

A Unified Information Flow Model of Poisson-Type Brain Neuronal Network Activity

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Abstract—Understanding information transfer and representation in the brain is one of the most challenging scientific endeavors since neuroscientists are still far from converging to a solution with exact description. The main challenge in deciphering the neural code is the probabilistic nature of the neural codebook which maps stimuli to neural responses and vice versa. With the advent of recording techniques from single and multiple cells, it is becoming plausible to obtain large amount of experimental data against which theoretical models can be tested. In this respect, information theory can potentially provide a powerful framework for analyzing information content and representation in neuronal network activity. In this paper, we develop a simplified neuronal firing model which is mathematically complete and scalable. The model makes use of Poisson processes' properties and queuing theory. We also derive theoretical tools to measure, quantify, and set upper limits on information coded by the proposed model based on information theory. The designed measures take into account a general coding scheme in each neuron that combines temporal and rate coding of spike train responses of neurons. The proposed model along with the tools are generalized to quantify information in a population of neurons where correlation among neurons is modeled. The model also incorporates a spatial component which allows studying the amount of information gained from the spatial pattern of responses in a neuron population. Accordingly, the developed model and tools aim at providing a unified view of measuring information quantities and hence giving a better understanding of the neural coding.

I. INTRODUCTION

The mammalian brain is subject to a wide range of sensory stimuli ranging from simple to complex correlated stimuli. These stimuli are processed by a vast network of interconnecting neurons and are subsequently transformed into meaningful memories, decisions, and motor activities in relation to the outside world. The basic language by which neurons can communicate is composed of elementary alphabets known as spikes or action potentials -identical short discrete voltage pulses propagating among neurons over large distances without attenuation. Accordingly, neurons produce different spiking patterns which signify varying perceptions and give meaning to perceived stimuli. At a single neuron level, information about stimuli can be encoded by the number of spikes and their arrival times [1]. At a neural population level, stimuli could also be encoded in the spiking activity of many neurons with heterogenous properties and connectivity and hence distributed representation or spatial encoding becomes important.

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In trying to develop a general mathematical tool that describes the occurrence of spiking events in time and the nature of information transferred, noisy and random nature of neural coding quickly renders solutions incomplete. In fact, there is often a lack of one-to-one mapping between incoming stimuli and neural spiking, which necessitates developing probability dictionaries that map responses to stimuli and quantify the underlying randomness [2]. Discrete time processes such as Poisson models have been adopted in many studies as they have been considered relatively accurate in many scenarios and more importantly they are analytically tractable. It is plausible that several forms of coding actually coexist in varying proportions in different sensory systems. The different forms of neural codes often described by neuroscientists are either the time average of spiking or the firing rate (called rate coding), or the timing of individual spikes on a discretized time axis or spike-timing (called temporal coding) [3], or a combination of both.

With the advent of single and multiple microelectrodes recording techniques as well as new brain imaging methods, it is becoming increasingly plausible to observe neural responses in awake animals. This data availability can subsequently allow for developing and testing various statistical and information-theoretic approaches that aim at understanding the neural code. Statistical approaches are widely used in literature to solve the neural encoding/decoding problem (relating stimuli to responses and vice versa) as in the stimulus-response curves or tuning curves [4], [5], [6], spike-triggered average stimulus, and response-conditional ensembles [7]. Additionally, system identification techniques may be used to find the optimal estimator or decoding algorithm [7]. Information-theoretic approaches aim on the other hand at understanding the information content and transfer among neurons. While most commonly encountered in communication engineering, information theory [8] also provides a general framework for information analysis in many other fields [9].

In computational neuroscience, information theory allows to set limits on information transfer, quantify the amount of information carried and neuronal capacity, as well as estimate the neural code reliability and efficiency. Several examples in the literature use information theoretic measures and associated concepts, such as entropy, mutual information and capacity to (i) compare information content between rate and temporal coding [7], (ii) to set upper and lower bounds in estimating information between responses and stimuli in encoding/decoding neural problems [7], [10], and (iii) to study the effect of correlations among neurons in estimation

problems [11].

In this paper, we develop a scalable model to represent firing responses of neurons and subsequently use information theory, specifically an entropy measure, to quantify the amount of information conveyed by the response of a neuronal population. This developed measure incorporates the aforementioned forms of neural coding: rate, temporal, and spatial. It can therefore be used *as a benchmark to evaluate how close a neural system or subsystem come to the performance limits specified by the theory under each or combination of the coding schemes*. We develop the theoretical tools that can help understand the underlying properties of neurons and measure the amount of information which can be processed in the brain in a unified view starting from a single neuron and generalizing to a population of neurons. For single neurons, we model the spike train sequence as a homogeneous Poisson process thus combining the rate coding and temporal coding into one general scheme. For populations of neurons, we come up with a correlation model that can describe dependence among neurons in a population and induce this quantity in the entropy information measure of neuron population. We also incorporate an original concept of adding a spatial component when dealing with neuronal populations that is believed to induce additional information different from that induced by correlations.

II. BACKGROUND

A. Spike Generation

For simplicity, we will think of neurons as three parts: synapses which the input ports along the dendritic tree and cell body and allow for spike-to-current conversion (D/A conversion), the soma and intracellular channels which accumulate current (conductances, capacitance) and thus perform computations in the analog domain, and the axonal initial segment which generates stereotypical pulses when membrane potential reaches a critical threshold (A/D conversion). A single neuron interconnects with others via thousands of input ports (synapses). An arriving spike to a synapse creates a Post Synaptic Potential (PSP) which changes in the membrane potential, either by positive current injection towards spike threshold (called excitatory or EPSP) or negatively away from threshold (called inhibitory or IPSP). Note that EPSPs can summate spatially or temporally to generate an action potential whereas even if the number of EPSPs is sufficient to generate a spike, IPSP can prevent the generation as depicted in Fig. 1.

B. Information Theory Definitions

The basic element in information theory is the concept of entropy whose properties agree with the intuitive notion of information measure. The entropy of a discrete random variable X with realizations x is defined as

$$H(X) = - \sum_x p(x) \log p(x), \quad (1)$$

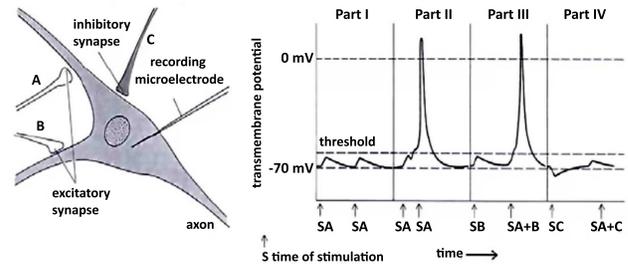


Fig. 1. Action Potential Generation [12]. Neurons A and B have excitatory synapses with the neuron whereas C has an inhibitory synapse. In part I, the occurrence of two spikes from neuron A is not sufficient to raise the membrane potential beyond the spiking threshold since they are far temporally from each other. In part II, the difference in time is sufficient to generate a spike. In part III, spikes from neurons A and B add up spatially to induce a spike. In part IV, the spike from neuron C inhibits the generation of spikes in the neuron.

where $p(\cdot)$ is the Probability Mass Function (PMF) of X . Entropy measures the uncertainty or "surprise" of a random variable and hence quantifies the inherent information in a random variable.

The entropy of a random variable X taking n possible values may be lower and upper bounded by

$$0 \leq H(X) \leq \log(n). \quad (2)$$

The left-hand side inequality is satisfied with equality if and only if X is deterministic ($p = 1$ for some event and 0 for others), while the right-hand side is satisfied with equality if and only if X has uniform distribution, i.e. all outcomes are equiprobable. This is intuitively consistent as there is maximum uncertainty and knowing any outcome provides us with maximum amount of information.

When a random variable with only two realizations is defined with probabilities λ and $1 - \lambda$, the entropy is referred to as *binary entropy* and denoted as

$$H(X) = -\lambda \log \lambda - (1 - \lambda) \log(1 - \lambda) \stackrel{def}{=} H(\lambda). \quad (3)$$

For a continuous random variable Y , a similar measure is defined known as *differential entropy* expressed as

$$h(Y) = - \int_{\mathcal{S}} f(y) \log f(y) dy, \quad (4)$$

where $f(\cdot)$ is the probability density function (pdf) of Y and \mathcal{S} is its support.

Differential entropy may also be used as an information measure by comparing the gain of information for one continuous random variable relative to another, and hence can be negative.

The conditional entropy of a random variable X given another random variable Y is

$$H(X|Y) = - \sum_x \sum_y p(x, y) \log p(x|y). \quad (5)$$

The chain rule of entropy is defined as

$$H(X_1, \dots, X_n) = H(X_1) + H(X_2|X_1) + \dots + H(X_n|X_{n-1}, \dots, X_1). \quad (6)$$

If $X_1 \cdots X_n$ are independent, this implies that

$$H(X_1, X_2 \cdots X_n) = H(X_1) + \cdots + H(X_n). \quad (7)$$

Random variables X, Y, Z are said to form a *Markov chain* in that order denoted as $X \rightarrow Y \rightarrow Z$ if X and Z are conditionally independent given Y . Then,

$$\begin{aligned} H(Z, X|Y) &= H(Z|Y) + H(X|Y) \\ H(Z|X, Y) &= H(Z|Y). \end{aligned} \quad (8)$$

Another important concept in information theory is the mutual information between two random variables X and Y expressed as:

$$I(X; Y) = H(X) - H(X|Y). \quad (9)$$

Mutual information quantifies the amount of information X tells about Y and viceversa and hence it is a measure of strength of dependence between random variables having a zero value when the latter are independent.

A more exhaustive treatment of information theory concepts, definitions and proofs can be found in [9].

C. Information Theory and Neural coding

Information theory has the advantage of taking into account exact probability distributions with various complexities, it allows us to compute maximum rate of information transfer (capacity), and it can deal with nonlinear models [2]. It also results in a meaningful measure of information because it is dimensionless, and thus enables the comparison of the performance of the neural code across neurons, stimulus modalities, sensory systems, and species [13]. In this paper, we will focus on computing the entropy based on the developed Poisson model, so that available information can be quantified, and that reliability and efficiency can be investigated.

Mutual information is widely used in the literature on encoding/ decoding problems since it reveals the dependence between stimulus and response. Although we are not currently seeking to solve such problems, calculating the entropy of neuron responses is a key element in mutual information estimation since it limits the amount of information revealed by the response about the stimulus (mutual information is upper bounded by the entropy as shown in (9)). Accordingly, coming up with a model that describes neuron spiking along with computing its inherent entropy is the first step towards solving neural coding problems and information transfer among neurons.

III. NEURON MODELING

A. Individual Neuron Model

Based on the neurophysiology of neural spiking in mammalian brain, a description of the firing response in a single neuron should take into account two main properties: (i) The occurrence times of any number of events or spikes, and (ii) The stochastic nature of the response.

The most appropriate mathematical tool that can characterize the response taking into account these two properties

is the point process theory where the neuron response spike train can be fully represented by a discrete stochastic point process characterized by a specific Conditional Intensity Function (CIF). The type of the point process model, is chosen to match experimental data collected on neural response variability. We will here approximate the neuron's spike train response by a Poisson process* as is observed experimentally by several workers in different sensory systems (see for example [10], [6] and references therein). In particular, recordings in the brain from regularly spiking neurons (non-bursting neurons) in the medial temporal (MT) area of the extrastriate cortex, a region that plays an important role in processing motion information, of trained monkeys while performing direction discrimination tasks often show an interspike interval distribution similar to the exponential distribution [14], [15], [16], which is a characteristic of a Poisson process. In addition, recordings from neurons in other regions of the brain such as the primary visual cortex (VI) of trained monkeys in response to bars and textured stimuli [17] also show similar distribution. Some studies adopted inhomogeneous (i.e., variable firing rate) processes and noisy models [18], [19], other studies assumed inhomogeneous model under natural conditions or stimuli [20]. Even though they establish that inhomogeneous Poisson models are richer in terms of information and may be more appropriate, we limit ourselves to homogeneous model in this paper. Also note that neurons with bursting behavior and those whose responses in general deviate from the Poisson description are excluded from our study.

Quantifying the amount of information in a neuron is achieved by computing the entropy of the spike train. Assuming a homogeneous process with fixed rate ρ , we need to calculate the entropy $h(P)$ where the response P is described by a Poisson process [21], [22]. If t is the length of a window under consideration, the number of spikes n in t follows a Poisson distribution denoted as

$$p(n, t) = Pr(N(t) = n) = \frac{(\rho t)^n e^{-\rho t}}{n!}, \quad \text{for } n \geq 0 \quad (10)$$

where $N(t)$ is the number of arrivals from 0 to t sec.

The vector of spike arrival times is denoted by the random vector $\mathbf{s} = \{s_1, s_2, \cdots, s_n\}$ where s_i is the arrival time of the i^{th} spike in t or is also known as the i^{th} epoch. The joint distribution of the arrival epochs conditional on a specific number of spikes $N(t) = n$ follows an ordered uniform distribution described as

$$\begin{aligned} f\{(s_1, \cdots, s_n) | N(t) = n\} &= k_n(\mathbf{s}, t) = \frac{n!}{t^n}, \\ \text{for } 0 < s_1 < \cdots < s_n < t \end{aligned} \quad (11)$$

Using (1) and (4), $h(P)$ is calculated using the product of

*The conditional Intensity function of a Poisson process is independent of history. In other words, a Poisson process is a point process whose inter-event arrival times are Independent and Identically Distributed (IID) and follow an exponential distribution. It is also noted that the number of events in a specified window of time follows a Poisson distribution.

the two probability distributions (10) and (11) as:

$$\begin{aligned} h(P) &= - \sum_{n=0}^{\infty} \int_{s_1, s_2, \dots, s_n} ds_1 \cdots ds_n p(n, t) \cdot k_n(\mathbf{s}, t) \cdot \\ &\quad \ln[p(n, t) \cdot k_n(\mathbf{s}, t)] \\ &= \rho t (1 - \ln \rho). \end{aligned} \quad (12)$$

The entropy of a Poisson process computed in (12) is a general information measure that combines the entropy measures of spike count and temporal coding which are usually computed separately in literature [23], [7], [3]. It is advantageous to compute the entropy of the whole process rather than computing two components separately since the latter method overestimates the amount of information. On the other hand, combining both coding schemes is more realistic since the number and arrival times of the spikes are related by the assumed underlying point process.

Since the entropy calculated in (12) is a differential entropy, it can be negative and does not reveal information on absolute scale, hence it should always be measured in relative to another quantity as discussed in section II-B. In our subsequent work, we use the discrete entropy rather than the differential entropy for several purposes. First, it can represent information on an absolute scale. Second, in the model we propose in section III-B, we compute the entropy of some discrete random variables that follow a Bernoulli distribution to describe the connection between neurons, and for the objective of consistency, we consider solely discrete entropies.

To find the discrete version of $k_n(\mathbf{s}, t)$ denoted as $k'_n(\mathbf{s}, t)$, the window t under consideration is binned with resolution δ into t/δ bins and hence

$$k'_n(\mathbf{s}, t) = \frac{n! \cdot \delta^n}{t^n}. \quad (13)$$

Now the discrete entropy to be used in our modeling is calculated by substituting $k'_n(\mathbf{s}, t)$ in (12)

$$H(P) = \rho t (1 - \ln(\rho \delta)). \quad (14)$$

Note here that the “discretization” is biologically justified. The resolution δ can be thought of as the absolutely refractory period[†] and based on our approximation, the probability of having more than one spike in this period is to the first order zero.

The developed measure is mathematically complete and may be readily calculated.

B. Neuron Pair Modeling

In this section, we model a neuron pair P_1 and P_2 and quantify the amount of information available in the pair by computing the joint entropy $H(P_1, P_2)$. Fig. 2 shows a pair of connected neurons and is translated to the block diagram shown in Fig. 3.

[†]Absolutely refractory period is the time interval following a generated spike through which a second stimulus, no matter how strong it is, cannot initiate a second action potential. The absolutely refractory period lasts for about 1ms limiting the firing rates to a maximum of 1000Hz [3].

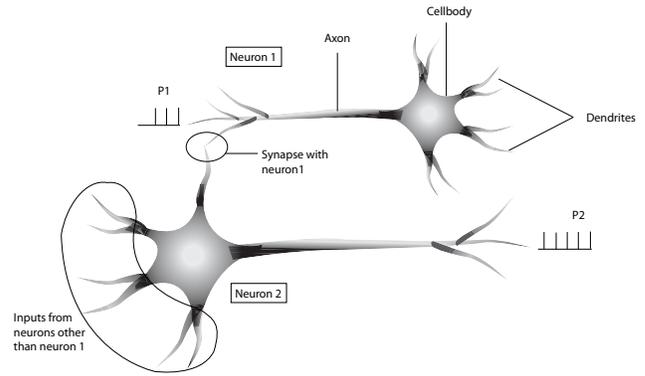


Fig. 2. Neuron Pair Model: the axon of neuron 1 terminates at the dendrites of neuron 2; the output of neuron 2 is affected by the output of neuron 1.

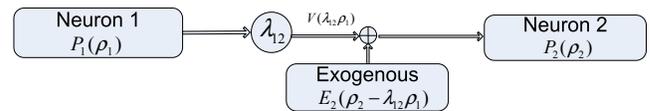


Fig. 3. Neuron Pair block diagram: $M(\mu)$ notation refers to a Poisson process M with rate μ . Parameter λ represents the synaptic connection.

1) *Model Description:* Neurons 1 and 2 are two Poisson processes denoted by P_1 and P_2 described by their rates ρ_1 and ρ_2 respectively. The spike train of P_2 is divided into two components. (i) One component is the result of the input/s from neuron 1 that synapse with neuron 2. Neuron 1 affects neuron 2 in the following manner; given that neuron 1 generates a spike at some time t_0 , neuron 2 generates a spike with probability λ_{12} resulting in V which is a Poisson process with rate $\lambda_{12}\rho_1^{\ddagger}$ [21]. (ii) The other component is the result of some exogenous contribution from neurons that synapse with neuron 2 dendrites and cell body other than neuron 1. All these inputs are lumped and modeled as a Poisson process E_2 with rate ρ_{E_2} . Since V and E_2 are independent Poisson processes, P_2 is a Poisson process with rate equals to the summation of the input rates ($\rho_2 = \rho_V + \rho_{E_2}$) [21]. Hence, the rate ρ_{E_2} is equal to $\rho_2 - \lambda_{12}\rho_1$ (see Fig. 3). The parameter λ_{12} is a parameter that depends on the strength of correlation between the two neurons as well as the state of neuron 2 in terms of how close its membrane potential is to the critical threshold of spiking. Two extreme cases are identified:

- (i) If $\lambda_{12} = 0$, this means that the generation of a spike in neuron 2 is independent of neuron 1. This can be due to a very low membrane potential relative to the threshold such that spikes from neuron 1 are insufficient to provoke a spike in neuron 2. Another interpretation could be the lack of common synapses between the two neurons.
- (ii) If $\lambda_{12} = 1$, this means that every spike in neuron 1 generates a spike in neuron 2. This can be due to either a strong connection between the two neurons (axon synapses with multiple dendrites) or a very high

[‡]This is a property of subdividing a Poisson process used in queuing applications.

membrane potential relative to the threshold that a single spike can trigger a spike in the other neuron.

Depending on the scenario under study, the parameter λ could include many factors such as the number of common synapses, physical distance between neurons, activity of neurons, degree of synchrony, or other factors that might contribute to correlations among neurons.

2) *Joint entropy*: The information content in the described neuron pair scheme is quantified by calculating $H(P_1, P_2)$ as follows, using (6)

$$H(P_1, P_2) = H(P_1) + H(P_2|P_1). \quad (15)$$

In order to find $H(P_2|P_1)$, we note that

$$H(P_2|P_1) = H(P_2|V, P_1) - H(V|P_1, P_2) + H(V|P_1). \quad (16)$$

Computing the first term of (16) is based on the fact that $P_1 \rightarrow V \rightarrow P_2$ form a Markov chain. By (8)

$$\begin{aligned} H(P_2|V, P_1) &= H(P_2|V) = H(E_2 + V|V) \\ &= H(E_2|V) = H(E_2), \end{aligned} \quad (17)$$

since E_2 and V are independent processes. Next, note that the second term of (16)

$$H(V|P_2, P_1) = 0, \quad (18)$$

since given the spike sequences of P_1 and P_2 , V can be perfectly identified. This is true under the assumption that given a spike at a some time t_0 in P_1 , the probability of having a spike in P_2 at t_0 as a result of E_2 is zero to the first order, hence the spike is the result of V (see Fig. 4).

To find the last term of (16) $H(V|P_1)$, we define a random vector Z^n , where given the occurrence of the i^{th} spike in P_1 , $Z_i = 1$ if a spike occurs in V and $Z_i = 0$ otherwise. The length of Z^n is n_1 such that the total number of spikes in P_1 , $N_1 = n_1$. Using (6), we have

$$\begin{aligned} H(V, Z^n|P_1) &= H(V|P_1, Z^n) + H(Z^n|P_1) \\ &= H(V|P_1) + H(Z^n|V, P_1) \\ H(Z^n|V, P_1) &= H(V|P_1, Z^n) = 0, \end{aligned}$$

since if V and P_1 are known, Z^n can be identified, and given Z^n and P_1 , V can also be identified uniquely. Therefore,

$$H(V|P_1) = H(Z^n|N_1), \quad (19)$$

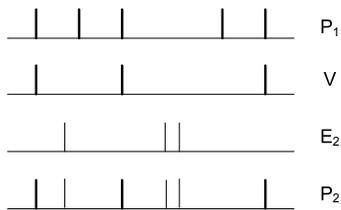


Fig. 4. Example of spiking patterns of the processes in the neuron pair model. V is the result of P_1 , P_2 is the sum of E_2 and V .

Since Z_1, \dots, Z_n are independent and identically distributed random variables,

$$H(Z^n|N_1 = n_1) = n_1 H(Z_1) = n_1 H(\lambda),$$

where $H(\lambda)$ is the binary entropy defined in (3). Averaging $H(Z^n|N_1 = n_1)$ over n_1 , we get

$$H(V|P_1) = H(Z^n|N_1) = \rho_1 t H(\lambda). \quad (20)$$

Substituting (17), (18), and (20) in (16), we get

$$H(P_2|P_1) = H(E_2) + \rho_1 t H(\lambda) \quad (21)$$

Substituting (21) in (15) and using (14), the total amount of information quantified in the modeled neuron pair is

$$\begin{aligned} H(P_1, P_2) &= \rho_1 t (1 - \ln(\rho_1 \delta)) \\ &\quad + (\rho_2 - \lambda_{12} \rho_1) t [1 - \ln((\rho_2 - \lambda_{12} \rho_1) \delta)] \\ &\quad + \rho_1 t H(\lambda_{12}). \end{aligned} \quad (22)$$

If $\lambda_{12} = 0$, $H(P_1, P_2) = H(P_1) + H(P_2)$, and the neurons' responses are independent. If $\lambda_{12} = 1$, $H(P_1, P_2) = H(P_1) + H(E_2)$.

The neuron pair model described above is a simple model where the connection is unidirectional, i.e. neuron 2 response is affected by neuron 1 response and not vice versa. However, we might have reciprocal connections between neurons, that is the axon of neuron 1 might terminate at the input ports of neuron 2 whose axon terminates at the input ports of neuron 1, hence forming a closed loop. This type of connection is currently being studied especially that it introduces some constraints on our mathematical model (the Poisson model) which should be treated in a biologically justified way.

C. Neuron Population Modeling

The nervous system is a hierarchy of organized interconnected structures starting from the neuron, the basic structure, to networks, maps, systems, and central nervous system (CNS). Interconnected neurons can show complex behavior and lead to higher information processing capabilities not present in a single neuron. One repeated stimulus, even a highly specialized stimulus with a single feature, can elicit responses in different neurons. In addition, a single neuron responds in different ways to multiple features. These two observations support distributed coding (population of neurons) rather than localized coding (single neuron) [3]. Furthermore, in most tasks, behavioral decisions are done during short times after stimulus presentation where only few spikes are relevant, which supports the idea of population averaging referred to as instantaneous rate [3], [7]. Population coding also makes sense in terms of brain robustness against loss of neurons which is a powerful advantage in information processing [3]. Accordingly, and since neurons may convey information collectively, quantifying the information present in a neuron population as a whole rather than individually is an important research question.

For a population of neurons of size $N \geq 2$, the amount of information can be quantified in a similar analysis to that performed in section III-B and the joint entropy $H(P_1, \dots, P_N)$

is quantified. For example, three neurons can be modeled as shown in Fig. 5. The amount of information, $H(P_1, P_2, P_3)$ is calculated to be

$$\begin{aligned} H(P_1, P_2, P_3) &= H(P_2, P_1) + H(P_3|P_2, P_1) \\ &= \rho_1 t(1 - \ln(\rho_1 \delta)) + \rho_2 t(1 - \ln(\rho_2 \delta)) \\ &+ [\rho_3 - \lambda_{13}\rho_1 - \lambda_{23}\rho_2] t \left[1 - \ln[(\rho_3 - \lambda_{13}\rho_1 - \lambda_{23}\rho_2)\delta] \right] \\ &+ \rho_1 t H(\lambda_{13}) + \rho_2 t H(\lambda_{23}). \end{aligned}$$

If $\lambda_{23} = 0$, then $H(P_1, P_2, P_3) = H(P_2) + H(P_1, P_3)$ which is the joint entropy of neurons 1 and 3, in addition to the information in the remaining neuron (neuron 2) in the population under consideration.

Other topologies including closed loops among neurons in addition to reciprocal connections are currently being investigated. We seek to extend the model along with the information theoretical measures, to a matrix of neurons with all possible interconnections in between as depicted in Fig. 6 and its connectivity matrix:

$$\mathbf{C} = \begin{pmatrix} 1 & \lambda_{12} & \lambda_{13} \\ \lambda_{21} & 1 & \lambda_{23} \\ \lambda_{31} & \lambda_{32} & 1 \end{pmatrix}$$

Other schemes can be studied by direct application of the developed theoretical results. Depending on an experimental paradigm with some given parameters, the amount of information can be quantified and studied as a function of the model variables, i.e. neurons' rates, exogenous inputs, and connection parameters. From the above discussed measures, we notice that the application of the developed tools to realistic models is computationally simple. Furthermore, the tools can be easily scaled to larger neuronal networks.

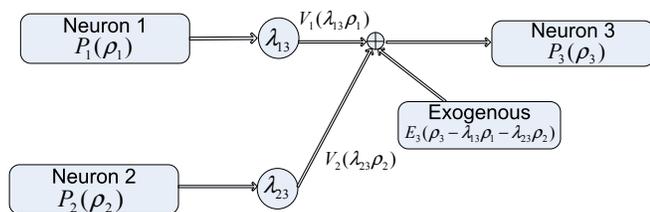


Fig. 5. Three Neurons block diagram: Neurons 1 and 2 are independent. $M(\mu)$ notation refers to a Poisson process M with rate μ

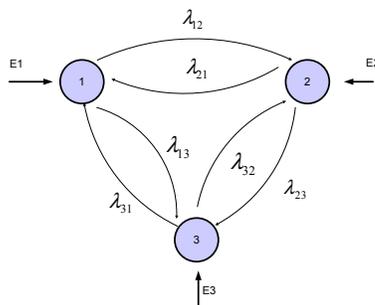


Fig. 6. Triplet bidirectional model.

D. Spatial Component

In the previous sections, we have quantified the amount of information present in a population of neuron taking correlations into account. We believe that even if a set of neurons in a population are independent, the different patterns of their activity spatially can induce additional information to that obtained from their individual activity. Denote the spatial component by an *independent* random variable Y . Now, the total amount of information in a neuron population of size N is

$$H(P_1, \dots, P_N, Y) = H(P_1, \dots, P_N) + H(Y).$$

$H(P_1, \dots, P_N)$ can be computed as described above, so we need to evaluate $H(Y)$. For N neurons, Y has a maximum of $N!$ different arrangements. Using (2), the information content of this arrangement assuming all states are identically and independently distributed is

$$H(Y) = \ln(N!). \quad (23)$$

Equation (23) is an upper limit or a maximum value since it assumes that all responses are different and IID.

For example, in a pair of neurons, the spatial component can add one bit of information to the total information. Hence, the amount of information gained from the contribution of the spatial component in a neuron population could be a significant amount.

Assume we have a population consisting of N independent neurons, and we need to study the percentage gain induced by the spatial component (23) to the total amount of information present in the population as a function of N and the firing rate. Using (7), (14) and (23), the total amount of information present in a population of N independent neurons each firing with rate ρ is

$$\begin{aligned} H_{total} &= H(P_1(\rho)) + H(P_2(\rho)) + \dots \\ &+ H(P_N(\rho)) + \ln(N!) \\ &= N \cdot \rho t(1 - \ln(\rho \delta)) + \ln(N!). \end{aligned} \quad (24)$$

To study the effect of the spatial component, we plot the ratio of $\ln(N!)$ to the total information (24) in Fig. 7. Note that the resolution δ is set to 1msec and t which is the window over which spike sequences are observed is set to 100 msec. The value of t is chosen in accordance to a typical behavioral decision time. For example in the primary visual cortex of monkeys, texture discrimination can range from 50 to 100 msec [17]. Similar response time is found in comparable cells in cats [24] and in 'place cells' of rats [25]. We can notice that for any fixed firing rate of the neurons, as N increases, the contribution of the information induced by the spatial component to the total amount of information in the neuron population increases as well. However, at high rates, there is no significant contribution of the spatial component as the population size increases. Increasing the population size N at high rates doesn't increase the amount of information. On the other hand, at relatively low rates, i.e. up to 50 Hz, the contribution of the spatial component is significant and can reach up to 30%. As the rate increases,

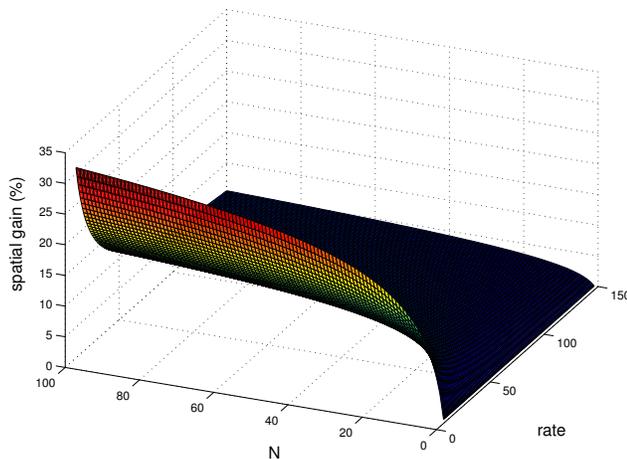


Fig. 7. Spatial gain in percentage as a function of the number of neurons N and the rate ρ .

increasing the population size becomes irrelevant in terms of information representation. This observation is justified from experimental evidence in neuroscience. It is observed that most sensory and cognitive tasks which are general, i.e. need general description such as viewing a picture as a whole, stimulate large population of neurons that oscillate at low rate to insure the spread of the message reliably among neurons. Whereas specific tasks such as those that describe fine details or delicate motor activities stimulate specific individual neurons with relatively higher rates.

Another observation is that at some fixed relatively low rates, the increase in the spatial gain is higher for lower values of N . In other words, the slope is sharper for smaller population sizes and flattens out for large populations. The interpretation here is that there is some "optimal" population size involved in representing information beyond which the information gain is not significant.

IV. CONCLUSIONS AND FUTURE WORK

In this work, we modeled neuronal responses as Poisson processes and developed a correlation model describing multiple neurons. We quantified the amount of information present in our model taking into account the inherent information in an individual neuron, correlations among multiple neurons, and information gained from spatial pattern of activity. Combining all of these components in the presented information measures enables getting a full picture of the information content in neurons and hence setting more realistic and meaningful limits on information with a minimal number of assumptions as possible.

The importance of the developed model lies in the theoretical analysis of the brain in a unified view taking into account biological justifications. Moreover, the theoretical results are scalable to larger neuronal networks and are computationally simple. Another important aspect of the Poisson modeling of neurons which takes into account the number and arrival times of the spikes in one scheme is that it allows us to set more realistic and meaningful information limits. This

is due to the fact that the two components describing the spikes (number and arrival times) are related by the assumed underlying process whereas thinking of the components as separate entities can overestimate the amount of information.

Other complex schemes in terms of cyclic and reciprocal connections among neurons are currently being investigated with some induced constraints and assumptions that should be mathematically and biologically justified.

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