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The Effects of Input Rate and Synchrony on a Coincidence Detector: Analytical Solution

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We derive analytically the solution for the output rate of the ideal coincidence detector. The solution is for an arbitrary number of input spike trains with identical binomial count distributions (which includes Poisson statistics as a special case) and identical arbitrary pairwise cross-correlations, from zero correlation (independent processes) to complete correlation (identical processes).

1 Introduction

Individual neurons typically receive thousands of inputs that vary temporally with respect to both mean rate and cross-correlation. Much experimental evidence underscores the importance of mean input rate and cross-correlation as determinants of neural firing, though the relative contributions of each are not so clear (Abeles, 1982, 1991; Softky & Koch, 1992, 1993; Shadlen & Newsome, 1994; Alonso, Usrey, & Reid, 1996; Decharms & Merzenich, 1996; König, Engel, & Singer, 1996; de Oliveira, Thiele, & Hoffmann, 1997; Riehle, Grün, Diesmann, & Aertsen, 1997; Steinmetz et al., 2000; Salinas & Sejnowski, 2000; Niebur, Hsiao, & Johnson, 2002; Williams & Stuart, 2002). Given the importance of rate and cross-correlation in neural coding, the determination of how inputs modulated with respect to both affect neural firing assumes significance if the impact of these different neural codes is to be fully appreciated. Employing simple probabilistic and combinatorial methods, we derive the exact analytical solution for the output rate of a coincidence detector receiving an arbitrary number of inputs modulated with respect to both mean rate and cross-correlation

2 Binomial Spike Trains with Specific Cross-Correlation

In this section, we introduce a systematic method for the generation of an arbitrary number of spike trains with specified pair-wise mean cross-correlations and firing rates.[1] Spikes are distributed according to binomial counting statistics in each spike train. Mean firing rates and cross-correlations are the same for all spike trains (or all pairs of spike trains, respectively), but they can be chosen independently of each other. The algorithm that we describe here is as suitable for the analytical computations in this report as for the implementation of such spike trains in numerical simulations. We emphasize that although we use this particular algorithm to illustrate the derivation of the output rate of the coincidence detector, our results are of general validity since the properties of the spike trains are entirely specified by their correlation coefficient and the statistics of the individual spike trains. However, no higher-order effects (correlations of order 3 and higher; see, e.g., Bohte, Spekreijse, & Roelfsema, 2000) are included.

First, we establish some notation. Let m be the number of input spike trains, each one having n time bins. All bins are of equal length Δt, chosen sufficiently small so that each contains a maximum of one spike, that is, each bin is guaranteed to contain either one or zero spikes. The probability that a spike is found in any given time bin is p; no spike is therefore found with probability $1 - p$. Bins in any given spike train are independent, which implies that all the following analysis can be limited to a single time bin. Note that the physiologically important Poisson statistics are the special case of low rates and long spike trains.

Generation of m spike trains with specific correlation starts by generating $m + 1$ independent spike trains with the desired mean firing rate (which is just $p/\Delta t$). Let us assume we want a correlation coefficient q (with $0 \leq q \leq 1$) between each and any pair of the m spike trains. We designate spike train number $m + 1$ as the reference spike train. In order to introduce the correlation coefficient q between spike trains $1, \ldots, m$, we will switch, with a probability $\sqrt{q}$, the state of a time bin in each of these spike trains to that found in the reference spike train. This yields a mean correlation coefficient of q between any two of the spike trains $1, \ldots, m$ without changing the mean firing rate.[2] No further use is made of the reference spike train.

[1] The method proposed here is not the only possible way to introduce correlations between spike trains. For instance, one could add spikes generated by a common Poisson process to each individual spike train (Stroeve & Gielen, 2001), or start from a common spike train and generate two different spike trains by removing spikes independently. The method presented here has the advantage of being straightforward and efficient and of generating spike trains with controlled rates and correlation coefficients, both determined in a direct way.

[2] Since all spike trains, including the reference spike train, have the same mean firing rate, changing the state of any bin to the state of any bin in another spike train does not change the probability of this bin's containing a spike. Therefore, this manipulation does not change the mean firing rate of the spike train.

3 Coincidence Detection for Vanishing Input Correlation

The coincidence detector is a computational unit that fires if the number of input spikes received within a given time bin equals or exceeds the threshold, θ. It is instructive to first derive a solution for independent inputs ($q = 0$) with mean rate $p/\Delta t$. Using the binomial distribution and elementary combinatorics, we find that the probability of obtaining exactly j coincident input spikes from a set of m input spike trains with probability p for a spike (to exist within each time bin) is

$$P(j) = \binom{m}{j} p^j (1-p)^{m-j}. \tag{3.1}$$

Since we are interested only in cases where the coincidence detector receives at least θ coincident input spikes, the probability for the coincidence detector to produce an output spike is

$$P_{out}(p, m, \theta; q = 0) = \sum_{j=\theta}^{m} \binom{m}{j} p^j (1-p)^{m-j}. \tag{3.2}$$

Dividing equation 3.2 by Δt, we obtain the mean output rate of a coincidence detector in the case of vanishing input correlation:

$$N_{out}(p, m, \theta; q = 0) = \frac{1}{\Delta t} \sum_{j=\theta}^{m} \binom{m}{j} p^j (1-p)^{m-j}. \tag{3.3}$$

4 Finite Correlation

Let us continue to the case of input spikes that vary with respect to both mean rate and cross-correlation. In the notation introduced in section 3, we have to compute $P_{out}(p, m, \theta, q)$, the probability that the coincidence detector produces an output spike (in this time bin) when it receives m input spike trains with cross-correlation q. Conceptually, it is helpful to start with independent input spike trains, $q = 0$, and then apply the modification of the result as the procedure described in section 2 is applied to generate input spike trains with finite q. Thus, the generation of our correlated input spike trains has two parts: (1) the generation of independent spike trains and (2) the imposition of our cross-correlation procedure to introduce cross-correlation between the input spike trains.

Without loss of generality, we treat $P_{out}(p, m, \theta, q)$ as the following joint probability, again derived from the binomial distribution:

$$P_{out}(p, m, \theta, q) = \sum_{j=\theta}^{m} \binom{m}{j} p^j (1-p)^{m-j} C_1(j, q) + \sum_{j=0}^{\theta-1} \binom{m}{j} p^j (1-p)^{m-j} C_2(j, q). \tag{4.1}$$

In this equation, both $C_1(j, q)$ and $C_2(j, q)$ are conditional probabilities; in addition to j and q, they depend on θ and m, but these arguments are suppressed to alleviate the notation. Specifically, $C_1(j, q)$ is the probability of obtaining at least θ coincident input spikes given that initially (i.e., before applying our cross-correlation procedure), there were $j \geq \theta$ coincident input spikes. The factor $C_2(j, q)$ is the probability of obtaining at least θ coincident input spikes given that initially there were $j < \theta$. From their definition, it is obvious that $C_1(j, 0) \equiv 1$ and $C_2(j, 0) \equiv 0$, which will later be found to be the case explicitly (see equations 4.2 and 4.4). As it must be, equation 3.2 is thus just the special case of $q = 0$.

Equation 4.1 expresses the joint probabilities for a two-part experiment: the generation of independent spike trains and the correlation procedure applied to these spike trains that is described in section 2. Let us first consider C_2, the conditional probability for a suprathreshold event (that is, among the m input neurons, θ or more have a spike) occurring in the (whole) experiment given that initially (after completion of only the first part) it was subthreshold. This can happen only if the reference spike train has a spike in the time bin under consideration since otherwise, a subthreshold event can never be converted to a suprathreshold event (if the state of any neuron will be switched, it will be switched to that of the reference spike train). This occurs with a probability p.[3]

Since by assumption $j < \theta$ neurons already have a spike (and their state will not be influenced even if a switch should occur since the reference spike by assumption also has a spike), we have to compute the probability that a sufficient number of the remaining $(m - j)$ neurons that do not spike before application of the correlation procedure will be switched. Since all switches are independent and occur with a probability $\sqrt{q}$, we can expect i switches among the available $(m - j)$ neurons with a probability $\binom{m-j}{i} \sqrt{q}^i (1 - \sqrt{q})^{(m-j)-i}$. This gives rise to a suprathreshold event if $i \geq \theta - j$

[3] Formally, the procedure could also be viewed as a three-part experiment: (1) the generation of spike trains, (2) the correlation procedure described in section 3 for any reference spike train, and (3) the drawing of either a spike or a nonspike in the reference spike train, with probabilities p and $(1 - p)$, respectively. We have simplified the analysis somewhat by taking only those parts in equations 4.2 and 4.3 that actually contribute to the output of the coincidence detector.

since in this case, the total number of spikes is $j + i \geq \theta$. We therefore have to sum the probabilities for all cases with $i \geq \theta - j$ and obtain $C_2(j, q)$ in equation 4.1 as

$$C_2(j,q) = \sum_{i=\theta-j}^{m-j} \binom{m-j}{i} \sqrt{q}^{i} (1-\sqrt{q})^{m-j-i} p. \tag{4.2}$$

Now we turn to the derivation of $C_1(j, q)$ in equation 4.1, which is the probability that an initially (i.e., at $q = 0$) suprathreshold event remains suprathreshold after cross-correlation. This is more difficult to compute directly, and therefore we compute its complement, that is, one minus this probability. The latter is the probability of switching a suprathreshold event to a subthreshold event. Assuming now $j \geq \theta$, this probability is found by an argument completely analogous to that leading to equation 4.2 as

$$\sum_{i=j-\theta+1}^{j} \binom{j}{i} \sqrt{q}^{i} (1-\sqrt{q})^{j-i} (1-p). \tag{4.3}$$

It can be seen that this is the probability that i (with $i > j - \theta$) input spikes get switched to the value in the reference spike train during the generation of correlated spike trains. This expression also takes into account the requirement that the bin in the reference train contains no spike (from which the $(1 - p)$ term results). Therefore, we have the following:

$$C_1(j,q) = 1 - \sum_{i=j-\theta+1}^{j} \binom{j}{i} \sqrt{q}^{i} (1-\sqrt{q})^{j-i} (1-p). \tag{4.4}$$

This completes the computation of equation 4.1 for $P_{out}(q)$. To compute the mean output rate of the coincidence detector $N_{out}(p, q, \theta)$ as a function of input rate $p/\Delta t$, cross-correlation q, and threshold θ, we collect terms and multiply equation 4.1 by the inverse of the time bin width, Δt, to yield the following:

$$\begin{aligned} N_{out}&(p, m, \theta, q) \\ &= \frac{1}{\Delta t}\left[\sum_{j=\theta}^{m} \binom{m}{j} p^{j} (1-p)^{m-j} \left(1 - \sum_{i=j-\theta+1}^{j} \binom{j}{i} \sqrt{q}^{i} (1-\sqrt{q})^{j-i} (1-p)\right)\right. \\ &\quad \left. + \sum_{j=0}^{\theta-1} \binom{m}{j} p^{j} (1-p)^{m-j} \sum_{i=\theta-j}^{m-j} \binom{m-j}{i} \sqrt{q}^{i} (1-\sqrt{q})^{m-j-i}\right]. \end{aligned} \tag{4.5}$$

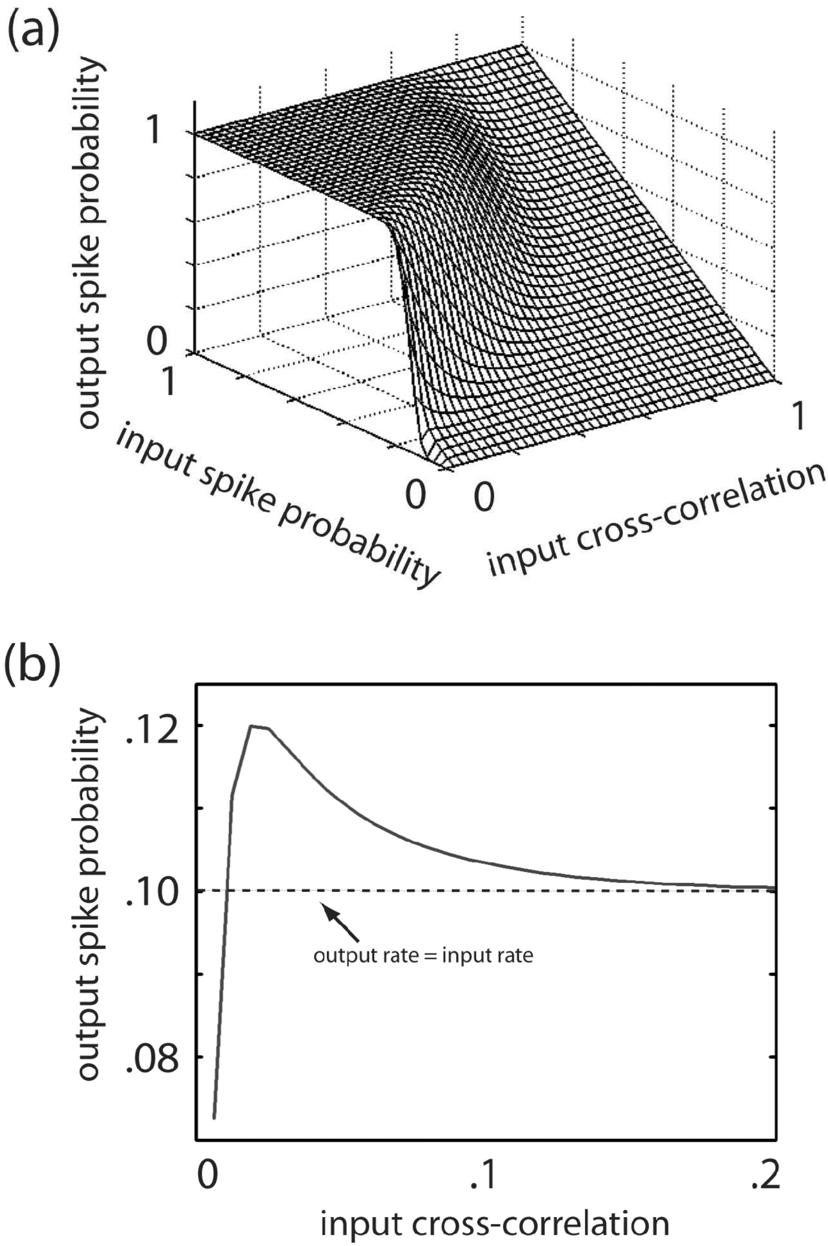
We have thus obtained our main result: the exact analytical solution for the output rate of a coincidence detector receiving an arbitrary number of inputs with identical binomial statistics and modulated with respect to both mean rate and cross-correlation. The validity of equation 4.5 is confirmed by simulation (not shown).

5 Example

An illustration of equation 4.1 for a coincidence detector receiving $m = 100$ binomial input spike trains and with a threshold $\theta = 15$ is shown in Figure 1a. For low values of cross-correlation, the output rate of the coincidence detector is sigmoidal as a function of the input rate, and it rapidly saturates as the input rate increases. For increasing cross-correlation, this behavior approaches more and more a linear increase with input rate, which is, of course, nothing but the solution in which each synchronous volley of incoming action potentials leads to exactly one output spike.

In Figure 1b, we show a cut through Figure 1a for the case of constant probability $p = 0.1$, corresponding to a firing rate of 50 Hz for $\Delta t = 2$ ms, which is physiologically realistic in many cases. For this low probability, the binomial distribution of input spike trains can be reasonably well approximated by a Poisson distribution. Bernander, Koch, and Usher (1994) emphasized that increasing synchrony does not necessarily lead to an increased output rate since synchronous volleys with more spikes than required to overcome the threshold are wasted. They demonstrated by way of simulation of different neuron models that the output firing rate as a function of input correlation in this case takes on the shape of an inverted U. Figure 1b shows an example of this behavior in the case of our exact solution. While synchrony in this example always increases the efficacy of the incoming firing rates beyond that obtained for independent spike trains, this increase reaches a maximum for small q, after which the output rate decreases again. For this value of p, the trivial solution in which one input volley generates exactly one output spike (i.e., output rate $\equiv p$) is obtained for all $q \sim> 0.1$.

Figure 1: *Facing page.* The plots illustrate the main equation (4.1) derived in this article for a coincidence detector receiving $m = 100$ binomial input spike trains with a threshold $\theta = 15$. (a) The probability for a coincidence detector to fire an action potential per unit time (see equation 4.1). (b) An iso-frequency (p = .1) slice through the surface of a, showing the output probability of the coincidence detector as a function of input cross-correlation. At this relatively low input frequency (corresponding to 50 Hz for $\Delta t = 2$ ms), the input spike trains are approximately Poisson. Note the inverted U shape of the plot, whereby higher cross-correlated inputs result in a lower output due to inefficient allocation of input spikes.The horizontal dashed line shows $p = 0.1$.


(a)
output spike probability
1
0
1
input spike probability
0
0
1
input cross-correlation
(b)
output spike probability
.12
.10
.08
output rate = input rate
0
.1
.2
input cross-correlation

6 Discussion

In this article, we have derived analytically the solution for the output firing rate of an ideal coincidence detector as a function of the input rate and correlation between input spike trains. Our derivation was based on a simple model and it is important to make explicit the key assumptions of our model: (1) the bins in any given input spike train are independent, (2) the coincidence detector "neuron" integrates over a very short time window, and (3) there is no inhibition. The first condition means that there might be additional effects that depend on the structure of the individual spike trains; the second condition makes this model memoryless, which serves to differentiate it from integrator models with long time constants; and the last condition means that the applicability of our model to neurons that receive strong, structured inhibitory input may be limited. All of these conditions are significant simplifications; for instance, it is well known (for a recent example, see Tiesinga, Fellous, & Sejnowski, 2002) that neurons are not memoryless processes (assumption 1 for incoming spike trains and assumption 2 for the neural processing). We feel that these simplifications are justified in the interest of obtaining an analytical solution.

Others have noted that output frequency varies with the correlation of input spike trains in a nontrivial and frequently nonmonotonic way. In particular, the existence of a maximum, as shown in Figure 1b, has been predicted by Bernander et al. (1994), based on simulations. We can compute the location of this maximum from our solution by differentiating equation 4.5 with respect to the cross-correlation q and setting the right-hand side equal to zero. The computation is straightforward but not particularly illuminating. Instead, we plotted iso-frequency curves through the surface given by equation 4.5 to obtain the position of this maximum (not shown). We observed that the prominence of this peak increases with increasing number of inputs and that it is confined to low input rates (the Poisson regime), disappearing altogether above a certain input rate where monotonically decreasing iso-frequency curves are obtained. This general behavior can be seen in Figure 1a. These observations lead us to infer that correlations modulate firing rate best when the number of inputs is high and the input rates are low, which corresponds to the most neurally plausible scenario. Thus, our results may have relevance for synchrony-based models of neural computing.

In sum, we believe our derivation will prove useful both as a theoretical example highlighting the power of combinatorial methods and for explaining the relative contributions of rate versus synchrony in neural coding.

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References

Abeles, M. (1982). *Local cortical circuits*. New York: Springer-Verlag.

Abeles, M. (1991). *Corticonics—Neural circuits of the cerebral cortex*. Cambridge: Cambridge University Press.

Alonso, J. M., Usrey, W. M., & Reid, R. C. (1996). Precisely correlated firing in cells of the lateral geniculate nucleus. *Nature*, *383* (6603), 815–819.

Bernander, O., Koch, C., & Usher, M. (1994). The effect of synchronized inputs at the single neuron level. *Neural Computation*, *6*(4), 622–641.

Bohte, S. M., Spekreijse, H., & Roelfsema, P. R. (2000). The effects of pair-wise and higher-order correlations on the firing rate of a postsynaptic neuron. *Neural Computation*, *12*, 153–179.

Decharms, R. C., & Merzenich, M. M. (1996). Primary cortical representation of sounds by the coordination of action potential timing. *Nature*, *381*, 610–613.

de Oliveira, S. C., Thiele, A., & Hoffmann, K. P. (1997). Synchronization of neuronal activity during stimulus expectation in a direction discrimination task. *J. Neurosci.*, *17*(23), 9248–9260.

König, P., Engel, A. K., & Singer, W. (1996). Integrator or coincidence detector? The role of the cortical neuron revisited. *Trends in Neurosciences*, *719*(4), 130–137.

Niebur, E., Hsiao, S. S., & Johnson, K. O. (2002). Synchrony: A neuronal mechanism for attentional selection? *Current Opinion in Neurobiology*, *12*(2), 190–194.

Riehle, A., Grün, S., Diesmann, M., & Aertsen, A. (1997). Spike synchronization and rate modulation differentially involved in motor cortical function. *Science*, *278*, 1950–1953.

Salinas, E., & Sejnowski, T. J. (2000). Impact of correlated synaptic input on output firing rate and variability in simple neuronal models. *Journal of Neuroscience*, *20*(16), 6193–6209.

Shadlen, M. N., & Newsome, W. T. (1994). Noise, neural codes and cortical organization. *Current Opinion in Neurobiology*, *4*, 569–579.

Softky, W., & Koch, C. (1992). Cortical cells should fire regularly but do not. *Neural Computation*, *4*(5), 643–646.

Softky, W., & Koch, C. (1993). The highly irregular firing of cortical cells is inconsistent with temporal integration of random EPSPs. *J. Neurosci.*, *13*(1), 334–350.

Steinmetz, P. N., Roy, A., Fitzgerald, P., Hsiao, S. S., Johnson, K. O., & Niebur, E. (2000). Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature*, *404*, 187–190.

Stroeve, S., & Gielen, S. (2001). Correlation between uncoupled conductance-based integrate-and-fire neurons due to common and synchronous presynaptic firing. *Neural Computation*, *13*, 2005–2029.

Tiesinga, P. H. E., Fellous, J.-M., & Sejnowski, T. J. (2002). Attractor reliability reveals deterministic structure in neuronal spike trains. *Neural Computation*, *14*, 1629–1650.

Williams, S. R., & Stuart, G. J. (2002). Dependence of EPSP efficacy on synapse location in neocortical pyramidal neurons. *Science*, *295*, 1907–1910.

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