THE NEURAL MULTIPLE ACCESS CHANNEL

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Abstract. In many systems, independently encoded information must at some point be transmitted over the spike train of one neuron. We introduce a method for quantitatively studying the effects of the signal encoding and transmission processes on the rates of transmission of multiple sources of information over one spike train, using the multiple access channel model from network information theory. To illustrate this method we study the effects of a small set of synaptic input patterns and input signal power spectra on the capacity region of a simple three-neuron system.

1. INTRODUCTION

Many people have been interested in recent years in characterizing the information transmission capabilities of sensory neurons. The typical approach to these problems is roughly as follows. One records spike trains from one or a few neurons while varying a single external sensory stimulus. One then attempts to approximately calculate the Shannon mutual information between the sensory input signals and the neural output signal ([2]). In such an approach, the underlying mechanims determining the stochastic input/output mapping are treated as an inaccesible "black box."

In this paper, we present results and simulations which extend this paradigm to include situations where single neurons encode and transmit information contained in more than one incoming signal. "Multiplexing" or combining of information is likely to be important at multiple levels of neural information processing. For example, simple cells in primate primary visual cortex are thought to receive convergent input from P and M retino-thalamo-cortical streams. These streams encode image information in distinct, though partially overlapping, spatial and temporal frequency bands. Presumably, simple cell responses reflect an integration of information from both P and M streams, so that simple cells simultaneously transmit P and M cell derived information. We consider the question: Supposing multiple "senders" of neural information must transmit their information through a common neuron, what strategies will allow (1) maximal transmission of information from only one of the senders, or (2) maximum simultaneous transmission of information from both senders? We have begun to explore the issue of transmission of multiple information sources over the spike train of one neuron by considering a highly simplified model system involving only three neurons, two presynaptic and one postsynaptic. The universe of alternative encoding strategies is severly limited for tractability: each presynaptic neuron encodes random signals from one of three power spectra and makes synaptic contacts with the postsynaptic neuron in one of four patterns; see below. We develop a way of comparing the 78 possible scenarios (taking account of symmetric configurations) by mapping these issues onto the well studied multiple access channel from network information theory. The aim of this
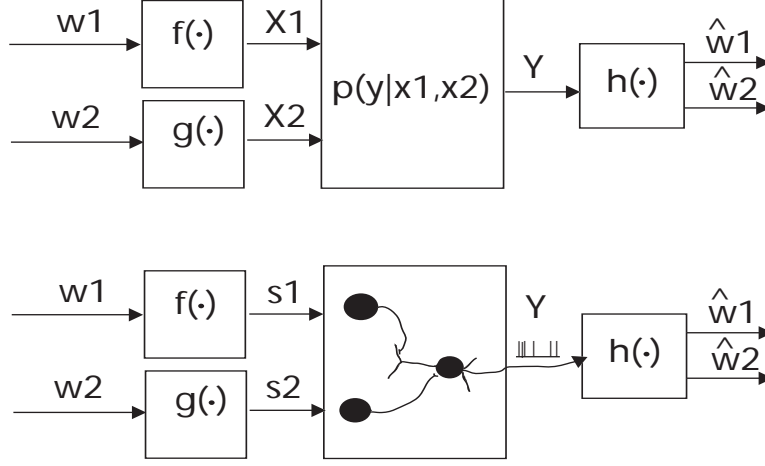
FIGURE 1.1. Multiple Access Channel and Equivalent Neural Model

paper is to develop this mapping, as well as methods for approaching more realistic and interesting specific scenarios in the future.

1.1. **Multiple Access Channel.** We want to determine optimal transmission rates of information from two sources over a common channel, a single neuron. The specific problem of calculating the maximum rate at which information from two sources can be transmitted over one channel falls in the domain of network information theory and the multiple access channel. We show that the problem of calculating the limits on information transmission of two independent signals by one spike train can be mapped to an equivalent model of a multiple access channel. The problem then becomes that of calculating the capacity region of the channel defined by the neural circuit in question and provides a theoretical foundation on which various encoding strategies and various levels of circuitry detail can be compared.

The multiple access channel is characterized by the presence of two or more sources of information and one receiver; here we discuss the case of two sources. The multiple access channel communication system consists of two message sets, two encoding functions, a collection of probability transition functions relating the input to the output, and a decoding function (see figure 1). Each message set is a set of integer message indices, $\{1, 2, \ldots, 2^{nR_i}\}$. The encoding functions map the indices of the messages to signals appropriate for transmission by the channel. Communication of information over physical devices is inherently a probabilistic process and thus the relationship between the input and output of the channel must be expressed in terms of probability transition functions. The deterministic decoding function produces an estimate of the input from the output. The message sets are included for completeness in the description of the multiple access channel.The computation of the capacity region only depends on the relationship between the input and the output. For reference, the basic definitions and theoretical results regarding the multiple access channel are produced below, from Cover and Thomas, ([1]).

Definition 1. *A $((2^{nR_1}, 2^{nR_2}), n)$ code for the multiple access channel consists of two sets of integers $W_1 = \{1, 2, \ldots, 2^{nR_1}\}$ and $W_2 = \{1, 2, \ldots, 2^{nR_2}\}$ called the*

message sets, two encoding functions, $X_1 : W_1 \to X_1^n$ and $X_2 : W_2 \to X_2^n$ and a decoding function $g : Y^n \to W_1 \times W_2$.

Definition 2. *A rate pair (R_1, R_2) is said to be achievable for the multiple access channel if there exists a sequence of $((2^{nR_1}, 2^{nR_2}), n)$ codes with $P_e^{(n)} \to 0$, where $P_e^{(n)}$ is the average probability of error.*

Definition 3. *The capacity region of the multiple access channel is the closure of the set of all achievable (R_1, R_2) rate pairs.*

The important well known theoretical result regarding the multiple access channel is the fact that the capacity region is determined by the mutual information between the input and the output random variables. This is stated precisely in the following theorem.

Theorem 1. *The capacity region of the multiple access channel $(X_1 \times X_2, p(y|x_1, x_2), Y)$ is the closure of the convex hull of all (R_1, R_2) satisfying*

$$R_1 < max_{p(X_1)p(X_2)} I(X_1; Y|X_2) \ , \ R_2 < max_{p(X_1)p(X_2)} I(X_2; Y|X_1) \ , \ R_1 + R_2 < max_{p(X_1)p(X_2)} I(X_1, X_2; Y)$$

for some product distribution $p(x_1)p(x_2)$ on $X_1 \times X_2$.

We are interested in the effects of the spatial organization of inputs onto a postsynaptic neuron and the content of the input signals on the ability of the neuron to transmit information about the two input signals. Each selection of a spatial organization of inputs defines a new channel consisting of the presynaptic neurons and the postsynaptic neuron (see fig 1). To quantify the performance of the system, we approximately compute the capacity region of the channel for each input location combination. For each realization of the channel, the elements of our model can be mapped to the above diagram for the multiple access channel in the following way. The message sets remain sets of integers representing the indices of the messages to be sent. The encoding functions map the elements of the message sets to stationary Gaussian random signals characterized by one of three power spectra. We compute the maximum mutual informations in theorem 1 by performing a complete search over pairs of signals from the three power spectra. The channel consists of the pre and postsynaptic neurons. The output is taken to be the spike train of the postsynaptic neuron.

2. METHODS

2.1. **Model.** Our neural multiple access channel consisted of two presynaptic neurons and one postsynaptic neuron. Signals, $s_i(t)$ i=1,2, of length $5sec$ were generated using MATLAB and were encoded by two identical presynaptic leaky integrate and fire (LIF) neurons. Signals were Gaussian random signals with one of three power spectra: (1) low pass, (2) $\frac{1}{f^2}$, and (3) bandpass peaked at 30 Hz. The two LIF neurons formed the presynaptic input to a more biophysically detailed model neuron, created using NEURON ([5]). The postsynaptic neuron consisted of a soma, axon, two basal dendrites, an apical trunk, and two distal apical branches. The axon, soma, and apical trunk contained Hodgkin Huxley type Na^+ and K^+ channels while the remaining branches were passive.

Although synaptic dynamics and the reliability of synaptic transmission are large factors in determining the amount of information transmission between real neurons ([6],[7]), in this investigation we used only a simplified, deterministic, model of synaptic transmission. The input signals, $s_i(t)$, were encoded by the LIF neurons;

the output of these neurons were taken as lists of spike times $\{t_1, \ldots, t_n\}$. At each synaptic contact made by a presynaptic LIF neuron onto the postsynaptic neuron, the onset of a conductance increase occurred at each time that the presynaptic neuron spiked. The synapses were modelled as alpha synapses with a time constant of $\tau = 3msec$.

Input LIF spike trains carrying each signal $s_i(t)$ were transmitted to the postsynaptic neuron via 60 (except in the default case of no input) identical synaptic inputs arranged in one of the four following patterns: (1) no input, (2) uniformly distributed over the soma and all dendritic branches, (3) uniformly distributed over the distal apical branches, and (4) uniformly distributed over the soma. We emphasize that this setup is a simplification. The paradigm and methods developed here apply equally well to more realistic configurations.

2.2. Calculating The Capacity Region.
To analyze the effects of both the distribution on the signals and the location of the inputs on information transmission, we have defined separate multiple access channels for each of the 16 combinations of location patterns. To calculate the boundary of the capacity region for each of these channels we compute three quantities:

$$max_{p(s_1)p(s_2)}I(s_1; Y|s_2) \ , max_{p(s_1)p(s_2)}I(s_2; Y|s_1) \ , max_{p(s_1)p(s_2)}I(s_1, s_2; Y)$$

where s_1, s_2 are the input signals and Y is the list of spike times $\{t_1, \ldots, t_n\}$ of the postsynaptic neuron in our model system. For each of these quantities the maximum over all distributions on the input signals will be taken with respect to the set of three possible distributions defined above. Therefore, for each channel defined by a location pair, the maximum will be taken over the nine distribution pairs on the input signals.

Calculating the mutual information between Gaussian random signals and spike trains exactly is impractical because of the large amount of data required to estimate spike train probability densities. ([2]). Consequently, we calculate lower bounds on the mutual information using the reconstruction method advocated by Rieke et. al. ([2]). In brief, this involves computing optimal linear reconstruction filters for the spike trains; the mutual information is then computed by comparing the signal with the spike filtered estimate and assuming a standard Gaussian channel model relationship between the signal and estimate. The novelty of our calculation here is that we compute the *conditional* mutual information. To our knowledge, this is the first presentation of such calculations.

Let $\tilde{s}_1 = \tilde{s}_1(s_2, Y)$ be any estimator of s_1 using s_2, and Y. Then,

$$I(s_1; Y|s_2) = I(s_1; Y, s_2) - I(s_1; |s_2) \geq_a I(s_1; \tilde{s}_1, s_2) - I(s_1; |s_2) = I(s_1; \tilde{s}_1|s_2)$$

$$= H(s_1|s_2) - H(s_1|\tilde{s}_1, s_2) \geq_b H(s_1|s_2) - H(s_1|\tilde{s}_1) =_c H(s_1) - H(s_1|\tilde{s}_1) = I(s_1; \tilde{s}_1)$$

where we have used: (a) the data processing inequality because $(\tilde{s}_1, s_2)$ is a function of (Y, s_2) , (b) conditioning reduces entropy, and (c) s_1 and s_2 are independent. Now, let $\tilde{s}_1 = s_1 + g(s_2, \eta)$ where $g(s_2, \eta)$ represents the noise in the approximation of s_1 due to the presence of s_2 and noise inherent in the approximation procedure, η. Let $\tilde{s}_1 = \tilde{s}_1(\omega)$, $s_1 = s_1(\omega)$, and $g = g(\omega)$. Then, the information as a function of frequency satisfies:

$$I(s_1; \tilde{s}_1) = H(\tilde{s}_1) - H(\tilde{s}_1|s_1) = H(\tilde{s}_1) - H(s_1 + g|s_1) = H(\tilde{s}_1) - H(g|s_1)$$

$$\geq_a H(\tilde{s}_1) - H(g) =_b \frac{1}{2}log_2(1 + SNR(\omega))$$

where we have used: (a) conditioning reduces entropy and (b) assuming that g is Gaussian; $SNR(\omega)$ is the ratio of the power spectra of the output to the input. The total information is obtained by integrating over ω. To approximate $I(s_1; Y|s_2)$ we treat s_2 as noise and average over trials reduce fluctuations in the output spike train due to s_2. Specifically, we fix s_1 and average the spectrum of the output spikes, $Y(\omega)$, over 10 independent trials. We then estimate s_1 using the averaged spike train spectrum and compute the information as described above. Note that this estimate of the conditional mutual information is a lower bound, but is larger than what would be obtained without knowledge of s_2.

Similarly it can be shown that $I(s_1, s_2; Y) = I(s_2; Y) + I(s_1; Y|s_2) \geq I(s_2; \hat{s}_2) + I(s_1; \tilde{s}_1)$ where $\tilde{s}_1$ is the estimator obtained by averaging spike train spectra to reduce the noise and $\hat{s}_2$ is the estimator obtained in the standard way without averaging.

We perform these calculations for all s_1,s_2 pairs and search over these to find the distributions which achieve the maximum. These are the points that we use to construct the capacity regions for each channel.

3. Results and Discussion

This experiment was performed to illustrate that formulating questions about the transmission of multiple signals over a neural system in terms of the multiple access channel model facilitates a quantitative interpretation of the performance of the system. Our experiment addressed the simple question of how the location of synaptic inputs onto a neuron and the content of the signals determines the maximum information rates at which the two signals can be sent over the spike train of one neuron.

As expected, the results show that it is possible to send more information about the signals with certain spatial configurations of synaptic inputs than in others. This is easily seen by the varying sizes of the capacity regions in figure 3.1. Points (i,j) on the figure indicate the boundary of the capacity region obtained when sender 1 uses location pattern i and sender 2 uses location pattern j. Surprisingly, the maximum rate that a single sender can use is increased by the presence of input from the other source. The points on the R2 axis, (1,2), (1,3), and (1,4), correspond to the maximum rate that a single sender can use when inputs are placed in patterns 2,3, and 4 respectively. Contrasting these points on the R2 axis with those of the curves for location pairs (2,2), (4,4), (2,4), (3,3), and (2,3) shows that the maximum rate that a sender can use is increased when input from another source is present. Another unexpected result is that the maximum rate for a single source is achieved when input is located in the distal apical branches. This can be seen by looking at the curves for location pairs (2,3) and (3,3) on the R2 axis and pairs (3,3) and (3,4) on the R1 axis (figure 3.2). The similar maximum values attained in each of these cases suggests that input to the distal apical branches was affected in similar ways by input to the soma, the entire neuron, or the distal apical branches from the second sender. For the case of the combined rates for the two senders, the maximum was achieved when both senders had either some or all of their input at the soma (figure 3.2). These results show quantitatively that different patterns of synaptic inputs provide the system with the capability to either transmit information from one source at a high rate or transmit information from multiple sources at high
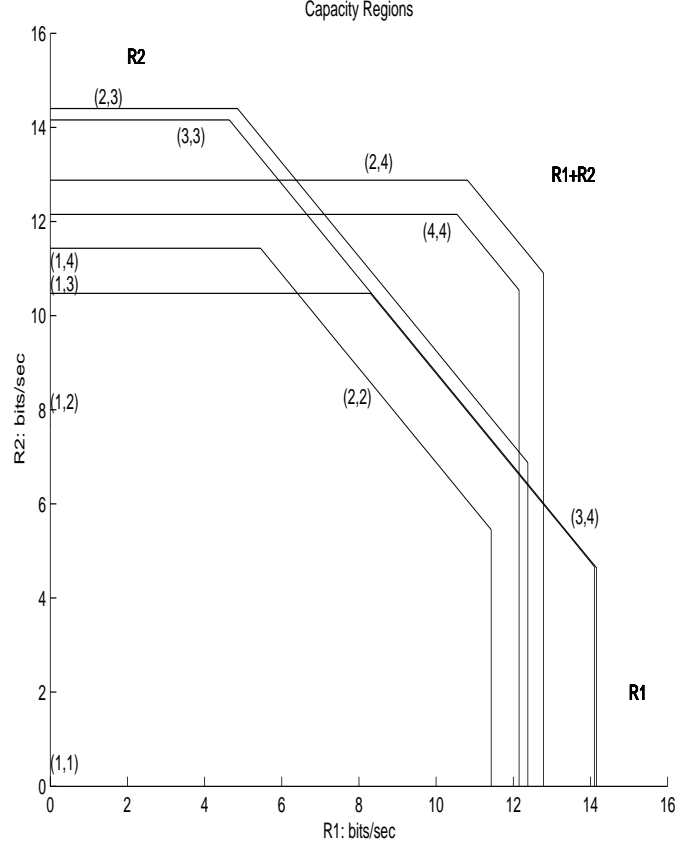
FIGURE 3.1. Capacity regions.

rates simultaneously.

In our experiment we have used input signals of varying power spectra. The results show that for a given location pair, the amount of information that can be sent reliably about the two input signals depends on their relative power spectra (table 1). In table 1 we present the power spectrum pairs that were used to achieve the maximum of the mutual informations at each location pair (taking into account symmetry). There are two interesting results. First, the power spectrum used to achieve the maximum rate for a single sender was the bandpass spectrum, #3, for each location pair. Second, the maximum combined rate for the two senders was achieved in all cases by the power spectrum pairs (3,3). This is contrary to what would be expected based on standard multiplexing wisdom, which dictates that the two power spectra should not overlap.

The methods developed here, and illustrated by our simple model system, are a starting point for analyzing the transmission of information from multiple sources over a common channel. We intend to apply this method to more detailed and realistic systems in future work.
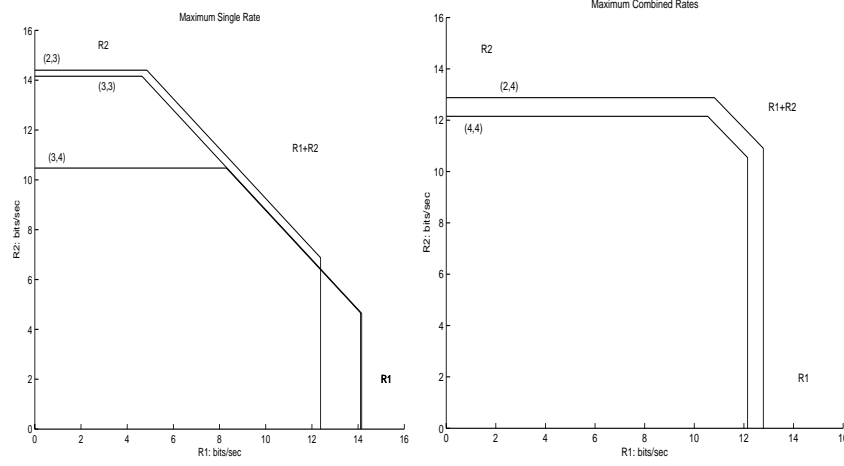
FIGURE 3.2. Selected capacity regions.

Location Pairs	max R1	max R2	max R1+R2
(1,1)	NA	NA	NA
(1,2)	NA	(2,3)	NA
(1,3)	NA	(2,3)	NA
(1,4)	NA	(1,3)	NA
(2,2)	(3,2)	(2,3)	(3,3)
(2,3)	(3,1)	(1,3)	(3,3)
(2,4)	(3,3)	(3,3)	(3,3)
(3,3)	(3,1)	(1,3)	(3,3)
(3,4)	(3,1)	(2,3)	(3,3)
(4,4)	(3,3)	(3,3)	(3,3)

TABLE 1. Maximum-achieving power spectrum pairs.

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