SPECTRAL PROPERTIES OF NEURONAL PULSE INTERVAL MODULATION

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ABSTRACT

We determine the power spectrum of an ideal neuron which encodes information using a pulse interval modulation scheme in continuous time. We develop this by considering the rigorous derivation of the Digital Pulse Interval Modulation (DPIM) coding scheme spectra of L. Vangelista et al. in the limit of the coding slot size approaching zero. We show in this limit the spectrum is identical to that of a filtered renewal process frequently used to model neuroscience time series data. Using this renewal theory equivalence we then use the ‘Fundamental Isometry Theorem’ developed by Win & Ridolfi to show that introducing firing time jitter (as a simple model for noise effects) removes non-Poisson structure and reduces the utility of spectral feature selection. Lastly we show with sufficient jittering that the Bartlett spectrum of any renewal process reduces to that of a Poisson process, with a spectral density consistent with Carson’s theorem for shot noise.

Index Terms— DPIM, renewal process, Fundamental Isometry Theorem, neural time series analysis

1. INTRODUCTION

Digital Pulse Interval Modulation (DPIM) is a communications scheme where information content is transmitted in the variable number of idle slot times between pulses [1]. The DPIM information transmission methodology is ideally suited for optical fibre communications where classical amplitude or frequency modulation techniques are non-trivial. The wide bandwidth offered by optical fibre motivates the use of particularly narrow pulses with low duty cycles which allows for low average, but high peak power. This property provides accurate signal detection at the receiver end during transmission over a noisy channel [2]. Carrying the information between the pulses also eliminates the need for the pulse times to be defined relative to a central clock.

These properties of robust transmission over noise, lack of a central clock and minimal energy expenditure are also ideal for information transmission of neurons. Indeed the concept of neurons transmitting information in the space between firing events has been considered as far back as [3] where it was shown that a DPIM coding scheme offers a far greater channel capacity than a binary on/off keying (OOK) coding scheme. Fundamentally the debate about rate vs time dependent coding is about *how* neurons encode information in the timing between spikes. Nevertheless there is a key difference between neuron information exchange and DPIM on communications channels. DPIM processes are discrete time processes embedded in continuous time. Although the signals being sent and received are occurring in continuous time, the pulse intervals are constrained to be separated by a discrete number of packets, termed slots or chips. Neurons have no such embedding and the firing times can occur at any point along the continuous time line. This issue is philosophically complicated by the fact that at some fine enough level of temporal resolution a neuron must consider a spike arriving at two different times to be the same spike.

This paper will do the following: Firstly simplify the closed form expression for the DPIM power spectra developed in [1]. Secondly show in the limit of unconstrained firing times (transforming from discrete to continuous firing times) that the DPIM spectra is equivalent to that of a renewal process, which is frequently used to model neuroscience time series data. We then show using the Fundamental Isometry Theorem developed in [4] that randomly displacing the firing times attenuates, but does not distort, the non-Poisson structure of the measured spectrum. Lastly we show that both purely periodic & Poisson (uniformly distributed) firing patterns are resistant to this spectral dampening, whereas firing regimes in between these extremes are susceptible, with consequences for spectral feature selection.

2. SPECTRAL EQUIVALENCE OF DPIM AND RENEWAL THEORY

The time intervals between pulses in DPIM are driven by some encoding strategy and thus is strictly speaking deterministic. Nonetheless from the receiver’s perspective, who does not know the message a priori, the series of gaps between the pulses is a random process. Neurons are most likely similar in the sense that the action potential timings are generated by highly nonlinear processes, with exceptionally rich and complex synaptic/dendritic connections, such that from the ‘perspective’ of a neuron the arriving pulse times are random variables. This is the basis for mathematical modeling of neuron firing times as stochastic point processes.

The time history of DPIM, $v(t)$, can be represented as follows [1]:

$$v(t) = \sum_{m=-\infty}^{m=+\infty} g(t - \tau_m T) \tag{1}$$

Where $g(t)$ is the pulse shape, characteristically a rectangle with a given duty cycle, T is the slot length and τ_m is a set of random integers indicating when a pulse occurs in terms of numbers of slots.

The power spectrum of this process contains both a continuous and discrete part which are both functions of the energy spectrum, $G(f)$, of the pulse shape. They are also both dependent on the the average pulse rate ν_b which is the inverse of the expected length (in number of slots) between pulses. The continuous component, $R_c(fT)$, termed the *Bartlett spectrum* in point process literature

[5], is best understood from the Weiner-Khinchtine theorem as the Fourier transform of the autocorrelation structure of the pulse times. The discrete component forms a Dirac comb with Dirac delta distributions $\delta(\cdots)$ spaced $f_m = m/T, (m \in Z)$ apart. This discrete component arises because the expectation of the signal is non zero $(\mathbb{E}\left[v(t)\right] \neq 0)$ [6]. Intuitively the repetition of the Dirac delta pulses can be understood because the discrete process is embedded in the continuous time, creating an effective Nyquist frequency (the inverse of the slot time) for the frequency structure to be periodic about. The spectrum of the DPIM process is determined in [1] as:

$$\begin{aligned} S_{\text{DPIM}}(f) &= \underbrace{\frac{1}{T}\left|G(f)\right|^2 R_{c,\text{DPIM}}(fT)}_{\text{Continuous}} \\ &+ \underbrace{\sum_{m=-\infty}^{+\infty} \frac{1}{T^2}\left|G(f)\right|^2 \nu_b^2 \delta(f-f_m)}_{\text{Discrete}} \end{aligned} \tag{2}$$

The *Bartlett spectrum* is given in [1] by the following evaluation of the Z transform on the unit circle:

$$\underbrace{R_{c,\text{DPIM}}(u)}_{\text{Bartlett Spectrum}} = \nu_b\left[\nu_b - 1 + 2\text{Re}\left(X(z)\Big|_{z=e^{2\pi j u}}\right)\right] \tag{3}$$

Where $X(z)$ can be understood to be the Z transform of the cumulative probabilities associated with the spacing (in number of slots) between two arbitrary pulses. We use an alternate definition of $X(z)$ defined in [7]:

$$X(z) = 1 + X(z)\sum_{\lambda=0}^{\infty} p[\lambda] z^{-\lambda} - \nu_b \sum_{\lambda=0}^{\infty} p[\lambda] \sum_{k=0}^{\lambda-1} z^{-k} \tag{4}$$

Where $p[\lambda]$ represents the probability of the pulse interval being λ slots long. We algebraically re-arrange (4) and evaluate the z transform on the unit circle as defined in (3) to show that this term depends on the characteristic function associated with the pulse arrival time random variables:

$$\begin{aligned} X(e^{j2\pi u}) &= \frac{1}{1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}} \\ &\quad -\nu_b \cdot \underbrace{\left(\frac{\sum\limits_{\lambda=0}^{\infty} p[\lambda] \sum\limits_{k=0}^{\lambda-1} e^{-2\pi j u k}}{1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}}\right)}_{\text{simplify}} \end{aligned} \tag{5}$$

We will now develop a simplified expression for the bracketed term in (5) (labeled simplify) by recognizing that the nested sum in the numerator can be re-written *except at zero frequency* using the geometric series formula and identifying that the probability mass function, $p[\lambda]$, must sum to unity:

$$\begin{aligned} \sum_{\lambda=0}^{\infty} p[\lambda] \sum_{k=0}^{\lambda-1} e^{-2\pi j u k} &= \sum_{\lambda=0}^{\infty} p[\lambda]\left(\frac{1-e^{-2\pi j u\lambda}}{1-e^{-2\pi j u}}\right) \\ &= \frac{\left(1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}\right)}{1-e^{-2\pi j u}} \end{aligned} \tag{6}$$

Substituting (6) into the numerator of the bracketed part of (5) (labeled simplify) and cancelling the common denominator & numerator term yields the following simpler expression:

$$\left(\frac{\sum\limits_{\lambda=0}^{\infty} p[\lambda] \sum\limits_{k=0}^{\lambda-1} e^{-2\pi j u k}}{1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}}\right) = \frac{1}{1-e^{-2\pi j u}} \tag{7}$$

Therefore:

$$X(e^{j2\pi u}) = \frac{1}{1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}} - \nu_b \cdot \frac{1}{1-e^{-2\pi j u}} \tag{8}$$

Note the identity:

$$2Re\left(\frac{1}{1-e^{-2\pi j u}}\right) = 1 \tag{9}$$

Thus taking the real part of (8) and using (9) yields:

$$2\text{Re}\left[X(e^{2\pi j u})\right] = 2\text{Re}\left(\frac{1}{1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}}\right) - \nu_b \tag{10}$$

Substituting (10) into (3), adding and subtracting unity yields:

$$R_{c,\text{DPIM}}(u) = \nu_b\left[1 + 2\text{Re}\left(\frac{\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}}{1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u\lambda}}\right)\right] \tag{11}$$

Thus we can write the power spectrum for the DPIM scheme in [1] as:

$$\begin{aligned} S_{\text{DPIM}}(f) &= \frac{\nu_b}{T}\left|G(f)\right|^2\left[\sum_{m=-\infty}^{+\infty} \frac{\nu_b}{T}\delta(f-\frac{m}{T})\right. \\ &+ \left. 1 + 2\text{Re}\left(\frac{\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j f\lambda T}}{1-\sum\limits_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j f\lambda T}}\right)\right] \end{aligned} \tag{12}$$

Note that if the pulse slot time approach zero, the expected gap (in units of the number of slots) between pulses will approach infinity. Thus the average rate of pulses (in units of the inverse of the number of slots) ν_b, will also approach zero. These limits will both converge to zero such that their ratio remains the statistical average rate of the number of pulses, $N(t)$, in units of time:

$$\lim_{\substack{T\to 0\\ \nu_b\to 0}} \frac{\nu_b}{T} = \nu. = \lim_{t\to\infty} \mathbb{E}\left(\frac{N(t)}{t}\right) \tag{13}$$

Note that as the pulse slot time approaches zero the discrete component of the spectrum will change from a train of Dirac delta pulses (spaced 1/T apart) to a single Dirac delta pulse (the *m* = 0 solution) centered at zero frequency.

$$\lim_{\substack{T\to 0\\ \nu_b\to 0}} \sum_{m=-\infty}^{+\infty} \frac{\nu_b^2}{T^2}\delta(f-\frac{m}{T}) \longrightarrow \nu^2\delta(f) \tag{14}$$

Also note that reducing the pulse slot length to zero allows the pulse times to occur at any point on the continuous time line. Thus the characteristic function will transform from a periodic DTFT for a discrete random variable to a non-periodic continuous Fourier transform for a continuous random variable:

$$\sum_{\lambda=0}^{\infty} p[\lambda] e^{-2\pi j u \lambda} \longrightarrow \int_{0}^{+\infty} p(t) e^{-2\pi f t} dt \equiv H(\omega) \tag{15}$$

Where $H(\omega)$ is the characteristic function of the Inter Spike Interval (ISI) of firing times. Thus the DPIM spectrum in the continuum reduces to:

$$\lim_{\substack{T\to 0\\ \nu_b \to 0}} S_{\text{DPIM}}(f) = \nu |G(f)|^2 \Bigg[\underbrace{1 + 2\text{Re}\left(\frac{H(\omega)}{1-H(\omega)}\right)}_{R_{c,DPIM}} + \nu\delta(f) \Bigg] \tag{16}$$

3. NEURAL RENEWAL SPECTRUM PROPERTIES

This spectrum (16) is the same as that derived for filtered renewal processes in [8], [9], [10]. Renewal theory describes a general class of continuous time stochastic processes where the time between events (in this case the firing of an action potential) is an independent identical distributed (i.i.d.) random variable. There is a wealth of literature using renewal processes to model neuroscience time series data [11], [12], [8]. A renewal process can be described by its *renewal density function*, $m(t)$, which can be written as an infinite series of convolutions of the ISI density function:

$$m(t) = \sum_{n=0}^{\infty} p(t)(*)^n p(t) \equiv p(t) + p(t) * p(t) + \cdots, \quad t \geq 0 \tag{17}$$

Each term in the series expansion of (17) represents the probability of any spike (the first, second, third etc ...) occurring at time t. Therefore the renewal density function can be seen as a 'spiking density function', indicating the probability of seeing a spike, irrespective of which spike, at time t. Note that this function does not integrate to unity, so the renewal density is not a true probability density. It can be shown by the Erdos-Feller-Pollard theorem [13] that the renewal density function asymptotes to the mean firing rate $\lim_{t\to\infty} m(t) = \nu$. This result can also be obtained in the less general case by applying the final value theorem to the Laplace transform of (17).

This renewal density function can be related to the Bartlet spectrum [8]:

$$2\text{Re}\left(\frac{H(\omega)}{1-H(\omega)}\right) = \mathcal{F}\left\{m(t) + m(-t) - \nu\right\}(\omega) \tag{18}$$

Thus the Bartlett spectrum can be seen to represent the deviation of the spiking density from uniformly distributed firing (Poisson counting statistics) as a function of frequency. This suggests that measurement of the Bartlett spectrum can provide insight into the underlying neural firing patterns. Indeed spectral analysis of neural time series data is widespread [8], [14] and feature selection based upon spectral properties of neurons modeled as point processes (a generalisation of renewal processes) was considered in [15].

A significant problem with this approach is that this Bartlett spectrum of the renewal process is remarkably resistant to closed form analysis. For example it is not possible to develop closed form expressions for the conditions for the presence of peaks, their locations or width or how rapidly the spectrum decays to zero. Instead we are forced to rely on heuristics to understand the Bartlett spectrum. For example if a neuron is firing perfectly periodically we would expect to see peaks in the power spectrum at the firing rate and its harmonics. Purely periodic firing represents one of the few cases we can develop an analytic expression:

$$\begin{aligned} H(\omega)_{\text{periodic}} &= \int_{0}^{\infty} \delta(t - \frac{1}{\lambda}) e^{i\omega t} = e^{(i\omega)/\lambda} \\ \sum_{n=1}^{\infty} H(\omega) + \sum_{n=1}^{\infty} H^*(\omega) &= \sum_{n=-\infty}^{\infty} \delta(\omega - n\lambda) \\ R_{\text{c,DPIM}}(\omega)_{\text{periodic}} &= \nu + \nu^2 \sum_{n=-\infty}^{\infty} \delta(\omega - n2\pi\lambda) \end{aligned}$$

As the variance increases we would expect to see the peaks get wider, and the higher order harmonics begin to disappear. As the variance is increased such that the firing pattern becomes maximally random (that is, it becomes a *Poisson* counting process) there would be no statistically expected deviation from uniformly distributed firing times and thus we would expect the Bartlett spectrum to be a constant. This is another case where an analytic expression for the Bartlett spectrum can be developed, and it can be shown [9], in agreement with Carson's theorem the Bartlett spectrum is a constant:

$$\begin{aligned} H(\omega)_{\text{Poisson}} &= \frac{\lambda}{\lambda - i\omega} \longrightarrow 2\text{Re}\left(\frac{H(\omega)}{1-H(\omega)}\right) = 0, \\ R_{\text{c,DPIM}}(\omega)_{\text{Poisson}} &= \nu + \nu^2 \delta(f) \end{aligned}$$

These two firing patterns represent extremes of the Weibull family of distributions for the ISI random variable:

$$p(t)_{\text{ISI}} = \left(\frac{k}{\lambda}\right) \left(\frac{t}{\lambda}\right)^{k-1} e^{-(t/\lambda)^k}, \qquad t, \lambda, k \geq 0 \tag{19}$$

Where λ and k are termed the scale & shape parameter respectively. When k is unity the maximally random Poisson statistics are recovered, whereas periodic firing occurs in the limit of the shape parameter, k, approaching infinity. The variance of the Weibull distribution is given by: $\sigma^2 = \lambda^2\Gamma(1 + 2/k) - \mu^2$. Notice that as k increases the variance decreases, and the Poisson solution has maximal variance. Between the two extremes of periodic and Poisson count firing statistics we can observe the Bartlett spectrum by parametrically fitting the ISI density function to the Weibull distributions and tuning the shape parameter. Examples of this process are shown for k = 1,5,10 and validate this heuristic approach.

There are two important points to observe from figure 1. Firstly, for the neuron firing with physiological rate of 30Hz there is no structure (beyond constant behavior) for all classes of firing (at least from the Weibull family) in the Bartlett spectrum above roughly 100 Hz. This intuitively makes sense, as you would not expect to see correlations in neuron firing patterns at frequencies which are not physiological possible for the neuron to fire at. Secondly there is no structure in the Bartlett spectrum for a Poisson counting process beyond constant amplitude equal to the mean firing rate.

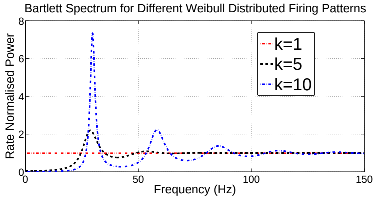


Fig. 1. Bartlett spectrum of Weibull distributions with different shape parameters k=1,5,10 for a neuron with mean firing rate of 30Hz. Notice that as the firing becomes less periodic (k decreases) the higher order harmonics will disappear, the remaining peaks get smaller and wider until eventually with Poisson counting statistics (k=1) the Bartlett spectrum shows no features.

4. SPECTRAL EFFECT OF JITTERING

In this section we explore how robust the spectral features of a neuron following renewal statistics are to noise. The noise sources on a neuron in a network are exceptionally complex. We model noise effects to the PIM encoding scheme in the simplest possible fashion of Gaussian displacements of the firing times. In the most general sense we can consider that noise will introduce variation to the membrane voltage, which in turn will introduce variation to when the neuron reaches threshold and fires, thus jittering the firing times. These ideas were formalised in [16] with a leaky integrate and fire model of a neuron subject to Gaussian white noise input. We show that the effect of the jittering is to attenuate, but not distort, the non-Poisson features of the Bartlett spectrum.

We consider the effect of the jittering on the spectral properties of the Bartlett spectrum rather than the full time series power spectrum. This is equivalent to considering the action potentials to be Dirac delta pulses ($g(t) = \delta(t)$, $|G(f)|^2 = 1$). This spectrum can be determined with aid from the Fundamental Isometry Theorem. Briefly this theorem allows for the determination of the spectrum of a *marked* point process when the spectrum of the original process and the statistics of the *marks* are known. It can be shown [4] that the jittering is easily accounted for as follows:

$$R_{\text{c,DPIM}}(\omega)_{\text{jittered}} = |\phi_z(2\pi f)|^2 R_{\text{c,DPIM}}(\omega) + \nu(1 - |\phi_z(2\pi f)|^2) \quad (20)$$

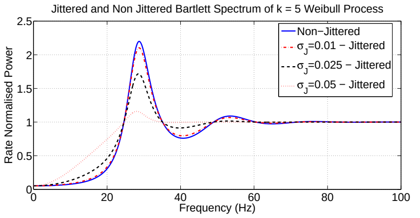
We consider that the firing times are independently jittered by a Gaussian random variable with mean μ_{J} and variance σ_{J}^2. Thus the absolute value squared of the characteristic function is $|\phi_z(2\pi f)|^2 = e^{-\sigma_J^2 f^2}$. Note that the effect of jittering is to randomise firing patterns, remove correlation structure and thus make the observed firing times more uniform. Using (20) the Gaussian jittered Bartlett spectrum is given by:

$$R_{\text{c,DPIM}}(\omega)_{\text{jittered}} = \nu \left[1 + 2e^{-\sigma_J^2 \omega^2} \text{Re}\left(\frac{H(\omega)}{1 - H(\omega)} \right) \right] \qquad (21)$$

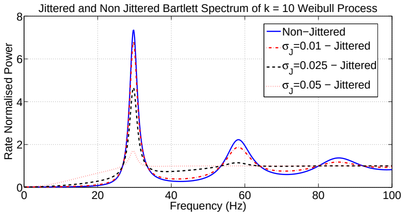
There are two points to notice about (21). Firstly jittering removes the non-Poisson structure, which represents deviations from uniformly distributed patterns, from the Bartlett spectrum at a rate exponentially proportional to the jittering variance. Secondly jittering has no effect on the Bartlett spectrum of a Poisson process, which already has uniform distributed firing times.

Figure 2 shows the jittered Bartlett spectrum of Weibull processes with shape parameters of k=5 (pseudo-periodic) & k=10 (strongly periodic) for different strengths of jittering ($\sigma_J = 0.01, 0.025, 0.05$ seconds). As a comparison the time constant of a leaky integrate and fire model of a Sub Thalamic Nucleus is 0.01 seconds [17]. Notice that, as expected, the larger the variance of jitter the more the features of the Bartlett spectra are reduced but not distorted. Notice also that the spectra of the more periodic Weibull process is more robust to jittering. This intuitively makes sense, as we expect it would require jitter of a higher variance to transform the more 'strongly' periodic processes to a maximally random Poisson process.

This result shows that the spectra of both the maximum (Poisson) and minimum (purely periodic) information entropy firing distributions are highly resistant to firing time jitter, whereas patterns in between these extremes are sensitive. This is especially true for nearly Poisson ($k \approx 1$) firing patterns. This is interesting for neural spectral feature selection because neurons can have highly variable firing patterns under different anatomical and physiological conditions. For example cortical neurons alone can display firing statistics ranging from Poisson to weakly periodic depending on anatomical area, anaesthetic state and behavioural task [18].



(a) Weibull Bartlett Spectrum, k =5



(b) Weibull Bartlett Spectrum, k =10

Fig. 2. Rate normalised jittered Bartlett Spectrum of a Weibull process with shape parameters (k) = 5 & 10, mean firing rate of 30Hz for different strengths of jittering (σ_J)

5. CONCLUSION

We have shown that the spectrum of a neuron performing a DPIM encoding strategy in continuous time is equivalent to a renewal process. We have shown that non-Poisson effects in the firing statistics manifest as features which may be detected in the low (<100Hz) frequency portion of the measured spectrum. We have shown that the effect of firing time jitter (as a simple model for noise) is to attenuate (but not distort) the non-Poisson features of the spectrum. We have shown that with sufficiently noisy jitter, all non-Poisson structure in the Bartlett spectrum is lost. We have identified that the spectra of near Poisson firing statistics are especially sensitive to this jitter. These identified properties may help guide future work attempting to estimate firing statistics of neurons from spectral analysis.

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