

Information transfer with small-amplitude signals

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We study the optimality conditions of information transfer in systems with memory in the low signal-to-noise ratio regime of vanishing input amplitude. We find that the optimal mutual information is represented by a maximum-variance of the signal time course, with correlation structure determined by the Fisher information matrix. We provide illustration of the method on a simple biologically-inspired model of electro-sensory neuron. Our general results apply also to the study of information transfer in single neurons subject to weak stimulation, with implications to the problem of coding efficiency in biological systems.

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Theoretical approach to the problem of information processing in biological (neuronal) systems has received significant attention over the past few decades [1, 2], with information theory [3–5] providing the fundamental framework [6–12]. Of particular interest are the optimality conditions under which the information between stimuli and responses is maximized [13–17], leading to the idea of *efficient coding hypothesis* [18]. Due to non-linear nature of information-theoretic measures, explicitly formulated optimality conditions are relatively rare [4, 19, 20], nevertheless numerical methods exploiting properties of mutual information are available [4, 16, 21]. Recently, the asymptotic relation between mutual information and Fisher information [22, 23] has been employed for the analysis of optimality conditions in the setting of large neuronal populations and large output signal-to-noise (SNR) ratios [6, 24].

In this paper we examine the effect of vanishing signal amplitude on the information transfer. We are motivated by the situation observed in sensory neurons, which are in many cases known to be responding to weak stimuli intensities (relative to the external or internal noise sources) [2, 25, 26]. Information transfer in channels subject to input cost constraints, with implications to low SNR conditions, has also been of interest in information-theoretic literature [20]. In this paper we employ a different setting and examine information transfer in channels with memory under vanishing stimulus amplitude constraint. We explicitly consider the effect of channel memory, since many realistic systems exhibit this property on various time scales, and furthermore the presence of memory is known to enhance information transfer in many cases [4, 27–29]. Finally, we apply the theory to calculate the effect of memory on information transmission in a simple neuronal model [30, 31]. This system exhibits the stochastic resonance effect, which is commonly understood to be the noise-induced enhancement of the system sensitivity to a *weak* signal [32] (although signal weakness is not a necessary condition for the stochastic resonance to occur [33]).

Throughout this paper we assume *discrete-time* setting, i.e., we denote the consequent responses of a single stochastic neuronal unit as a vector of random variables (discrete or continuous) $\mathbf{R} = (\{R_i\}_{i=1}^n)^\top$, where i indexes the time and $(\cdot)^\top$ denotes the transposition. The response, $R_i = r_i$, is invoked by stimulus, $\Theta_i = \theta_i$, where the stimulus course in time is described by a n -dimensional vector of random variables (r.v.) Θ . We account for the *memory* of the neuron, so that R_i generally depends on current, but also on past stimulations and responses. In the following we assume that the neuronal model is realized by the stationary causal discrete-time information channel with continuous input, fully described by the conditional probability density function $f(\mathbf{r}|\boldsymbol{\theta})$, which factorizes as [3]

$$f(\mathbf{r}|\boldsymbol{\theta}) = \prod_{i=1}^n f_i(r_i|\theta_i, \theta_{i-1}, \dots, \theta_1, r_{i-1}, \dots, r_1). \quad (1)$$

In our setting we do not consider channel *feedback*, i.e., dependence of current stimulus on past responses.

The two most well-known information measures, Fisher information (FI) and Shannon's mutual information (MI), rely on $f(\mathbf{r}|\boldsymbol{\theta})$. The FI (matrix) is often employed as a measure of the efficiency of the population coding [6, 11],

$$\mathbf{J}(\boldsymbol{\theta}|\mathbf{R}) = \langle [\nabla \ln f(\mathbf{r}|\boldsymbol{\theta})][\nabla \ln f(\mathbf{r}|\boldsymbol{\theta})]^\top \rangle_{\mathbf{r}|\boldsymbol{\theta}}, \quad (2)$$

where the gradient is with respect to $\boldsymbol{\theta}$, and $\langle \cdot \rangle_{\mathbf{r}|\boldsymbol{\theta}}$ denotes averaging with respect to $f(\mathbf{r}|\boldsymbol{\theta})$. Throughout this paper we assume that $f(\mathbf{r}|\boldsymbol{\theta})$ is sufficiently continuous in $\boldsymbol{\theta}$, so that the following regulatory conditions [34] hold

$$\int_{\mathbf{R}} \nabla f(\mathbf{r}|\boldsymbol{\theta}) d\mathbf{r} = \mathbf{0}, \quad \int_{\mathbf{R}} \nabla \nabla^\top f(\mathbf{r}|\boldsymbol{\theta}) d\mathbf{r} = \mathbf{0}. \quad (3)$$

FI imposes limits on the precision of $\boldsymbol{\theta}$ estimation from the responses, namely, for the variance of any unbiased estimator of θ_i holds $\text{Var}(\hat{\theta}_i) \geq [\mathbf{J}^{-1}(\boldsymbol{\theta}|\mathbf{R})]_{ii}$ [34].

MI is the fundamental quantity measuring information transfer in channels [4]. MI gives the degree of statistical dependence between stimuli and responses and is defined

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as

$$I(\Theta; \mathbf{R}) = \left\langle \left\langle \ln \frac{f(\mathbf{r}|\theta)}{p(\mathbf{r})} \right\rangle_{\mathbf{r}|\theta} \right\rangle_{\theta}, \quad (4)$$

where $p(\mathbf{r}) = \langle f(\mathbf{r}|\theta) \rangle_{\theta}$ describes the marginal distribution of responses, and the averaging is with respect to the distribution of stimuli, $\pi(\theta)$, so that MI is essentially property of the joint distribution of stimuli and responses. The maximum value of MI per time step, taken over all possible stimuli distributions, is the information capacity (or capacity rate), \mathcal{C} , defined as [4],

$$\mathcal{C} = \lim_{n \rightarrow \infty} \max_{\pi(\theta)} \frac{1}{n} I(\Theta; \mathbf{R}). \quad (5)$$

FI is a local quantity in the sense that for some θ_0 , $\mathbf{J}(\theta_0|\mathbf{R})$ takes into account stimuli from an infinitesimal neighbourhood of θ_0 . In other words, if we assume that FI is a real quantity, i.e., something that can be measured and taken into account, then the stimuli from the neighbourhood of θ_0 have to be physically present, which makes FI analogous to MI in the following sense. Let the stimuli be restricted in amplitude, so that for some θ_0 and $\Delta\theta$ holds $\Theta \in [\theta_0 - \Delta\theta, \theta_0 + \Delta\theta]$ and $\Delta\theta_i > 0$. We define a shifted r.v. $\delta\Theta$ as $\delta\Theta = \Theta - \theta_0$ and rewrite the MI from Eq. (4) in terms of r.v. $\delta\Theta \sim \pi(\delta\theta)$ as

$$I(\Theta; \mathbf{R}) = \left\langle \int_{\mathbf{R}} [\varphi(\mathbf{r}, \theta_0 + \delta\theta) - \psi(\mathbf{r}, \theta_0 + \delta\theta)] d\mathbf{r} \right\rangle_{\delta\theta}, \quad (6)$$

by further introducing

$$\varphi(\mathbf{r}, \theta_0 + \delta\theta) = f(\mathbf{r}|\theta_0 + \delta\theta) \ln f(\mathbf{r}|\theta_0 + \delta\theta), \quad (7)$$

$$\psi(\mathbf{r}, \theta_0 + \delta\theta) = f(\mathbf{r}|\theta_0 + \delta\theta) \ln \langle f(\mathbf{r}|\theta_0 + \delta\theta) \rangle_{\delta\theta}. \quad (8)$$

Now we consider the case of vanishing amplitude, $\|\Delta\theta\| \geq \|\delta\theta\| \rightarrow 0$, and expand $I(\Theta; \mathbf{R})$ in Eq. (6) around θ_0 in terms of $\delta\theta$. It can be shown [35] that,

$$\ln \langle f(\mathbf{r}|\theta_0 + \delta\theta) \rangle_{\delta\theta} \approx \ln f(\mathbf{r}|\theta_0) + \langle \delta\theta \rangle^{\top} \frac{\nabla f(\mathbf{r}|\theta_0)}{f(\mathbf{r}|\theta_0)}, \quad (9)$$

where $\langle \delta\theta \rangle = \langle \delta\theta \rangle_{\delta\theta}$, and thus the Taylor expansion of $\psi \equiv \psi(\mathbf{r}, \theta_0 + \delta\theta)$, is

$$\begin{aligned} \psi &\approx f \ln f + \delta\theta^{\top} \ln f \nabla f + \langle \delta\theta \rangle^{\top} \nabla f + \\ &+ \frac{1}{2} \delta\theta^{\top} \ln f \nabla \nabla^{\top} f \delta\theta + \delta\theta^{\top} \frac{\nabla f \nabla^{\top} f}{f} \langle \delta\theta \rangle + \\ &+ \frac{1}{2} \langle \delta\theta \rangle^{\top} f \left[\frac{\nabla \nabla^{\top} f}{f} - \frac{\nabla f \nabla^{\top} f}{f^2} \right] \langle \delta\theta \rangle, \end{aligned} \quad (10)$$

where $f \equiv f(\mathbf{r}|\theta_0)$ and $\nabla f \equiv \nabla f(\mathbf{r}|\theta)|_{\theta=\theta_0}$. The analogous expansion of φ is straightforward. By substituting the expansions into Eq. (6) the zeroth- and first-order terms cancel and what remains can be written in terms of FI matrix evaluated at $\theta = \theta_0$, by employing $\mathbf{J}(\theta_0|\mathbf{R}) = [\mathbf{J}(\theta_0|\mathbf{R})]^{\top}$, as

$$I(\Theta; \mathbf{R}) \approx \frac{1}{2} \left\langle [\delta\theta - \langle \delta\theta \rangle]^{\top} \mathbf{J}(\theta_0|\mathbf{R}) [\delta\theta - \langle \delta\theta \rangle] \right\rangle_{\delta\theta}, \quad (11)$$

and after taking the expectation

$$I(\Theta; \mathbf{R}) \approx \frac{1}{2} \text{tr} [\mathbf{J}(\theta_0|\mathbf{R}) \mathbf{C}_{\Theta}], \quad (12)$$

where \mathbf{C}_{Θ} is the covariance matrix of Θ and $\text{tr}(\cdot)$ is the matrix trace. Eq. (12) holds for a broad class of channels with memory, both biologically-inspired and artificial, and represents the main result of this paper.

Next we concentrate on the interpretation and some immediate implications of Eq. (12). First, the information capacity from Eq. (5) follows readily from Eq. (12): FI matrix is the property of the neuronal model, so the stimulus properties are represented by \mathbf{C}_{Θ} . Maximizing $I(\Theta; \mathbf{R})$ thus corresponds to extremizing the values of $[\mathbf{C}_{\Theta}]_{ik}$ for which the corresponding elements $[\mathbf{J}(\theta_0|\mathbf{R})]_{ik}$ are non-zero (with appropriate sign). E.g., for a memoryless channel, $f(\mathbf{r}|\theta) = \prod_{i=1}^n f_i(r_i|\theta_i)$, so the FI matrix is diagonal with elements $[\mathbf{J}(\theta_0|\mathbf{R})]_{ii} = J(\theta_0|R)$ (omitting the index i due to channel stationarity). The capacity is thus achieved by maximizing the variance of the amplitude-constrained stimulus, so the capacity-bearing distribution is realized by two equiprobable probability masses located at the interval extremes, and

$$\mathcal{C} = \frac{1}{2} (\Delta\theta)^2 J(\theta_0|R), \quad (13)$$

a result obtained by different means in [20]. Generally, $I(\Theta; \mathbf{R}) \rightarrow 0$ as the stimulus amplitude vanishes. It is thus advantageous to introduce the MI (and capacity) per maximum stimulus power, i.e., $\bar{I}(\Theta; \mathbf{R}) = I(\Theta; \mathbf{R})/\|\Delta\theta\|$, so for the memoryless channel $\bar{\mathcal{C}} = J(\theta_0|R)/2$, as obtained in [20]. While the previously mentioned asymptotics of MI in terms of FI [6, 24] deals with the low-noise limit of information transmission (i.e., large neuronal populations), Eq. (12) describes the opposite ‘‘large-noise’’ limit situation.

In the following we apply Eq. (12) on the classical McCulloch-Pitts (MP) neuronal model, accounting for the memory of the noise component. Memoryless variant of the MP model has been successfully employed in describing the stochastic resonance effect in electrosensory neurons of paddlefish [30], and further analyzed in detail in [31, 36]. The MP model is based on thresholding of the stimulus (corrupted by an additive noise \mathbf{X}), so that the discrete-valued response in time-step i is

$$R_i = U(\theta_i + X_i - a), \quad (14)$$

where a is the threshold, $U(\cdot)$ is the Heaviside step function and $\theta_i \in [-\Delta\theta + \theta_0, \theta_0 + \Delta\theta]$ for all i . The occurrence of action potential at time i is indicated by $R_i = 1$. In the following we consider the noise r.v. $\mathbf{X} = \{X_1, \dots, X_n\}^{\top}$ to be identically distributed but *dependent*, which provides the memory effect for the MP neuron. For simplicity, we assume in the following that $\mathbf{X} \sim p(\mathbf{x})$ is gaussian with covariance matrix $[\mathbf{C}_{\mathbf{X}}]_{ik} = \sigma^2 \varrho_{ik}$, where $\varrho_{ik} = \text{corr}(X_i, X_k)$ is the serial correlation coefficient. Obviously, since U is not invertible, any simple form of dependence in the noise (such as

first order Markov) is not preserved in the time sequence of responses. Generally, the full joint distribution of \mathbf{R} is required, which means evaluation of n -dimensional gaussian integrals, which may not be numerically stable. In other words, the joint conditional probabilities $\Pr\{\mathbf{R}|\boldsymbol{\theta}\}$ are generally not tractable for reasonable values of n . The idea is to substitute the full and untractable log-likelihood, $\ell(\boldsymbol{\theta}|\mathbf{r}) = \ln f(\mathbf{r}|\boldsymbol{\theta})$, with a computable pseudo-log-likelihood [37], $\ell^{(P)}(\boldsymbol{\theta}|\mathbf{r})$, neglecting some high-order dependencies, i.e.,

$$\ell^{(P)}(\boldsymbol{\theta}|\mathbf{r}) = \sum_q \ell_q^{(P)}(\boldsymbol{\theta}|\mathbf{r}), \quad (15)$$

where $\ell_q^{(P)}(\boldsymbol{\theta}|\mathbf{r})$ are ‘‘computable’’ partitions. Here we concentrate on a variant of the second-order pseudo-log-likelihood, $\ell^{(P)}(\boldsymbol{\theta}|\mathbf{r}) = \ell_2(\boldsymbol{\theta}|\mathbf{r})$, based on *pairwise* dependence [38]

$$\ell_2(\boldsymbol{\theta}|\mathbf{r}) = \sum_{i=2}^n \sum_{k=1}^{i-1} \ln \Pr\{R_i, R_k|\boldsymbol{\theta}\} - (n-2) \sum_{i=1}^n \ln \Pr\{R_i|\boldsymbol{\theta}\}, \quad (16)$$

The advantage of ℓ_2 is, that most of the involved integrals can be expressed in a semi-closed form for the gaussian noise. The problematics of replacing $\ell(\boldsymbol{\theta}|\mathbf{r})$ by $\ell_2(\boldsymbol{\theta}|\mathbf{r})$ for non-Markov models has been investigated recently in statistical literature [38, 39]. The marginal probability P_1 of $R_i = 1$ (crossing the threshold) is independent of i due to stationarity, and since $R_i \in \{0, 1\}$, we can write $\Pr\{R_i|\theta_i\} = r_i P_1 + (1 - r_i)(1 - P_1)$, where

$$P_1 = \frac{1}{2} \left[1 - \operatorname{erf} \left(\frac{a - \theta_i}{\sqrt{2}\sigma} \right) \right] \quad (17)$$

by evaluation of the gaussian integral and $\operatorname{erf}(\cdot)$ is the error function. Similarly, for the bivariate joint response probability holds

$$\Pr\{R_i, R_k|\theta_i, \theta_k\} = r_i r_k P_{11} + r_i(1 - r_k)P_{10} + (1 - r_i)r_k P_{01} + (1 - r_i)(1 - r_k)P_{00}, \quad (18)$$

where $P_{mn} = P_{mn}(\theta_i, \theta_k)$ is the probability of $R_i = m, R_k = n$, so $\sum_{m,n} P_{mn} = 1$. Note, that $P_{11} + P_{01}$ is the marginal probability of $R_k = 1$, and $P_{11} + P_{10} = P_1$ is the marginal probability of $R_i = 1$. Eq. (17). These symmetries and Eq. (17) give

$$P_{11} = \int_0^\infty \frac{1}{2} \left[1 + \operatorname{erf} \left(\frac{\theta_i - a + (a - \theta_k + y)\varrho_{ik}}{\sigma\sqrt{2 - 2\varrho_{ik}^2}} \right) \right] \times \phi(y - \theta_k + a) dy, \quad (19)$$

$$P_{01} = \frac{1}{2} \left[1 - \operatorname{erf} \left(\frac{a - \theta_k}{\sigma\sqrt{2}} \right) \right] - P_{11}, \quad (20)$$

$$P_{10} = \frac{1}{2} \left[1 - \operatorname{erf} \left(\frac{a - \theta_i}{\sigma\sqrt{2}} \right) \right] - P_{11}, \quad (21)$$

$$P_{00} = 1 - P_{11} - P_{01} - P_{10}. \quad (22)$$

where $\phi(\cdot)$ is the probability density function of a gaussian r.v. with zero mean and variance equal to σ^2 (note

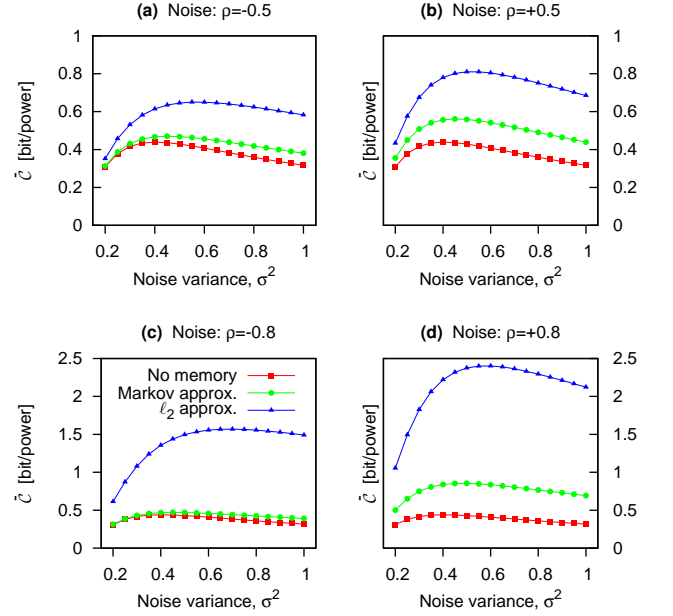


FIG. 1. Information capacity (in bits) per vanishing stimulus power of McCulloch-Pitts neuronal model with memory. The noise is a gaussian AR(1) process with first-order serial correlation ϱ and variance σ^2 . Stimulation parameters are: $\theta_0 = 0$ and threshold $a = 1$. Three situations are shown: *no memory* (see also [31, 36], corresponds to $\varrho = 0$), *Markov* (assuming the first-order Markov structure of responses) and *pseudo-log-likelihood*, ℓ_2 -approximation to the true situation, estimated for $n = 100$. The memory of the neuron enhances its information capacity, by reducing the disruptive power of the noise. Note, that positive noise correlations increase capacity more than negative ones.

that P_{mn} are functions of $\theta_i, \theta_k, a, \sigma$ and ϱ_{ik}). The FI matrix will have generally all elements non-zero, and its approximation by ℓ_2 is

$$[\mathbf{J}(\boldsymbol{\theta}|\mathbf{R})]_{ik} = - \sum_{r_1, \dots, r_n} \frac{\partial^2 \ell_2(\boldsymbol{\theta}|\mathbf{R})}{\partial \theta_i \partial \theta_k} \times \Pr\{[R_1 = r_1, \dots, R_n = r_n]|\boldsymbol{\theta}\}, \quad (23)$$

where the sum is over all possible n -dimensional vectors, consisting of 0's and 1's. Due to particular form of $\ell_2(\boldsymbol{\theta}|\mathbf{T})$, however, things are a lot simpler, although details of the following calculations will be published elsewhere. For the off-diagonal, $i \neq k$, and diagonal elements evaluated at $\theta_i = \theta_k = \theta_0$ holds

$$\mathbf{J}(\boldsymbol{\theta}|\mathbf{R})_{ik} = \gamma(\theta_0, a, \sigma, \varrho_{ik}, \tilde{P}_{11}, \tilde{\phi}_{01}), \quad (24)$$

$$\mathbf{J}(\boldsymbol{\theta}|\mathbf{R})_{ii} = \omega(\theta_0, a, \sigma, \varrho_{ii}, \tilde{P}_{11}), \quad (25)$$

where $\gamma(\cdot)$ and $\omega(\cdot)$ are complicated (but tabulated) functions of the indicated parameters, and

$$\tilde{P}_{11} = P_{11}(\theta_0, \theta_0), \quad (26)$$

$$\tilde{\phi}_{01} = \left. \frac{\partial}{\partial \theta_k} P_{11}(\theta_0, \theta_k) \right|_{\theta_k = \theta_0}. \quad (27)$$

Employing Eq. (12) gives the covariance matrix of the optimal stimulation as

$$[\mathbf{C}_\theta]_{ik} = (\Delta\theta)^2 \text{sgn}([\mathbf{J}(\theta_0|\mathbf{T})]_{ik}), \quad (28)$$

where $\text{sgn}(\cdot)$ is the signum function. The capacity rate per vanishing stimulus power is then

$$\bar{C} = \lim_{n \rightarrow \infty} \frac{1}{2n} \sum_{i,k} |[\mathbf{J}(\theta_0|\mathbf{T})]_{ik}|. \quad (29)$$

Fig. 1 shows how the memory of the neuron enhances its information capacity (shown as a capacity per vanishing stimulus power). We assumed that the noise r.v. \mathbf{X} is modelled by the AR(1) gaussian discrete-time process with first-order correlation ρ , so that $[\mathbf{C}_\mathbf{X}]_{ik} = \sigma^2 \rho^{|i-k|}$. The enhancement is compared to the already investigated $\rho = 0$ case (no memory) [31, 36], which exhibits the effect of stochastic resonance as the variance of the noise increases. The information transferred increases with memory, since the noise correlations effectively reduce its “corrupting” power (once the stimulus statistics is properly matched to the noise structure, as shown by Eq. (12)). The *no memory* values are identical in all cases, since the noise correlations are ignored. Besides the ℓ_2 -approximation, the first-order Markov approximation is also shown, obtained by setting $n = 2$ in Eq. (16). For Markov approximation the information capacity is lower, since the neuron employs only current and immediately preceding response value in the decoding, neglecting the possibilities of the essentially infinite-memory of the MP neuron. Additional numerical calculations show, that even small noise correlations ($\rho \approx 0.2$) increase the

capacity rates of the MP neuron by approx. 15% (not shown in Fig. 1).

Our results lead us to comment on the optimality of information transfer in real neurons. While the efficient coding hypothesis relies on the maximum information transfer, one should keep in mind, that from the information-theoretic perspective the coding-decoding operations are an integral part of the information transmission process. First, it is well known [4], that for some channels the optimal decoding process can be a very complex task – i.e., employing *all* the responses obtained so far, as illustrated in this paper on a relatively simple example of the MP neuron with memory. Since the nervous system is assumed to respond to spike trains in real time [29], it is questionable that real neurons try to achieve the true capacity and additional costs must be taken into account [40]. Second, the discrete, or impulse-like, character of capacity-bearing stimulation is not limited only to vanishing stimulus amplitudes. This phenomenon occurs in most channels examined in literature so far (with power-constrained AWGN channel, and low-noise limit channels being the only known exceptions) [41]. Another possible problem connected with the usage of a continuously varying stimulus is, that the complete specification of particular θ requires infinite amount of information, while real neurons probably do not strive for precise specification of θ .

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