract. Does synchronization between action potentials from different neurons in the visual system play a substantial role in solving the binding problem? The binding problem can be studied quantitatively in the broader framework of the information contained in neural spike trains about some external correlate, which in this case is object configurations in the visual field. We approach this problem by using a mathematical formalism that quantifies the impact of correlated firing in short time scales. Using a power series expansion, the mutual information an ensemble of neurons conveys about external stimuli is broken down into firing rate and correlation components. This leads to a new quantification procedure directly applicable to simultaneous multiple neuron recordings. It theoretically constrains the neural code, showing that correlations contribute less significantly than firing rates to rapid information processing. By using this approach to study the limits upon the amount of information that an ideal observer is able to extract from a synchrony code, it may be possible to determine whether the available amount of information is sufficient to support computational processes such as feature binding.

1 Introduction

Does synchronization (or more generally temporal correlations) between action potentials from different cells in the central visual system play a substantial role in solving crucial computational problems, such as binding of visual features or figure/ground segmentation? One theory suggests that synchrony between members of neuronal assemblies is the mechanism used by the cerebral cortex for associating the features of a coherent single object [1].

Although several groups have reported compelling experimental evidence from the visual system in support of this theory (for a review see [2]), the role played by synchronous firing in visual feature binding is still highly controversial [3–6], and far from being understood. In our view, it is possible that one or more methodological factors contribute to the continuing uncertainty about this issue.

In fact, almost all the reported neurophysiological evidence in favor or against the temporal binding hypothesis relies upon the assessment of the significance of peaks in cross-correlograms (CCG, [7]) and of their modulation with respect to stimulus configuration. While investigating stimulus modulation of peaks (or of other features) of CCGs can clearly bear some evidence on the role of synchrony in binding, it does not address the crucial issue of *how much* synchrony tells the brain about the configuration of objects in the visual field. This question is particularly important as it is well known that firing rates of individual cells are commonly related to features of the sensory world [8], and even to perceptual judgements (see e.g. [9, 10]). Firing rate modulations can potentially contribute to association of features through the use of population codes, or also in other ways[3]. Therefore the specific contribution of synchrony (or in general of correlations between firing of cells) as a coding mechanism for binding should be assessed against the contribution of independent firing rate modulation to the encoding of object configurations in the visual field.

To address these issues, a pure analysis of CCG characteristics is insufficient. In addition to CCG quantification, information theory can be used to address the specific contribution of synchronized or correlated firing to visual feature binding, and to compare the contribution of synchrony against that of firing rates. In fact, Information theory [11] allows one to take the point of view of an ideal observer trying to reconstruct the stimulus configuration just based on the observation of the activity of neuronal population, and to determine how much the presence of correlated firing helps in identifying the stimulus.

In this paper we present and develop a rigorous information theoretic framework to investigate the role of temporal correlations between spikes. We first discuss how information theory could overcome the limitations of the pure CCG analysis. We then present a mathematical formalism that allows us to divide the information into components which represent the information encoding mechanisms used by neuronal populations – i.e. it determines how many bits of information were present in the firing rates, how many in coincident firing by pairs of neurons, etc., with all of these adding up to the overall available information. The mathematical approach developed here is valid for timescales which are shorter than or of the order of a typical interval between spike emissions, and it makes use of a Taylor series approximation to the information, keeping terms up to the second order in the time window length. This approximation is not merely mathematically convenient; short timescales are likely to be of direct relevance to information processing by the brain, as there is substantial evidence that much sensory information is transmitted by neuronal activity in very short periods of time [12–14]. Therefore the mathematical analysis is relevant to the study of the computations underlying perceptual processes. In particular, it enables the quantitative study of the rapidly appearing correlational assemblies that have been suggested to underlie feature binding and figure/ground segmentation.

2 Problems with conventional Cross-Correlogram analysis

The CCG represents a histogram of the probability of a spike from one neuron at a given time relative to a reference spike of a second neuron [7]. Whilst cross-correlation is capable of identifying synchrony between neurons, several aspects of the analysis of CCGs present problems or are incomplete. First, CCG analysis itself does not provide a criterion to choose which periods of a response epoch should be analysed. Since, in many cases, moving stimuli are employed, the response varies with time and it may be that correlations are present or are stimulus modulated for only a short part of the response [15]. This short period is not necessarily related simply to the response peak, although some studies have analysed only the period in which the peak of the response is made to a moving stimulus [16]. Second, the width of the time window over which correlations should be assessed is arbitrary. CCG analysis does not entirely address over which time scales correlations contribute most information about object configuration. Using long windows (e.g. much larger than the width of CCG peaks) may “wash out” transient correlations. Narrow windows centered upon the PSTH peak may ignore the part of the responses that contains most of the information about the stimuli (e.g. in firing rate modulations). Third, if the window length used to assess correlations is varied between stimulus conditions (e.g [16]) then an undesirable extra source of variation is introduced when the stimulus conditions are compared. Information theory can mitigate some of these problems by providing a criterion for the selection of time windows, by identifying the windows in which most information is actually transmitted.

Many previous studies also differ in the methods used to quantify the temporal structure in CCGs. Some studies rely on the fitting of a damped sine wave to the CCG (e.g. [5, 17]). Other methods quantify solely the likelihood that the peak in the CCG did not arise by chance [18]. Analysis of the significance of a peak, or of structure in the CCG must be made in relation to the flanks of the CCG. What length of flank is chosen will affect the significance of peaks. However, downstream neurons are unlikely to be able to compare the likelihoods of spikes occurring at lags of tens of milliseconds against the likelihood of simultaneous spikes.

The parameters of a CCG do not themselves quantify the informational contribution of synchronous firing. Conventional CCG analysis techniques attempt to assess correlation in a manner independent of the firing rate in order to disambiguate synchronous modulations from firing rate variations. It is unlikely, though, that any downstream detector of the synchronous discharge of neurons would be capable of assessing the significance of correlation independent of the firing rate. It is more likely that it would make use of the actual number of coincident spikes available in its integration time window. Therefore cross-correlation peaks and firing rate modulation are probably intrinsically linked in transmitting information to downstream neurons, and an analysis of the functional role of synchrony should be able to take this into account. Most studies that appear to show stimulus-dependent synchrony have employed relatively strongly

stimulated cells. An important prediction of the temporal correlation hypothesis is that synchrony should encompass the responses of sub-optimally stimulated neurons [19]. A thorough test of this hypothesis requires the study of cells that fire very few spikes. The number of spikes included in the calculation of a CCG of course affects the precision with which correlations can be detected [20]. Variations in the number of evoked spikes, rather than a true change in correlation between the neurons, could thus affect comparisons between optimal and sub-optimal stimuli. While analysing cells firing at low rates may be a challenge for CCG analysis, it is tractable for analyses developed from information theory, as we shall see in Section 4.

3 Information Theory and Neuronal Responses

We believe that the methodological ambiguities that attend studies purely based on quantification of spike train correlograms can be greatly reduced by employing in addition methods based upon information theory [11], as we describe in this Section.

Information theory [11] measures the statistical significance of how neuronal responses co-vary with the different stimuli presented at the sensory periphery. Therefore it determines how much information neuronal responses carry about the particular set of stimuli presented during an experiment. Unlike other simpler measures, like those of signal detection theory, which take into account only the mean response and its standard deviation, information theory allows one to consider the role of the entire probability distributions. A measure of information thus requires sampling experimentally the probabilities $P(r|s)$ of a neuronal population response r to all stimuli s in the set, as well as designing the experimental frequencies of presentation $P(s)$ of each stimulus. The information measure is performed by computing the distance between the joint stimulus-response probabilities $P(r, s) = P(r|s)P(s)$ and the product of the two probabilities $P(r)P(s)$, ($P(r)$ being the unconditional response probability) as follows:

$$I(S; R) = \sum_s \sum_r P(s, r) \log_2 \frac{P(s, r)}{P(s)P(r)} \quad (1)$$

If there is a statistical relationship between stimuli and responses (i.e. if $P(r, s)$ is dissimilar from $P(r)P(s)$), our knowledge about what stimulus was presented increases after the observation of one neuronal spike train. Eq. (1) quantifies this fact. The stronger the statistical relationship between stimuli and responses, the higher is the information value. Eq. (1) thus quantifies how well an ideal observer could discriminate between different stimulus conditions, based on a single response trial. There are several advantages in using information theory to quantify how reliably the activity of a set of neurons encodes the events in the sensory periphery [21, 22]. First, information theory puts the performance of neuronal responses on a scale defined at the ratio level of measurement. For example, an increase of 30% of on the peak height of a cross-correlogram does not tell us how this relates to synchrony-based stimulus discrimination, but values of

information carried by synchronous firing have a precise meaning. Information theory measures the reduction of uncertainty about the stimulus following the observation of a neuronal response on a logarithmic scale. One bit of information corresponds to a reduction by a factor of two in the stimulus uncertainty. A second advantage of information theory in this context is that it does not require any specific assumption about the distance between responses or the stationarity of the processes, and it can therefore lead to objective assessments of some of the hypotheses.

In the above discussion we have mentioned that we are calculating information ‘about a stimulus’. In fact, more generally it can be information ‘about’ any quantifiable external correlate, but we shall continue to use the word stimulus in an extended sense. If we were studying information about the orientation of a grating, we would define our stimulus to be which of a number of different orientations the grating appeared at on any given experimental trial. If we wish to study problems such as binding or figure-ground segregation within this framework, we have to specify our stimulus description accordingly. An illustration of this is shown in the scene of Fig. 1, which contains two objects in front of a background. Also shown are a number of receptive fields, which are taken to be those of cells from which we are simultaneously recording the activity (‘spike trains’). We can define our stimulus, or external correlate, as a multidimensional variable representing the object to which each receptive field is associated. The dimensionality of our stimulus is in this case the number of cells from which we are recording at once. By quantifying the information contained in the spike trains about this variable, and breaking it down into individual components reflecting firing rates and correlations (or synchronisation), we can determine the aspects of the spike train which best encode the figure-ground (or object-object-ground) segregation. Furthermore, by examining how this relationship scales with the stimulus dimensionality (number of receptive fields recorded from), it may be possible to determine whether enough information is present in correlations to support binding in perceptually realistic environments.

It is worth noticing that information values are always relative to the stimulus set used, and that testing a neuron with different stimuli may lead to rather different information values. This has some interesting implications. On the one hand, it allows us to characterise neuronal selectivity by searching for a stimulus set that maximises the neuronal information transfer, a more rational characterisation strategy than searching for stimuli eliciting sustained responses. On the other hand, the intrinsic dependency of mutual information values on the nature of stimulus set allows us to test whether different encoding strategies are used by visual cortical neurons when dealing with external correlates of a different nature. The last property is of interest because one of the predictions of the binding-by-synchrony hypothesis is that synchrony is particularly important when stimulus configurations requiring some kind of associations are included, and less important in other situations. Information theory thus provides a natural framework to test this theory.

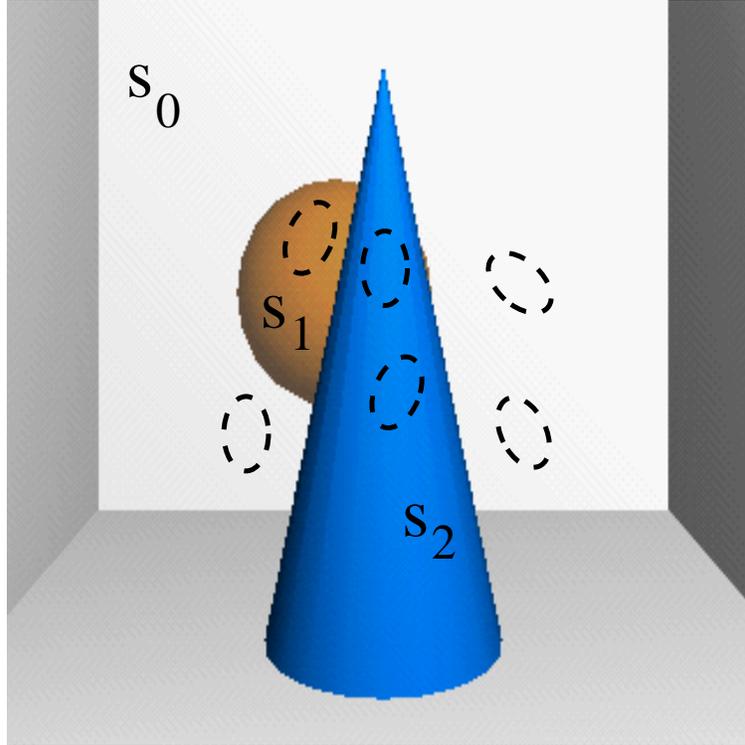


Fig. 1. An illustrative segregation problem in which there are two objects in front of a background. The background is labeled by s_0 , and the objects by s_1 and s_2 respectively. The dashed ellipses represent the receptive fields of visual cortical cells which we are recording the responses of simultaneously. This situation can be examined in the framework of information theory by considering the 'stimulus' to be a multidimensional variable indicating which object (s_0 , s_1 or s_2) is associated with each receptive field. The problem is thus to determine which response characteristics are most informative about the visual configuration.

4 Series expansion of the mutual information

Although information theory is, as explained, a natural framework to address the role of correlated firing on e.g. binding of visual features, some work is needed to separate out of the total information contained in a population response r into components, each reflecting the specific contribution of an encoding mechanism. We perform this separation in the limit in which the relevant window for information encoding is short enough that the population typically emits few action potentials in response to a stimulus. As discussed in the introduction and in [23], there is evidence that this is a relevant limit for studying the computations underlying perception, as cortical areas in several cases perform their computations within a time frame which is shorter than one typical interspike interval [13, 14].

We examine a period of time of duration t , in which a stimulus s is present. The neuronal population response r during this time is taken to be described by the number of spikes fired by each cell¹ in the window t . We study the information carried by the responses of a neuronal population about which stimulus is presented. It can be approximated by a power series

$$I(t) = t I_t + \frac{1}{2} t^2 I_{tt} + O(t^3). \quad (2)$$

The problem is thus to compute the first two time derivatives of the information, I_t and I_{tt} , which are all that survive at short timescales.

Two kinds of correlations influence the information. These are the “signal” (mean response to each stimulus) correlation and the “noise” (variability from the mean across different trials with the same stimulus) correlation between cells. In the short timescale limit the noise correlation can be quantified as

$$\gamma_{ij}(s) = \frac{\overline{n_i(s)n_j(s)}}{(\overline{n_i(s)}\overline{n_j(s)})} - 1, \quad (i \neq j) \quad \gamma_{ii}(s) = \frac{(\overline{n_i(s)^2} - \overline{n_i(s)})}{\overline{n_i(s)}^2} - 1, \quad (3)$$

where $n_i(s)$ is the number of spikes emitted by cell i in a given trial in response to stimulus s , and the bar denotes an average across experimental trials to the same stimulus. The signal correlation can be measured as

$$\nu_{ij} = \frac{\langle \bar{r}_i(s)\bar{r}_j(s) \rangle_s}{\langle \bar{r}_i(s) \rangle_s \langle \bar{r}_j(s) \rangle_s} - 1, \quad (4)$$

where $\bar{r}_i(s)$ is the mean firing rate of cell i to stimulus s , and $\langle \dots \rangle_s$ denotes an average across stimuli. These are scaled correlation densities ranging from -1 to infinity, which remain finite as $t \rightarrow 0$. Positive values of the correlation coefficients indicate positive correlation, and negative values indicate anti-correlation.

Under the assumption that the probabilities of neuronal firing conditional upon the firing of other neurons are non-divergent, the t expansion of response

¹ The additional temporal information contained in the spike times is studied in [24]

probabilities becomes an expansion in the total number of spikes emitted by the population in response to a stimulus. The probabilities of up to two spikes being emitted are calculated and inserted into the expression for information. This yields for the information derivatives

$$\begin{aligned}
I_t &= \sum_{i=1}^C \left\langle \bar{r}_i(s) \log_2 \frac{\bar{r}_i(s)}{\langle \bar{r}_i(s') \rangle_{s'}} \right\rangle_s \quad (5) \\
I_{tt} &= \frac{1}{\ln 2} \sum_{i=1}^C \sum_{j=1}^C \langle \bar{r}_i(s) \rangle_s \langle \bar{r}_j(s) \rangle_s \left[\nu_{ij} + (1 + \nu_{ij}) \ln \left(\frac{1}{1 + \nu_{ij}} \right) \right] \\
&\quad + \sum_{i=1}^C \sum_{j=1}^C \left[\langle \bar{r}_i(s) \bar{r}_j(s) \gamma_{ij}(s) \rangle_s \right] \log_2 \left(\frac{1}{1 + \nu_{ij}} \right) \\
&\quad + \sum_{i=1}^C \sum_{j=1}^C \left\langle \bar{r}_i(s) \bar{r}_j(s) (1 + \gamma_{ij}(s)) \log_2 \left[\frac{(1 + \gamma_{ij}(s)) \langle \bar{r}_i(s') \bar{r}_j(s') \rangle_{s'}}{\langle \bar{r}_i(s') \bar{r}_j(s') (1 + \gamma_{ij}(s')) \rangle_{s'}} \right] \right\rangle_s. \quad (6)
\end{aligned}$$

The first of these terms is all that survives if there is no noise correlation at all. Thus the *rate component* of the information is given by the sum of I_t (which is always greater than or equal to zero) and of the first term of I_{tt} (which is instead always less than or equal to zero). The second term is non-zero if there is some correlation in the variance to a given stimulus, even if it is independent of which stimulus is present; this term thus represents the contribution of *stimulus-independent noise correlation* to the information. The third component of I_{tt} is non-negative, and it represents the contribution of *stimulus-modulated noise correlation*, as it becomes non-zero only for stimulus-dependent correlations. We refer to these last two terms of I_{tt} together as the correlational components of the information.

In any practical measurement of these formulae, estimates of finite sampling bias must be subtracted from the individual components. Analytical expressions for the bias of each component are derived in the online appendix of [23].

5 Correlations and fast information processing

The results reported above for the information derivatives show that the instantaneous rate of information transmission (related to the leading order contribution to the information) depends only upon the firing rates. Correlations contribute to information transmission, but they play only a second order role. This has interesting implications for the neural code, that we develop further here.

It was argued [25] that, since the response of cortical neurons is so variable, rapid information transmission must imply redundancy (i.e. transmitting several copies of the same message). In other words, it should be necessary to average away the large observed variability of individual interspike intervals s by replicating the signal through many similar neurons in order to ensure reliability in short

times. Our result, eq. (6), shows that to have a high information rate, it is enough that each cell conveys some information about the stimuli (because the rate of the information transmitted by the population is the sum of all single cell contributions); therefore we conclude that it is not necessary to transmit many copies of the same signal to ensure rapidity.

Also, since firing rates convey the main component of information, correlations are likely to play a minor role in timescales of the order of 20-50 ms, in which much information is transmitted in the cortex. As an example, Fig. 2 shows the information conveyed by a population of simulated Integrate and Fire neurons, which share a large proportion (30%) of their afferents (see [23] for details of the neuronal model used). It can be seen that, despite the strong correlations between the cells in the ensemble correlations play only a minor role with respect to firing rates.

To model a situation where stimulus dependent correlations conveyed information, we generated simulated data using the Integrate-and-Fire model for another quintuplet of cells which had a stimulus dependent fraction of common input. This might correspond to a situation where transiently participate in different neuronal assemblies, depending on stimulus condition. This is therefore a case that might be found if the binding-by-synchrony theory is correct. There were ten stimuli in the sample. The spike emission rate was constant (20 Hz) across stimuli. One of the stimuli resulted in independent input to each of the model cell, whereas each of the other nine stimuli resulted in an increase (to 90%) in the amount of shared input between one pair of cells. The pair was chosen at random from the ensemble such that each stimulus resulted in a different pair being correlated. The change in responses of one such pair of cells to changes in the amount of common input is shown in Fig. 3a. The upper panel of Fig. 3a shows the fraction of shared connections as a function of time; the central and lower panel of Fig. 3a show the resulting membrane potentials and spike trains from the pair of neurons. This cross-correlation is also evident in the cross-correlograms shown in Fig. 3b. The results for the information are given in Fig. 3c: all terms but the third of I_{tt} are essentially zero, and information transmission is in this case almost entirely due to stimulus-dependent correlations. This shows that the short time window series expansion pursued here is able to pick up the right encoding mechanisms used by the set of cells. Therefore it is a reliable method for quantifying the information carried by the correlation of firing of small populations of cells recorded from the central nervous system *in vivo*. Another point that is worth observing is that Fig. 3c also shows that the total amount of information that could be conveyed, even with this much shared input, was modest in comparison to that conveyed by rates dependent on the stimuli, at the same mean firing rate. This again illustrates that correlations typically convey less information than what can be normally achieved by rate modulations only. Therefore they are likely to be a secondary coding mechanism when information is processed in time scales of the order of one interspike interval.

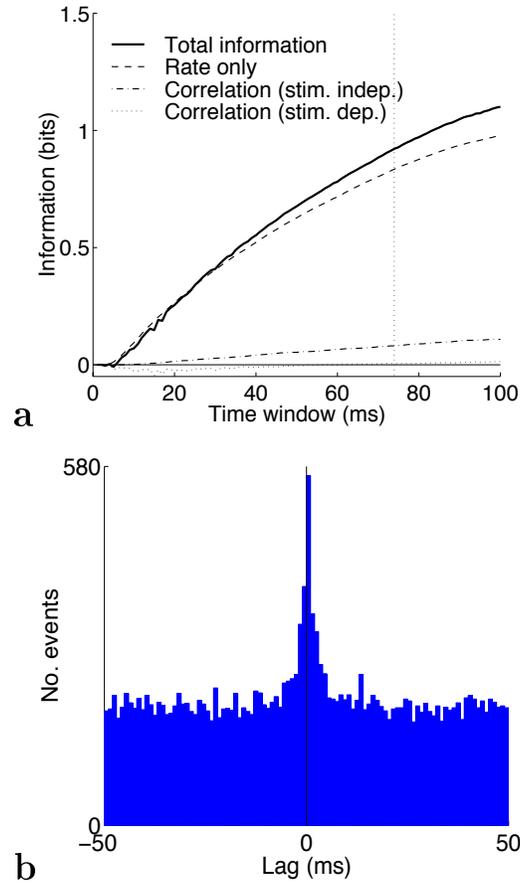


Fig. 2. (a) The short-timescale information components for a set of 5 simulated neurons sharing 30% of their inputs. (b) A typical example of the cross-correlogram between two of the simulated neurons. Despite of the strong correlation between neurons, the impact of the cross correlations on information transmission is minimal.

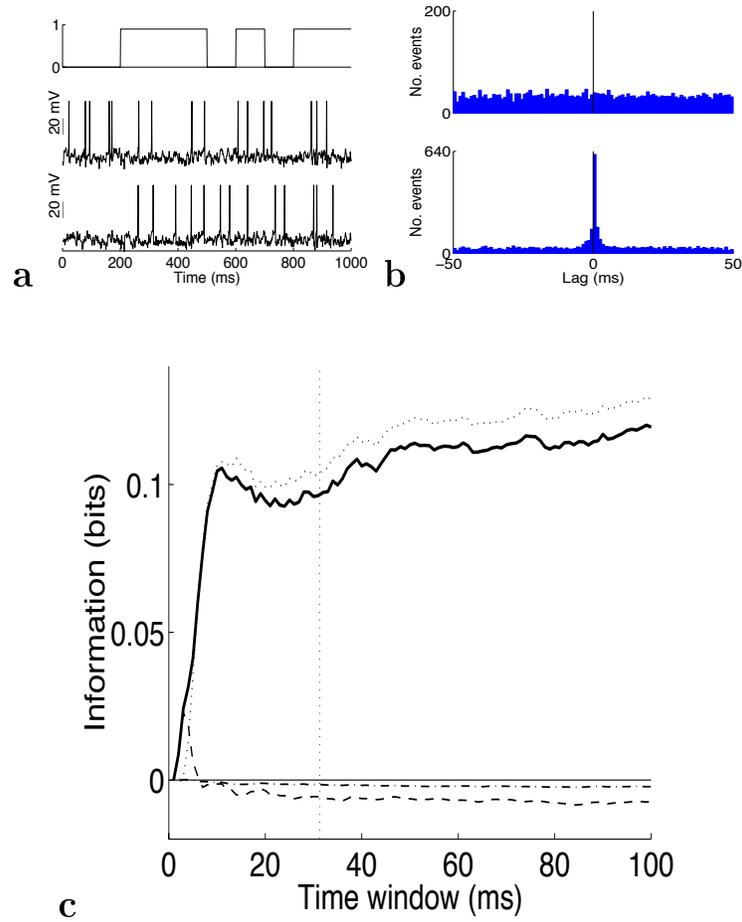


Fig. 3. A situation in which the stimulus dependent correlational component dominates: with a fixed mean firing rate, two of the five simulated cells (chosen randomly for that stimulus) increase their correlation by increasing the number of shared connections while the other two remained randomly correlated. The effect of this on cell spiking activity is shown in (a): upper panel shows the fraction of shared connections, while central and lower panels of (a) show the membrane potential and spike emission of the simulated cells. (b) shows the cross-correlograms corresponding to the low and high correlation states. The result of this is seen in (c): information due to correlations, although modest in magnitude, in this demonstration dominates the total information.

6 Optimality of correlational encoding

In the preceding sections we have shown that the correlational component is only second order in the short time limit, essentially because the probability of emission of pairs of spikes, and the reliability of this process, are much smaller than the corresponding quantities for single spikes. For this reason, one can expect a correlational code to carry appreciable information only when it is *efficient*, i.e. when each correlated spike pair carries as much information as possible.

In this section we investigate the statistical conditions that have to be satisfied by a correlational code in order to be efficient in the short time limit. If the population code is purely correlational (i.e. the firing rates are not modulated at all by the stimuli), then it is possible to show that the mean information per coincidence Ψ carried by a pair of cells (obtained dividing the total information by the mean number of observed coincidences) is bounded only by the sparseness of the distribution of coincident firing across stimuli α :

$$0 \leq \Psi \leq \log_2(1/\alpha) \quad (7)$$

The maximal (most efficient) value of information per coincidence $\Psi_{\max} = \log_2(1/\alpha)$ is reached by a binary distribution of correlations across stimuli, with a fraction of stimuli α eliciting positively correlated firing, and the other $1 - \alpha$ stimuli eliciting fully anti-correlated firing (i.e. coincident firing is never observed when presenting one of the latter stimuli). Nearly uniform, or strongly unimodal distributions of correlations across stimuli would give poor information, $\Psi \sim 0$.

By analyzing Eq. (7), it is easy to realize that there are two statistical requirements that are necessary to achieve high values of information per coincidence. The first one is that the correlational code should be *em sparse* (i.e. the fraction of stimuli leading to a “high correlation state” should be low). The sparser the code, the more information per coincidence can be transmitted. The second important factor for fast and efficient transmission of correlational information, is that the low correlational state must be strongly *anti-correlated* in order to achieve an information per coincidence close to its maximum $\log_2(1/\alpha)$. In fact correlations in short times have fluctuations that may be big compared with their mean value, and therefore for any observer it is difficult to understand in less than one ISI if an observed coincidence is due to chance or neuronal interaction. This is why low correlational states with no coincidences are so helpful in transmitting information. We note here that states of nearly complete anticorrelation have never been observed in the brain. Therefore the “low state correlational state” of a realistic correlational assembly should be the “random correlation state” (i.e. the state in which the number of coincident spikes is on average that expected by chance).

We have quantified the reduction in the information per coincidence, compared to its maximum Ψ_{\max} , that arises as a consequence of the presence of the random correlation state. Fig. 4 plots the ratio between the information per coincidence carried when the “low correlation state” is random and the optimal

amount of information per coincidence $\log_2(1/\alpha)$ obtained when the low correlation state is totally anticorrelated. The plot is shown as a function of the fraction α of stimuli eliciting a “highly correlated state”. Fig. 4 shows clearly that, if the “low correlation state” of the assembly elicits uncorrelated firing, then the information per coincidence is far from its maximum, unless the correlation in the “high state” is extremely high and the correlational code is not sparse at all. However, in which case the information per coincidence is very low anyway (see eq. (7)).

Therefore correlational assemblies in the brain, if any, are likely to be inefficient in the short time limit. This consideration further limits the possible role played by correlations in fast information encoding.

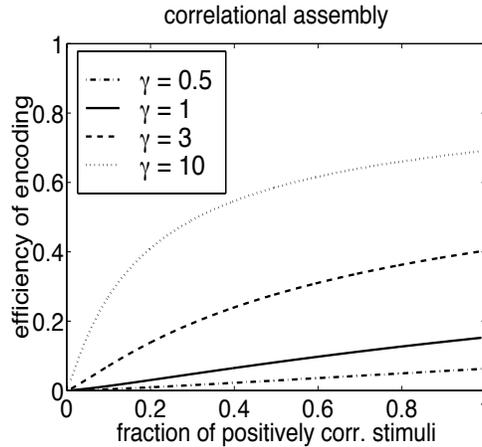


Fig. 4. The ratio between the information per coincidence carried by a binary correlational encoder with a fraction of stimuli eliciting positive correlation γ and the other stimuli eliciting no correlation, and the optimal information per coincidence carried in the same situation, but with full anticorrelation in the “low correlation state”. This ratio is plotted, for different values of the strength γ of the “high correlation state”, as a function of the fraction of stimuli eliciting positive correlation.

7 Discussion

If cells participate in context-dependent correlational assemblies [2], then a significant amount of information should be found in the third component of I_{tt} when analysing data obtained from the appropriate experiments. The series expansion approach thus enables the testing of hypotheses about the role of correlations in solving the binding problem, as opposed to other solutions, and about information coding in general. Data analyses based on the time-expansion approach have the potential to elucidate the role of correlations in the encoding of information by cortical neurons.

It is worth noticing that the formalism presented here evaluates the the information contained in the neuronal responses themselves, it does not make assumptions about the system that is going to read the code. For this reason, the information computed “directly” from neuronal responses is an upper bound to what any type of decoder can extract from the responses themselves. Therefore it is termed the information that an “ideal observer” can extract [22]. Of course, the relative contribution of rate and synchrony modulations to information transmission will depend on the specific read-out mechanism used by a downstream neural system that listens to the neuronal code. However, if the information that an ideal observer is able to extract from the synchrony code is small, as the mathematical analysis indicates for the fast information processing limit, one can be sure that any decoding device cannot extract more information in the synchrony than that small amount evaluated from the responses.

Whether this small amount is sufficient to support computational processes such as figure-ground segregation remains to be seen, and depends upon how it scales empirically with the number of receptive fields examined. Ultimately, as suggested by [3], the only way we will achieve any degree of confidence in a proposed solution to the binding problem will be to study recordings made from a monkey trained to make behavioural responses according to whether individual features are bound to particular objects. The information theoretic approach described here would be a natural way to analyse such data.

In conclusion, the methodology presented here can provide interesting and reliable bounds on the role of synchrony on cortical information encoding, and we believe that its application to neurophysiological experiments will advance our understanding of the functional interpretation of synchronous activity in the cerebral cortex.

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References

1. C. von der Malsburg. Binding in models of perception and brain function. *Current Opinion in Neurobiology*, 5:520–526, 1995.
2. W. Singer, A. K. Engel, A. K. Kreiter, M. H. J. Munk, S. Neuenschwander, and P. Roelfsema. Neuronal assemblies: necessity, signature and detectability. *Trends in Cognitive Sciences*, 1:252–261, 1997.
3. M. N. Shadlen and J. A. Movshon. Synchrony unbound: a critical evaluation of the temporal binding hypothesis. *Neuron*, 24(1):67–77, 111–25, September 1999.
4. G. M. Ghose and J. Maunsell. Specialized representations in visual cortex: a role for binding? *Neuron*, 24(1):79–85, 111–25, September 1999.
5. M. P. Young and S. Yamane. Sparse population coding of faces in the inferotemporal cortex. *Science*, 256:1327–1331, 1992.

6. H. D. R. Golledge, C. C. Hilgetag, and M. J. Tovee. A solution to the binding problem? information processing. *Curr Biol*, 6(9):1092–5, Sep 1 1996.
7. A. M. H. J. Aertsen, G. L. Gerstein, M. K. Habib, and G. Palm. Dynamics of neuronal firing correlation: modulation of “effective connectivity”. *Journal of Neurophysiology*, 61:900–917, 1989.
8. E. D. Adrian. The impulses produced by sensory nerve endings: Part I. *J. Physiol. (Lond.)*, 61:49–72, 1926.
9. K.H. Britten, M. N. Shadlen, W. T. Newsome, and J. A. Movshon. The analysis of visual-motion - a comparison of neuronal and psychophysical performance. *J. Neurosci.*, 12:4745–4765, 1988.
10. M. N. Shadlen and W. T. Newsome. Motion perception: seeing and deciding. *Proc Natl Acad Sci U S A*, 93(2):628–33, Jan 23 1996.
11. C. E. Shannon. A mathematical theory of communication. *AT&T Bell Labs. Tech. J.*, 27:379–423, 1948.
12. M. J. Tové, E. T. Rolls, A. Treves, and R. P. Bellis. Information encoding and the response of single neurons in the primate temporal visual cortex. *J. Neurophysiol.*, 70:640–654, 1993.
13. S. Thorpe, D. Fize, and C. Marlot. Speed of processing in the human visual system. *Nature*, 381:520–522, 1996.
14. E. T. Rolls, M.J. Tovee, and S. Panzeri. The neurophysiology of backward visual masking: Information analysis. *J. Cognitive Neurosci.*, 11:335–346, 1999.
15. C. M. Gray, A. K. Engel, P. König, and W. Singer. Synchronization of oscillatory neuronal responses in cat striate cortex: Temporal properties. *Visual Neuroscience*, 8:337–347, 1992.
16. A. K. Kreiter and W. Singer. Stimulus-dependent synchronization of neuronal responses in the visual cortex of the awake macaque monkey. *J Neurosci*, 16(7):2381–96, Apr 1 1996.
17. P. König, A. K. Engel, and W. Singer. Relation between oscillatory activity and long-range synchronization in cat visual cortex. *Proc. Natl. Acad. Sci. USA*, 92:290–294, 1995.
18. S. C. de Oliveira, A. Thiele, and K. P. Hoffmann. Synchronization of neuronal activity during stimulus expectation in a direction discrimination task. *J Neurosci*, 17(23):9248–60, Dec 1 1997.
19. P. König, A. K. Engel, and W. Singer. Relation between oscillatory activity and long-range synchronization in cat visual cortex. *Proc Natl Acad Sci U S A*, 92(1):290–4, Jan 3 1995.
20. Y. Hata, T. Tsumoto, H. Sato, and H. Tamura. Horizontal interactions between visual cortical neurones studied by cross-correlation analysis in the cat. *J Physiol (Lond)*, 441:593–614, September 1991.
21. F. Rieke, D. Warland, R. R. de Ruyter van Steveninck, and W. Bialek. *Spikes: exploring the neural code*. MIT Press, Cambridge, MA, 1996.
22. A. Borst and F. E. Theunissen. Information theory and neural coding. *Nat Neurosci*, 2(11):947–57, November 1999.
23. S. Panzeri, S. R. Schultz, A. Treves, and E. T. Rolls. Correlations and the encoding of information in the nervous system. *Proc. R. Soc. Lond. B*, 266:1001–1012, 1999.
24. S. Panzeri and S. R. Schultz. A unified approach to the study of temporal, correlational and rate coding. *Neural Computation*, *in press*, 1999.
25. M. N. Shadlen and W. T. Newsome. The variable discharge of cortical neurons: implications for connectivity, computation and coding. *J. Neurosci.*, 18(10):3870–3896, 1998.