Mutual Information of Population Codes and Distance Measures in Probability Space

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We studied the mutual information between a stimulus and a system consisting of stochastic, statistically independent elements that respond to a stimulus. Using statistical mechanical methods the properties of the Mutual Information (MI) in the limit of a large system size, N, are calculated. For continuous valued stimuli, the MI increases logarithmically with N and is related to the log of the Fisher Information of the system. For discrete stimuli the MI saturates exponentially with N. We find that the exponent of saturation of the MI is the Chernoff Distance between response probabilities that are induced by different stimuli.

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Population coding serves as a common paradigm of information processing in the brain. Its starting point is the fact that very often the response of a single neuron to a stimulus is noisy and is only weakly tuned to changes in the stimulus value. Hence, the information carried by a typical neuron is rather low. The brain may overcome this limitation by distributing the information across a large number of neurons which together carry accurate information about the stimulus [1]. This paradigm has inspired numerous studies of the statistical efficiency of population codes [2]-[7]. Of particular interest is the way in which the amount of information about the stimulus depends on both the size of the responding population and the response properties of the individual neurons.

Many theoretical studies [3,6,7] have employed the well-known concept of Fisher Information (FI) [11]. The FI is related to the derivative of the population response probability with respect to the stimulus. For a statistically independent population, the FI is an extensive quantity and is relatively easy to calculate. However, it is restricted to the case of a continuously varying stimulus. An alternative measure, applicable for arbitrary stimulus spaces, is provided by Shannon Mutual Information (MI) [11]. Unfortunately, except for special cases, exact calculation of the MI for a large population is difficult even for independent populations. This is because MI is bounded from above by the stimulus entropy, and thus is not an extensive quantity. Recently, a relationship between the MI of a continuous stimulus and the FI in a large population has been derived [6,7]. However, little theoretical progress has been made on the properties of the MI in large systems with discrete stimuli [8].

In this paper we introduce statistical mechanical methods to calculate analytically the behavior of the MI as the system size, N, of the population grows. For continuous valued stimuli our theory yields a logarithmic dependence of the MI on the FI, in agreement with previous results [6,7]. In the case of discrete stimuli, the MI saturates exponentially fast with N. We show that the exponential saturation rate is dominated by a contribution from the two stimulus values that induce the closest response-probabilities in the population. The contribution of this pair of stimuli to the saturation rate equals the Chernoff Distance between the corresponding response-probabilities, of Large Deviation Theory [11].

We consider a population of N stochastic units, which we call neurons, that respond simultaneously to a presentation of a stimulus. We denote their responses by a vector \( \mathbf{r} = \{r_1, r_2, \ldots, r_N\} \) where \( r_i \) represents the stochastic response of the i-th neuron to a stimulus. The stimulus states are denoted by the scalar variable \( \theta \), which can be either discrete or continuous, with a prior probability (or density) \( p(\theta) \). We denote the probability (or the density) of \( \mathbf{r} \) given a stimulus \( \theta \) by \( P(\mathbf{r}|\theta) \). In this paper we will focus on the case of statistically independent neurons (given a stimulus \( \theta \)), namely,

\[
P(\mathbf{r}|\theta) = \prod_{i=1}^{N} P_i(r_i|\theta).
\]

An important issue is how to quantify the efficiency of the coding of \( \theta \) in the population responses. For probabilities that are differentiable functions of a continuously varying stimulus, a well-known measure of the efficiency of the population code is the FI. In our case it is

\[
J(\theta) = -\sum_{i=1}^{N} \left\langle \frac{\partial^2 \ln P(r_i|\theta)}{\partial \theta^2} \right\rangle_{r_i|\theta}.
\]

\[
= \sum_{i=1}^{N} \left\langle \left\{ \frac{\partial}{\partial \theta} \ln P(r_i|\theta) \right\}^2 \right\rangle_{r_i|\theta}
\]

where \( \langle \cdots \rangle_{r_i|\theta} \) denotes an average with respect to \( P(r_i|\theta) \), which is clearly an extensive quantity. Here we study an alternative measure of efficiency, the MI of the system, which is the average amount of information on \( \theta \) that is added by observing the response, \( \mathbf{r} \). It is useful to define a local MI, \( I(\theta) \),
\[ I(\theta) \equiv \left\langle \log_2 \left\{ \frac{P(r|\theta)}{P(r)} \right\} \right\rangle_{r|\theta} \]

where \( P(r) = \sum_\theta P(r|\theta)p(\theta) \), and \( \langle \cdots \rangle_{r|\theta} \) denotes an average w.r.t. \( P(r|\theta) \). The full MI, \( I \), is

\[ I = \langle I(\theta) \rangle_\theta \]  

where \( \langle \cdots \rangle_\theta \) is an average over the stimulus distribution. A central quantity is the log-likelihood variable,

\[ S(r,\phi,\theta) = \ln \left[ \frac{P(r|\phi)}{P(r|\theta)} \right] = \sum_{i=1}^{N} S_i(r_i, \phi, \theta) \]

where \( S_i(r_i, \phi, \theta) = \ln P(r_i|\phi) - \ln P(r_i|\theta) \). Equation (3) can be written as

\[ I(\theta) = -\int \prod_{\phi \neq \theta} dS_\phi P_\theta \{S_\phi\} \log_2 \langle \exp S_\phi \rangle_{\phi'} \]  

where \( P_\theta \{S_\phi\} \) is the distribution of \( S_\phi \equiv S(r,\phi,\theta) \), calculated with respect to \( P(r|\theta) \). For large \( N \) this distribution is centered around the mean value of \( S_\phi \)

\[ \sum_{i=1}^{N} \langle S_i(r_i, \phi, \theta) \rangle_{r|\theta} = -D_{KL}(\phi||\theta) \]

where \( D_{KL}(\phi||\theta) > 0 \) is the relative entropy of \( P(r|\phi) \) and \( P(r|\theta) \), also known as the Kullback-Leibler (KL) distance between the two distributions. The correlation matrix of the fluctuations \( \delta S_\phi = S_\phi + D_{KL}(\phi||\theta) \) is also of order \( N \), and is given by

\[ C(\phi, \psi|\theta) = \sum_{i=1}^{N} \langle \delta S_i(r_i, \phi, \theta) \delta S_i(r_i, \psi, \theta) \rangle_{r|\theta}. \]

We first discuss the MI of a large system with a continuous varying stimulus. Here, all averages over stimulus space stand for integrals with a density \( p(\theta) \), and we assume that the probabilities vary smoothly with \( \theta \). In this case, the dominant contribution to Eq. (4) comes from values of \( S_\phi \) near their mean value and \( \phi \) which is near \( \theta \), i.e., \(|\phi - \theta| \lesssim 1/\sqrt{N}\). This is because \( S_\theta = S(r,\theta,\theta) = 0 \) while for \( \phi \) that is far from \( \theta \), \( S_\phi \approx -D_{KL}(\phi||\theta) \), which is large and negative. For small magnitudes of \( \delta \phi = \phi - \theta \), and \( \delta \psi = \psi - \theta \) we can write

\[ D_{KL}(\phi||\theta) \approx \frac{1}{2} J(\theta) \delta \phi^2, \quad C(\phi, \psi|\theta) \approx J(\theta) \delta \phi \delta \psi \]

where \( J(\theta) \) is the FI, Eq. (5). The low rank form of the correlation matrix in Eq. (6) implies that the fluctuations \( \delta S_\phi \) can be described as \( z \sqrt{J(\theta)} \delta \phi \), where by central limit theorem \( z \) is a Gaussian variable with zero mean and unit variance. Substituting this in Eq. (5) yields

\[ I(\theta) \approx -\int Dz \times \log_2 \left\{ \int dz p(\psi + \theta) \exp \left( -\frac{J(\theta) \psi^2}{2} + z \sqrt{J(\theta)} \psi \right) \right\} \]

where \( Dz = dz \exp(-z^2/2)/\sqrt{2\pi} \). Evaluating the integrals in the limit of a large \( J \), and substituting in Eq. (4), yields

\[ I \approx H_\theta - \frac{1}{2} \left\langle \log_2 \left( \frac{2\pi e}{J(\theta)} \right) \right\rangle_\theta \]

where \( H_\theta = -\int d\theta p(\theta) \log_2 p(\theta) \), in agreement with previous results [6,7].

We now turn to the more difficult case of discrete valued stimulus which takes the values \( \{\theta_i\}_{i=1}^{M} \) and \( M \) remains finite as \( N \to \infty \). The term \( \phi = \theta \) in the average \( \langle \exp S_\phi \rangle_{\phi} \) in Eq. (1) is \( p(\theta) \), yielding a total contribution to \( I \) which is the stimulus entropy \( H_\theta = -\sum_\theta p(\theta) \log_2 p(\theta) \). Naively, we would therefore expect that the main contribution to \( \log_2 p(\theta) - I(\theta) \) comes from the typical values of \( S_\phi \), namely, \(-D_{KL}(\phi||\theta)\), for a state \( \phi \) which is closest to \( \theta \). Such a contribution would be proportional to \( \exp(-D_{KL}(\phi||\theta)) \). However, we find that in fact, the dominant contribution comes from rare values of \( r \) such that \( S_\phi \neq 0 \) for one of the states \( \phi (\phi \neq \theta) \). This is because, as we will show, although this regime has an exponentially small probability, its contribution to \( I \) is exponentially larger than that of the typical value of \( S_\phi \) making it the dominant correction to \( I - H_\theta \).

To evaluate Eq. (7) in the discrete case we use an integral representation of the distribution of \( S_\phi \equiv S(r,\phi,\theta) \),

\[ P_\theta \{S_\phi\} = \int \prod_{\phi \neq \theta} \frac{dY_\phi}{2\pi} \exp \{-F_\theta(Y_\phi, S_\phi)\} \]

\[ F_\theta = -\sum_{i=1}^{N} \ln \langle \exp i\sum_\phi Y_\phi S_i(r_i, \phi, \theta) \rangle_{r|\theta} + i \sum_\phi Y_\phi S_\phi. \]

Note that there is no integration over variables with \( \phi = \theta \), since \( S_\theta \equiv S(r,\theta,\theta) = 0 \). The large \( N \) limit of Eq. (1) and (12) is evaluated by the saddle point method. Solving the saddle point equations for \( S_\phi \) and \( Y_\phi \) we find that there are \( M - 1 \) saddle points, each of which is characterized by having one \( S_\phi \) of \( O(1) \) while the remaining \( S_\phi' \) are negative and of \( O(N) \). The auxiliary variable \( Y_\phi = -\alpha \) where \( \alpha \) is a real number of order \( 1 \) while the remaining \( Y_\phi' \) are zero. At this saddle point, the value of \( F_\theta \), Eq. (13) is

\[ D_\alpha(\phi||\theta) \equiv -\sum_{i=1}^{N} \ln \langle \exp \alpha S_i(r_i, \phi, \theta) \rangle_{r|\theta} \]

where the order parameter \( \alpha \) is evaluated by maximizing Eq. (14).

\[ \frac{\partial}{\partial \alpha} D_\alpha(\phi||\theta) = 0. \]
where we denote the maximum value of $D_\alpha$ by $D_C(\phi, \theta)$. Out of these $M-1$ saddle points the dominant one is that with the smallest $D_C(\phi, \theta)$, yielding

$$\ln [-\log_2 p(\theta) - I(\theta)] \approx -\min_{\phi \neq \theta} D_C(\phi, \theta).$$

(16)

Finally, the full MI is given by

$$\ln [H_\theta - I] = -\min_{(\phi \neq \psi)} D_C(\phi, \psi) - \frac{1}{2}\ln N + A$$

(17)

where the $\ln N$ and the constant $A$ correction terms come from the Gaussian integration around the saddle point of Eqs. (3) and (4). The calculations of the constant $A$ will be presented elsewhere [9]. Finally, examining Eq. (12) at the saddle-point, it can be seen that $\exp(-D_C(\phi, \theta))$ equals the probability that $S_\phi/N \approx 0$ for a large $N$. This implies, as we have mentioned above, that the rate of saturation of the MI is dominated by the probability of the rare event that one of the log-likelihood ratios is close to zero.

The quantity $D_C(\phi, \psi)$ derived in the above theory is identical to the Chernoff Distance (or Chernoff Information) between the two distributions $P(\theta|\phi)$ and $P(\theta|\psi)$. More generally, the Chernoff Distance between two arbitrary distributions $P(x)$, and $Q(x)$, is defined [11] as

$$D_C(Q, P) = \max_{\alpha} D_\alpha(Q||P)$$

(18)

where

$$D_\alpha(Q||P) \equiv -\ln \sum_x Q(x)^\alpha P(x)^{1-\alpha}$$

(19)

$D_\alpha(Q||P)$ are proportional to the family of Renyi distances. [12] $D_\alpha(Q||P)$ vanishes at $\alpha = 0$ and $\alpha = 1$. It is positive (if $Q \neq P$) for $0 < \alpha < 1$, with a maximum at $\alpha^*$, $0 < \alpha^* < 1$, and is negative outside this regime. It is related to the KL distance through its slope at $\alpha = 0$, i.e., $\partial D_\alpha(Q||P)/\partial \alpha|_{\alpha = 0} = D_{KL}(Q||P)$. The Chernoff Distance chooses the value of $\alpha$ which maximizes $D_\alpha(Q||P)$. This value is not constant but depends on the pair of distributions $Q$ and $P$. Note, that in the case of a family of distributions parameterized by a continuous parameter $\theta$, the Chernoff Distance is related to the FI through $4D_C(\theta, \theta + \delta\theta) \approx D_{KL}(\theta, \theta + \delta\theta) \approx J(\theta)(\delta\theta)^2/2$.

Although $D_C(Q, P)$ is not symmetric with respect to $Q$ and $P$ for general $\alpha$, it obeys the symmetry $D_\alpha(Q||P) = D_{1-\alpha}(P||Q)$, which implies that $D_{\alpha^*}(Q||P) = D_{\alpha^*}(P||Q)$. Thus, the Chernoff Distance of $Q$ and $P$ is a symmetric function of the two distributions. It is smaller than $D_{KL}$, and in addition, it is less sensitive than the KL distance to outlier states. In particular, a single state which has a nonzero probability $P$ but zero probability $Q$, causes $D_{KL}(Q||P)$ to diverge whereas $D_C(Q, P)$ remains finite. In fact, it diverges only when the two distributions have zero overlap, i.e., the intersection of their support is empty.

Equation (17) implies that the Chernoff distance controls the rate of saturation of the MI. In order to test our theory we have studied the case of a population of statistically independent, binary neurons, where $r_i = \{0, 1\}$, and a stimulus which can take three values: $\theta_1, \theta_2$ and $\theta_3$. Each neuron has a preferred stimulus, denoted by $\theta$. The mean value of $r_i$ (i.e., the probability that $r_i = 1$) is

$$f_i(\theta) = z_i(\theta) + T\delta_{\theta, \theta^i}$$

(20)

For each neuron, the $\theta_i$ is chosen at random from $\{\theta_1, \theta_2, \theta_3\}$, with equal probability, and $z_i(\theta)$ are chosen at random uniformly from $[a, b]$, with $T \geq b - a$. Thus, the parameter $T$ measures the selectivity of the responses to the stimulus values. In this case, there is no statistical difference between the response probability of the population as a whole to the three stimuli, and changing the stimulus corresponds to permuting the mean responses of the individual neurons in the population. This is common in biological situations where different stimuli (such as different angles, spatial positions or abstract objects) elicit activity profiles that are similar in shape but shifted in position across the network.

FIG. 1. The Mutual Information between a population of $N$ independent binary neurons and an M-state stimulus, with $M = 3$, as a function of $N$. The response parameters $T, a$, and $b$ are 0.75, 0.05, and 0.15, respectively. The dots are the exact numerical calculation. The line is the approximation, Eq. (17). We have included a constant $\ln(M - 1)$ to account for the $M - 1$ equal contributions to $I(\theta)$ because of the symmetry of the stimuli. The Inset compares the two results on a log plot.

Figure 1 shows a nice agreement between the results of exact numerical calculation of the MI of this model up to size $N = 25$, and the asymptotic result of Eqs. (14)-(17), evaluated for the above distributions. Note that because of the symmetry between the different stimuli in this example, $D_C(\phi, \psi)$, is the same for all pairs of stimuli, $\theta \neq \theta'$, so that they all contribute equally to Eq. (17).
The importance of $D_C(\phi, \psi)$ in characterizing the efficiency of the population code is manifest not only in the MI of the system but also in the accuracy of the discrimination between stimuli on the basis of observation of the population responses. Plausible discriminatory often base their discrimination between a pair of stimuli on the log-likelihood ratio of the corresponding distributions. In particular, the Maximum-Likelihood (ML) discriminator makes a deterministic decision between a pair of stimuli, $\theta$ and $\phi$, upon observing $r$, according to whether the log-likelihood, $S(r, \phi, \theta)$, is larger or smaller than zero. As outlined below, our theory yields that the confusion error of an ML discriminator between two stimuli, $\theta$ and $\phi$, is dominated by the probability that $S(r, \phi, \theta)$ is close to zero, and thus is determined by $D_C(\phi, \theta)$.

![Graph](image)

**FIG. 2.** The probability of confusion in the case of an independent population of Poissonian neurons, incurred by an ML discriminator whose task is to discriminate between three stimuli. The mean response of each neuron is given by Eq. (12). Using the saddle point methods as described above, we find that in a large system the dominant contribution to the integrals over $S_\phi$ comes from the edge points where one $S_\phi$ is close to zero. Evaluating the saddle point equations for $Y_\phi$ under this condition, yields

$$\ln P_C = - \min_{\phi \neq \psi} D_C(\phi, \psi) - \frac{1}{2} \ln N + A'$$  \hspace{1cm} (22)

An example is shown in Fig. 2, where we have computed the confusion error of an ML discriminator between two stimuli in the case of a population of neurons responding to three stimuli as described above, except that in this case, the neurons are Poissonian with means $f_i(\theta)$, of the form Eq. (20). The numerical results obtained by simulating the ML discriminator are in very good agreement with the prediction of Eq. (22).

In conclusion, we have shown the relation between the MI of a large population coding for a stimulus and the distance between the response-probabilities that are induced by the different stimulus values. In the case of a continuous stimulus, the MI increases logarithmically with $N$, for large $N$, and is related to the FI which measures the vanishing rate of the distance for infinitesimally small stimulus differences. In the case of discrete stimuli, the MI saturates exponentially at a rate which is given by the Chernoff Distance between the closest pair of population response probabilities. In addition, we have shown that $D_C$ determines also the probability of discrimination error. This extends the classical Large Deviation Theory results \[1\] to cases where the elements of the population are not identical. Our finding that the Chernoff Distance controls both the MI and the error probability for a large population that code discrete stimuli, suggests that $D_C$ is a useful measure of the quality of neuronal population codes. We hope that these results will provide tractable tools to study the nature of population codes in the brain using experimental data on neuronal representations of sensory, motor and cognitive events.

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