QUALITY OF COINCIDENCE DETECTION AND ITD TUNING: A THEORETICAL FRAMEWORK

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Coincidence detector neurons increase their firing rate significantly if the input changes from random to coherent. Similarly, neurons in the avian nucleus laminaris vary their firing rate as a function of the interaural time difference (ITD). In both cases, neurons transform temporally coded input into a rate-coded output. To characterize the quality of this transformation we define a new measure, which explicitly takes noisy spike output of neurons into account. As an application, we investigate the coincidence detection properties of an integrate-and-fire (I&F) neuron in dependence on internal parameters and input statistics. We show that there is an optimal threshold and, furthermore, that there is a broad range of near-optimal threshold values. The theoretical results are applied to ITD-tuning of neurons in the laminar nucleus of the barn owl.

1 Introduction

Neurons have two basic operation modes: they can function either as integrators or as coincidence detectors. In the integration mode, the output rate changes as a function of the *mean* input rate and is independent of the temporal fine structure of input spike trains. Neurons act as coincidence detectors, if their mean output firing rate does depend on the temporal structure of input spike trains. Coincidence detection implies that the output firing rate is higher if spikes arrive 'coincidently' as compared to a random spike arrival.

There is, however, no sharp boundary that separates the two basic operation modes. It is known that the membrane time constant [10], the spike threshold and the number of input synapses [1] are relevant parameters. In this contribution we develop a framework that allows to assess how these parameters influence the quality of coincidence detection. We consider stochastic arrival of presynaptic spikes and ask the following question: How well can a neuron detect the degree of synchrony in the input? Can it convert a time-

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coded signal into a rate-coded one? For I&F neurons we show explicitly the dependence of the precision of neuronal coincidence detection upon, e.g., the membrane time constant, the input statistics, and the voltage threshold at which an action potential is generated. The theoretical results are applied to neurons in the laminar nucleus of the barn owl. For a more comprehensive and mathematically detailed account the reader is referred to Kempter *et al.* [7,8]. For a different model approach see Ref. (2).

2 Temporal Coding of the Input

Input spikes are generated stochastically and arrive at each of the $N \gg 1$ synapses of a single neuron with a time-dependent rate $\lambda^{\text{in}}(t) \geq 0$. The probability of having a spike in the interval $[t, t+\Delta t[$ is $\lambda^{\text{in}}(t)\Delta t$ as $\Delta t \to 0$. In this way we obtain a *nonstationary* or *inhomogenous* Poisson process. [8]

As a specific example we consider T-periodic rates, $\lambda^{\text{in}}(t) = \lambda^{\text{in}}(t+T)$, where input spikes are more or less phase-locked to a periodic stimulus. Phase locked spikes are an example of a temporal code. The average number of spikes that arrive during one period at a synapse will be called p. The time-averaged mean input rate is $\bar{\lambda}^{\text{in}} := 1/T \int_{t_0}^{t_0+T} \mathrm{d}t' \, \lambda^{\text{in}}(t')$ and equals p/T. To parameterize the input, we take the function

$$\lambda^{\text{in}}(t) := p \sum_{m=-\infty}^{\infty} G_\sigma(t - mT) \tag{1}$$

where $G_\sigma(.)$ denotes a normalized Gaussian distribution with zero mean and standard deviation $\sigma > 0$. At each input terminal spikes arrive with a probability density given by Eq. (1). Note that spikes arriving at different synapses are generated independently.

The standard deviation $\sigma \in [0, \infty[$ of the Gaussian distribution in Eq. (1) can be used to characterize the degree of synchrony of the input. In the case $\sigma = 0$, the input spikes arrive perfectly phase-locked and occur only at times $t_m = mT$ with integer m, and the number of spikes arriving at time t_m has a Poissonian distribution with parameter p. In the case $\sigma > 0$, there is also a temporal jitter of input spikes times around the t_m.

Instead of σ, another measure of synchrony, the so-called *vector strength* r^{in} may be used [5]. This measure can be defined as the ratio of the amplitude of the first Fourier component of the periodic rate $\lambda^{\text{in}}(t)$ and that of the Fourier component of order zero. For the input given in Eq. (1) we find $r^{\text{in}} = \exp[-(2\pi/T)^2 \sigma^2/2]$. By construction, we have $0 \leq r^{\text{in}} \leq 1$.

For example, neurons in the avian laminar nucleus are sensitive to the degree of coherence in the input. If a neuron in an *in vitro* preparation is stimulated by synchronized current pulses at times $T, 2T, 3T, \ldots$ (that means $r^{\text{in}} = 1$), then the neuron fires at a high rate. If the same amount of current is delivered by incoherent pulses or constant input current, the neuron is much less active [11]. In vivo, input spikes are not perfectly phase locked but have some jitter around a preferred phase. The maximum input vector strength to a neuron in the laminar nucleus of the barn owl is $r^{\text{in}} \approx 0.5$ for a 5 kHz sound wave. It is achieved, if input from the left and the right ear arrives at the optimal ITD. [3] If left and right ear stimulus are out of phase, the effective input vector strength is $r^{\text{in}} \approx 0$. The dependence of the output firing rate of a laminar neuron upon the relative phase of the stimulus is called the ITD-tuning curve of the neuron. We note that for different positions on the ITD-tuning curve the *mean* input is always the same – only the timing and, hence, the effective vector strength of the input changes.

3 Classification of Coincidence Detectors

In a standard firing rate description a neuron would be characterized by its gain function, which describes the dependence of the output firing *rate* upon the mean input *rate*. Here we take a different approach. We vary the temporal structure of the input under the constraint of a *constant* mean input rate, $\bar{\lambda}^{\text{in}} = \text{const}$. The example of ITD tuning shows that even with a constant mean input rate, a neuron's output rate $\bar{\lambda}^{\text{out}}$ can vary as a function of the temporal structure of the input. In other words, a neuron can 'read out' a temporal code. In order to quantify this effect, we define two measures: the *coherence gain* and the *quality factor*.

3.1 Coherence Gain and Modulation Depth of ITD Tuning

Let us suppose we change the vector strength r^{in} of the input while keeping the mean constant. For each value of r^{in} we measure the output rate $\bar{\lambda}^{\text{out}}(r^{\text{in}})$. We want to compare the output rate for a given vector strength, e.g., $r^{\text{in}} = 0.5$ with the rate for $r^{\text{in}} = 0$. To do so we define the *coherence gain*

$$E(r^{\text{in}}) := \bar{\lambda}^{\text{out}}(r^{\text{in}}) / \bar{\lambda}^{\text{out}}(0) \qquad (2)$$

Similarly, $E(1)$ would be the ratio between the mean firing rate for fully coherent input and the rate for completely incoherent input. $E(1) \gg 1$ is commonly interpreted as signaling a good coincidence detector. A coherence gain $E(r^{\text{in}} = 1) = E(r^{\text{in}} = 0.5) = 1$ means that a neuron is an integrator.

The notion of coherence gain can be directly interpreted as the modulation depth of an ITD tuning curve. To see how this works, let us return to the example of a 5 kHz neuron in the nucleus laminaris of the barn owl. As we have seen at the end of the previous Section, optimal ITD (that is the maximum of the ITD tuning curve) corresponds to stimulation with vector strength $r^{\rm in} = 0.5$. The minimum of the ITD tuning curve corresponds to nearly incoherent stimulation and may hence be identified with $r^{\rm in} = 0$. The modulation depth M of the ITD tuning curve may be defined as the maximum rate divided by the minimum rate, hence $M = E(r^{\rm in} = 0.5)$. For an example of ITD tuning in a model neuron, see Fig. 2.

3.2 Quality Factor of Coincidence Detection

The coherence gain E, which is a ratio of firing rates, is in general not sufficient for characterizing coincidence detectors. The reason is that in biological systems the mean output firing rate of a neuron cannot be determined exactly within a finite amount of time. The output rate of a neuron is defined as the number of spikes occuring in a time interval divided by the length I of that interval. Since spikes occur often highly irregularly, seemingly randomly [12], the number of spikes in an interval shows up variability. That is to say, the estimated output rate is subject to statistical errors — the shorter I and the smaller the firing rate, the larger the error. This has to be taken into account in characterizing a coincidence detector. To illustrate the limitations of E when quantizing coincidence detection, we consider a neuron that is silent for incoherent input and has a rate of 0.1 Hz for coherent input. Even though E is infinite in this case, the neuron's output could not be used to detect coherent input in a time interval of, say, $I = 100\,\text{ms}$ since most likely not a single spike will occur.

To overcome the shortcomings in the definition of E we introduce a more powerful notion of characterizing a coincidence detector. The output of a coincidence detector must convey a signal concerning the nature of a noisy input (coherent or incoherent) in a *finite* amount of time I. We assume that the number n of output spikes in I is a random quantity, which has some probability density $P(n)$. The mean value $\overline{n} = \sum_{n=1}^{\infty} n\, P(n)$ is $\overline{n} = \bar{\lambda}^{\rm out}\, I$, where $\bar{\lambda}^{\rm out}$ is the mean output rate. For two different input vector strengths, e.g., $r^{\rm in} = 0$ and $r^{\rm in} = 0.5$, we have two different distributions P with mean values $\overline{n}(r^{\rm in} = 0)$ and $\overline{n}(r^{\rm in} = 0.5)$, respectively. The task is to distinguish the two cases based on a single measurement of the number n of output spikes in I. This can be done by means of a number n' which acts as a decision boundary. If n is larger than or equal to the criterion n', then we classify the input to have $r^{\rm in} = 0.5$; if n is smaller than n', then we classify $r^{\rm in} = 0$.

Now the key idea is that we have to segregate *probability distributions.*

If the two distributions have a large overlap, a reliable decision is impossible, whatever n'. If the two distributions are well separated, then there is a high chance of making the right choice. The width of each distribution is characterized by the standard deviation ς. In order to quantify the discriminability of the two distributions we consider their normalized 'distance':

$$\gamma := \frac{\bar{n}(r^{\text{in}}) - \bar{n}(0)}{\varsigma(r^{\text{in}}) + \varsigma(0)} = \sqrt{\bar{n}(r^{\text{in}})} - \sqrt{\bar{n}(0)} \ . \tag{3}$$

For the second equality sign we have used that we have $\varsigma^2 = \overline{n}$ for Poisson distributed numbers. A Poisson distribution is a good approximation if spiking is driven by the variance of the neuron's input [13]. We call γ the *quality factor* for coincidence detection [a]. Using the definition of the coherence gain E [cf. Eq. (2)] we obtain from Eq. (3)

$$\gamma = \sqrt{I\,\bar{\lambda}^{\text{out}}(0)}\,\left(\sqrt{E(r^{\text{in}})} - 1\right) \ . \tag{4}$$

Equation (4) shows how the γ increases with increasing length of the time interval I, the mean output rate $\bar{\lambda}^{\text{out}}(0)$, and the coherence gain $E(r^{\text{in}})$. It is important to realize that $\bar{\lambda}^{\text{out}}(0)$ and $E(r^{\text{in}})$ are *not* independent variables.

4 Integrate-and-Fire Neurons

As a specific example we study the coincidence detection properties of an integrate-and-fire (I&F) neuron that receives stochastic input spike trains through N independent channels as specified in Sec. 2. We show that there is an optimal threshold for coincidence detection and that there is a broad range of near optimal threshold values. Fine tuning is not necessary. Finally, we show how the quality factor depends on neuronal parameters such as the width of the EPSP, the number of synapses N, and the mean input rate $p/T = \bar{\lambda}^{\text{in}}$. Based on an analytical expression for the quality factor we discuss coincidence detection as performed by laminar neurons.

4.1 Neuron Model

The I&F unit fires, if its membrane potential u approaches the threshold ϑ from below. This defines a firing time t^n with integer n. After an output spike, which need not be described explicitly, the membrane potential is reset

[a] Multiplying the quality factor γ by a factor 2 we obtain a quantity similar to the index d' commonly used in psychophysics, where d' is a measure of the discriminability of a signal in noise [6].

to 0. Between two firing events the membrane voltage changes according to the linear differential equation

$$\frac{\mathrm{d}}{\mathrm{d}t}\, u(t) = -\frac{1}{\tau_m} u(t) + i(t) \ , \tag{5}$$

where i is the total input current and $\tau_m > 0$ is the membrane time constant. The input is due to presynaptic activity. The spike arrival times at a given synapse j, with $1 \leq j \leq N$, are labeled by t_j^f where $f = 1, 2, \dots$ is a running spike index.

Each presynaptic spike evokes a small postsynaptic current (PSC) which decays exponentially with time constant $\tau_s > 0$. All synapses are equal in the sense that the incoming spikes evoke PSCs of identical shape and amplitude. The total input of the neuron is then taken to be $i(t) = \tau_s^{-1} \sum_{j=1}^{N} \sum_f \exp[-(t - t_j^f)/\tau_s] \theta(t - t_j^f)$ where $\theta(.)$ denotes the Heaviside step function with $\theta(s) = 1$ for $s > 0$ and $\theta(s) = 0$ for $s \leq 0$. It appears because of causality. We substitute the total input into Eq. (5) and integrate. This yields the membrane potential at the hillock,

$$u(t) = \sum\nolimits_{j=1}^{N} \left[\sum\nolimits_f \epsilon(t - t_j^f) \right] + \sum\nolimits_n \eta(t - t^n) \ . \tag{6}$$

The first term on the right in Eq. (6),

$$\epsilon(s) = \tau_m/(\tau_m - \tau_s)\ [\exp(-s/\tau_m) - \exp(-s/\tau_s)]\ \theta(s) \ , \tag{7}$$

describes the time course of an excitatory postsynaptic potential (EPSP). If $\tau_s = \tau_m$, we have instead of Eq. (7) the so-called alpha function, $\epsilon(s) = (s/\tau_m) \exp(-s/\tau_m)\, \theta(s)$. The second contribution to Eq. (6), $\eta(s) = -\vartheta \exp(-s/\tau_m)\ \theta(s)$, accounts for the reset of the membrane potential after each output spike and incorporates neuronal refractoriness.

4.2 The Threshold is not a Critical Parameter for Coincidence Detection

In a series of simulations, we have driven neurons by stochastic spike arrival generated at the time-dependent rate as given in Eq. (1). Figure 1 shows the quality factor γ as a function of the threshold ϑ. For various combinations of neuronal parameters (a–f in Fig. 1) there is always an *optimal* choice for ϑ that maximizes γ. Furthermore, γ exhibits a broad maximum and therefore depends only weakly on ϑ. In other words, the exact value of ϑ is *not* a critical parameter for coincidence detection. In contrast to that, γ varies strongly, if we change, e.g., the neuronal time constants τ_m and τ_s, the number N of synapses, or the number p of inputs spikes per period T, where $p/T = \bar{\lambda}^{\text{in}}$. We note that the mean output rate also depends strongly on ϑ. Along each

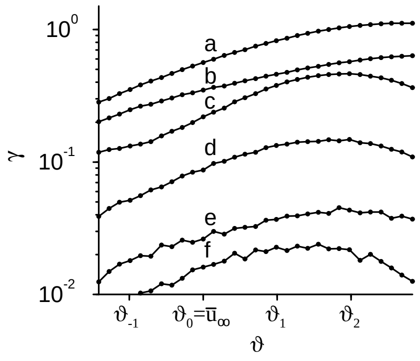

Figure 1. Coincidence detection properties depend on the value of the spiking threshold for different scenarios (a)–(f) of simulation parameters. The quality factor γ [in units of $T^{-1/2}I^{1/2}$, logarithmic scale; cf. Eq. (4)] shows a maximum always above the mean voltage $\bar{u}_\infty = \vartheta_0$, where $\bar{u}_\infty = N\,\bar{\lambda}^{\rm in}\,\tau_m = 200$. In practical situations it is immaterial, though, whether we take, e.g., $\vartheta_1 = 207$ or $\vartheta_2 = 213$. That is to say, the choice of the threshold is not critical because the maximum is broad. Simulation parameters are: (a) $\tau_m = \tau_s = T/4$, $Np = 800$; (b) $\tau_m = \tau_s = T/2$, $Np = 400$; (c) $\tau_m = T/2$, $\tau_s = T$, $Np = 400$; (d) $\tau_m = \tau_s = T$, $Np = 200$; (e) $\tau_m = 2\,T$, $\tau_s = T$, $Np = 100$; (f) $\tau_m = \tau_s = 2\,T$, $Np = 100$. To simplify comparison, parameters have been chosen so that the mean input current and, hence, $\bar{u}_\infty$ does not change between one simulation and the next. Each point corresponds to 10^4 output spikes (taken from Ref. 8).

graph in Fig. 1 the output rate $\bar{\lambda}^{\rm out}(0)$ varies by orders of magnitudes (data not shown).

Why is there an optimal threshold? If the threshold is low, the neuron basically acts as an integrator and is not sensitive to the temporal structure of the input. Hence, the coherence gain E is unity and the right-hand side of Eq. (4) vanishes. On the other hand, for very high values of ϑ the firing rate $\bar{\lambda}^{\rm out}$ approaches zero and so does the right-hand side of Eq. (4). Hence there must be an optimal value of ϑ in between. The idea dangling in the background is that of stochastic resonance [14]. Because of the stochastic spike arrival the membrane potential will always fluctuate around its asymptotic mean $\overline{u}$. The optimal threshold is around $\vartheta \approx \overline{u} + \Delta u$ where Δu is the standard deviation of the fluctuations [9].

In contrast to the quality measure γ, the coherence gain E increases monotonically with ϑ. [7,8] Using the coherence gain E as a measure for coincidence detection, we would therefore have totally missed the fact that there is an *optimal* threshold.

4.3 Analytical Expression for the Quality Factor

We are going to discuss and simplify a mathematical expression [8] for the quality factor of an I&F neuron at its optimal threshold. For $N\,\bar{\lambda}^{\rm in}\,\tau_m \gg 1$

an approximation to the maximum value of the quality factor is

$$\gamma_{\rm opt} \approx r^{\rm in}\,\sqrt{2\,N\,\bar{\lambda}^{\rm in}\,\tau}\,\frac{|\tilde{\epsilon}(\omega)|}{A\,\tau}\cdot\sqrt{\frac{I}{\tau^{\rm dec}+\tau^{\rm ref}}\,\frac{4}{\sqrt{54\pi}}}\quad. \tag{8}$$

The term $r^{\rm in}\,\sqrt{2\,N\,\bar{\lambda}^{\rm in}\,\tau}\,|\tilde{\epsilon}(\omega)|/(A\,\tau)$ on the right in Eq. (8) is the signal-to-noise ratio of the membrane potential of a neuron that receives spike input with vector strength $r^{\rm in}$ (cf. Sec.2) and rate $\bar{\lambda}^{\rm in}$ through N synapses. The symbol τ denotes the width of the integration window of a neuron (that can be approximated by the full width at half maximum of the EPSP), $|\tilde{\epsilon}(\omega)|$ is the absolute value of the Fourier transform of the EPSP at frequency $\omega = 2\pi/T$, A is the amplitude of the EPSP, I is the length of a time interval, $\tau^{\rm dec}$ is the time necessary for a decay of any fluctuation in the membrane voltage of the neuron (which is of the same order of magnitude as τ_m), and $\tau^{\rm ref}$ is the refractory period of the neuron. Equation (8) remains valid as long as the signal-to-noise ratio is smaller than or at least of order of 1.

We now simplify Eq. (8). Using $\tau_m = \tau_s$ the EPSP in Eq. (7) reduces to an alpha function. The absolute value of the Fourier transform then is $|\tilde{\epsilon}(\omega)| = \tau_m/\left(1+\omega^2\tau_m^2\right)$. If τ_m exceeds T, we obtain $|\tilde{\epsilon}(\omega)| \approx 1/(\omega^2\,\tau_m)$. Following Kempter *et al.* [8] we take $\tau^{\rm dec} = 3/2\,\tau_m$, $\tau^{\rm ref} = 2\tau_m$, $A\sqrt{\tau} = \sqrt{\tau_m/2}$ for I&F neurons, and are left with

$$\gamma_{\rm opt} \approx C\,r^{\rm in}\,\sqrt{N\,\bar{\lambda}^{\rm in}\,I}\;(T/\tau_m)^2 \tag{9}$$

where $C = 8.3\cdot 10^{-3}$. The membrane time constant τ_m and the number N of synapses are the relevant *neuronal* parameters for coincidence detection. Furthermore, the statistics of the input ($r^{\rm in}$, $\bar{\lambda}^{\rm in}$, and T) as well as the width of the time interval I determine a neuron's ability to read out a temporal code. The dimensionless fraction of time scales T/τ_m enters quadratically.

4.4 Application to Laminar Neurons

The membrane time constant (=decay time of the EPSP) of neurons in the nucleus laminaris is extremely short whenever the neuron is depolarized above resting potential. This is due to an outward rectifying current [11]. The data of Reyes *et al.* [11] on chicken – not an auditory specialist – suggest a time constant in the range of 0.2–0.5 ms, but for barn owls it may be even shorter. We therefore take $\tau_m = 0.1$ ms. [4] We consider a neuron in the 5 kHz channel, hence $T = 0.2$ ms. As for the other parameters, $N = 200$, $\bar{\lambda}^{\rm in} = 500$ Hz, and $r^{\rm in} = 0.5$ are reasonable [3]. We suppose an interval or 'waiting time' of $I = 100$ ms. From Eq. (9) we get an estimate $\gamma_{\rm opt} = 1.7$. In simulations with optimal threshold we obtain $\gamma = 0.9$ (Fig. 2), which is off by a factor of two.

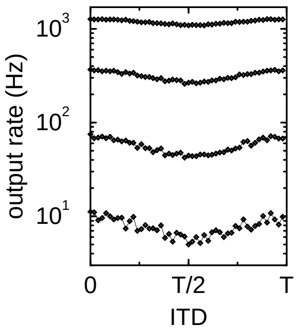

Figure 2. Numerical simulation of an I&F unit with parameters as given in Sec. 4.4 for a laminar neuron. We have plotted the output rate as a function of the ITD for four different threshold values ($\vartheta = 8, 7, 6, 5$ from bottom to top). To obtain ITD tuning curves, we have divided the synapses into two groups, viz., left and right, and 'delayed' one with respect to the other by the ITD as plotted on the horizontal axis. The minimum output rate is always at ITD $= T/2$, where input spikes arrive almost randomly with an effective input vector strength $r^{\text{in}} \approx 0$ [$\bar{\lambda}^{\text{out}} = 5.7, 43, 270, 1100\,\text{Hz}$]. The maximum output rate for coherent input ($r^{\text{in}} = 0.5$) occurs at ITD $= m\,T$ with integer m [$\bar{\lambda}^{\text{out}} = 10, 70, 370, 1260\,\text{Hz}$]. Though for different threshold values we obtain different coherence gains and output rates, which vary by orders of magnitude, the quality factor does not change that much ($\gamma = 0.2, 0.6, 0.9, 0.7$). Data points have been obtained by measuring the number of output spikes in a time interval of 10 s.

What does a quality factor of $\gamma \approx 1$ mean? We remind the reader of the definition of γ in Eq. (3). The quality factor measures the distance between the spike count distributions for random and coherent input. For $\gamma = 1$ the two distributions are just distinguishable and for $\gamma \gg 1$ they are well separated [6].

Even for values of γ smaller than 1, the system as a whole could still function as a coincidence detector, if there is a *pool* of neurons operating in the same pathway and receiving the same type of input. A system can either use the output spike count of a single neuron in an interval I or count the number of spikes of L statistically independent, identical neurons operating in the same pathway during a period of time I/L. [4]

Equation (9) is rather general and could be applied just as well to cortical neurons. With a realistic set of parameters, we [8] find that cortical neurons are as good in reading out a 40 Hz signal as laminar neurons are in reading out a 5 kHz signal, a result that may stimulate further discussions on the role of cortical neurons (integrator or coincidence detector) [1,10].

Acknowledgments

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