

Efficient Coding Hypothesis and an Introduction to Information Theory

Lay Kuan Loh & Mihovil Bartulovic

September 15, 2014

Abstract

The Efficient Coding Hypothesis, proposed by Barlow 1961, suggests that sensory relays recode sensory messages, so that their redundancy is reduced, but little information is lost. Coding to reduce redundancy not just eliminates wasteful neural activity, but also organizes sensory information such that an internal model of the environment causing the past sensory inputs to build up, while the current sensory situation is represented in a way that simplified the task of the part of the nervous system which is responsible for learning and conditioning. To investigate animal's sensory mechanisms, Barlow 1961 suggests that one should examine the ways in which animals use their senses, as these ways are likely reflected in the design of the sense organs and their nervous pathways.

I. INTRODUCTION

Information Theory represents the necessary basis of the modern information and communication technologies. Without it, many of today's technologies would be unavailable or less developed.

Bits are the standard choice of unit in Information Theory. The core theorems of Information Theory set measures for the quantity of information, upper bound for loss-less compression of information, and for the highest speed for the information to be transferred through a channel with or without noise.

Although Information Theory does not give practical solutions for upper bounds that it sets, the theory behind it is a vital step to practical implementation. The transfer of information should be fast, precise, energy efficient and it should work regardless the inevitable interference and noises in the channel. Information Theory presents the necessary basis for efficiently coding and compressing various types of information such as text, images, and sound.

The Efficient Coding Hypothesis is one of the quantitative links between the statistical and structural properties of our visible surroundings. It is a core theory in Information Theory and has inspired new directions in neuroscience. This hypothesis suggests that a group of neurons should encode information as compactly as possible in order to maximize efficient utilization of resources, meaning that the information carried by one

neuron should not be redundant to the information which is carried by the other neurons.

Testing the Efficient Coding Hypothesis is impractical as estimating information-theoretic quantities requires large amounts of data, and common estimators of information are heavily biased. Therefore, it is hard to achieve a good estimation from any set of given data. Nonetheless, successful experimental results have been achieved, which will be described in the following sections.

II. POSSIBLE PRINCIPLES UNDERLYING THE TRANSFORMATIONS OF SENSORY MESSAGES

Barlow 1961 discusses three hypotheses about sensory relays:

- Hypothesis 1: Sensory relays detect certain "passwords" in incoming messages that have a particular key significance.
- Hypothesis 2: Sensory relays are filters whose "pass characteristics" can be controlled in accordance with the requirements of the other part of the nervous system.
- Hypothesis 3: Sensory relays recode sensory messages, extracting signals of high relative entropy from the highly redundant sensory input.

His paper is not a discussion of the physiological mechanisms of sensory pathways, but an attempt to formulate ideas about operations which these mechanisms do. The idea behind all of the three above mentioned hypothesis comes from experimental results, not merely from abstract speculations on this topic.

In Hypothesis 1, specific classes of stimuli act as "releasers" and evoke specific responses. These classes of stimuli are thought of as "passwords" which have to be distinguished from other stimuli and it is suggested that their detection may be the important function of sensory relays. For instance, a frog's visual system has a limited range of visual responses. A moving object elicits a sequence of reactions, such as the frog going into alert, or hopping forward and snapping at it. This hypothesis says that since animals respond differently to specific stimuli, their sensory pathways must have mechanisms for detecting such stimuli and discriminating between them.

In Hypothesis 2, sensitivity of one type of stimulus might be increased while another is decreased. Combined with Hypothesis 1, this means the whole characteristic of relay could change, so that, in effect, the "password" is altered. Thus, relays act as control points at which the flow of information is modulated according to the requirements of the other parts of the nervous system.

Hypothesis 1 argued about existence of preset mechanisms for detecting and passing on restricted classes of key signals. Hypothesis 2 postulated that the acceptance or rejection of messages might be controlled from somewhere else - either be a temporary change or a permanent adjustment for the sensory relays. The remaining question is: is the current input new information? If not, it should be marked as redundant and rejected.

Several assumptions need to be made for Hypothesis 3:

- Sensory pathways are noiseless and use discrete time signals.
- The discrete time signals for any one fiber and time interval are binary impulses which are either present or absent.
- The capacity of a nerve pathway is constrained as such: number of fibers F is constant, number

of discrete time intervals per second R is also constant, and the average number of impulses per second in one fiber I is variable.

These assumptions are not justified by experimental results, but are mentioned due to potential generality of the problem. FitzHugh 1957 criticized these assumptions where an evidence is produced which tells us that it is not important if a single impulse in the short time interval is there or not but the cumulative number of impulses in a longer time interval is the one who carries the information.

Hypothesis 3 states that sensory relays recode sensory messages so that their redundancy is reduced, but little information is lost. A "message" it is assumed to be a set of signals, i.e. a particular pattern of impulses along a set of N fibers during the time interval T . Denoting \mathbb{P}_m as the probability of the message m in such an ensemble, the information attributed to m is $H_m = -\log \mathbb{P}_m$. The average information of all of the messages is thus the summation of information of all members of the ensemble.

$$H_{av} = \sum_m \mathbb{P}_m \log \mathbb{P}_m \quad (1)$$

The rate of flow of information is $\frac{H_{av}}{T}$, where T is the average duration of messages from the ensemble.

$$T = \sum_m \mathbb{P}_m T_m. \quad (2)$$

The capacity C of a channel is equal to the greatest rate of flow of information that can be passed down it. The capacity of a nerve pathway is

$$C = -FR \left[\frac{I}{R} \log \frac{I}{R} + \left(1 - \frac{I}{R} \right) \log \left(1 - \frac{I}{R} \right) \right]. \quad (3)$$

The relative entropy of the messages is $\frac{H}{CT}$, and thus making the redundancy $[1 - (H/CT)]$. The channel capacity is maximum if $I = \frac{R}{2}$. In normal circumstances $I < \frac{R}{2}$, thus a decrease in redundancy of the sensory relay can only be done by decreasing the average frequency of impulses being used to transfer a message. Therefore, for a given class of input messages, relays will choose the code that requires the smallest average expenditure of impulses in the output signal.

Hence, reduction of redundancy is an important principle guiding the organization of sensory messages and it is carried out at relays in the sensory pathways.

The main difference between the last hypothesis and the first two is that the first two consist of possible principles for selecting some sensory messages while rejecting others. The selected messages are considered to be infrequent, and all of the rejected messages would be classified in the same way, thus disregarding a large part of the data. Hypothesis 3, however, preserves the given information.

III. RETINAL GANGLION CELLS ACT LARGELY AS INDEPENDENT ENCODERS

Correlated firing among neurons is widespread in the visual system, but its importance for encoding visual information is unclear. To study this, Nirenberg et. al., 2001 presented the retina with natural stimuli and computed the responses of the output cells, the ganglion cells. They used information theoretic techniques to measure the amount of information about the stimuli that can be obtained from the cells under correlated firing and non-correlated firing. They found that more than 90% of the information about the stimuli can be obtained from the cells with uncorrelated firing, suggesting that ganglion cells act largely independently to encode information, simplifying the problem of decoding their activity.

Nirenberg et. al., 2001 stimulated pairs of isolated mouse retina using natural movies. The stimuli were each 7 seconds long and repeated 300 times, and the ganglion cell responses were recorded. Data used had to be clean of contaminating spikes from other cells, and that both responses had to have average firing rates.

To find the degree of correlated activity for each pair, the excess correlated fraction (ECF) was found. ECF is the fraction of correlated spikes produced by the pair above chance, taking into account correlations induced by the stimulus. The ECFs ranged from -1% to 34%.

To measure the amount of information the pairs of ganglion cells carried about the stimuli when their correlations were taken into account, information theoretic techniques were used. Each movie was treated as a series of segments of fixed temporal length, with each segment regarded as a separate stimulus. The movie was presented several hundred times to generate a large set of responses (spike trains) to each segment. This allowed the authors to estimate the probability of getting a particular pair of responses given a particular movie segment - that is, to estimate $\mathbb{P}(r_1, r_2|s)$,

where r_1 was the response of cell 1, r_2 was the response of cell 2 and s was the movie segment. Given these conditional probabilities, the amount of information I between the responses and the stimulus segments was found using the expression:

$$I = - \sum_{r_1, r_2} \mathbb{P}(r_1, r_2) \log_2 \mathbb{P}(r_1, r_2) \quad (4)$$

$$+ \sum_s \mathbb{P}(s) \sum_{r_1, r_2} \mathbb{P}(r_1, r_2|s) \log_2 \mathbb{P}(r_1, r_2|s) \quad (5)$$

where $\mathbb{P}(r_1, r_2)$ is found by taking $\mathbb{P}(r_1, r_2) = \sum_s \mathbb{P}(r_1, r_2|s)\mathbb{P}(s)$, and $\mathbb{P}(s)$ is the probability that a given stimulus segment s occurred.

To examine how important correlation is in encoding visual information, the amount of information that would be lost if the correlations in the responses of the pair of ganglion cells were ignored was examined. To ignore the correlations, the conditional probability distributions of the two responses, $\mathbb{P}(r_1, r_2|s)$, as the product of their individual probability distributions, $\mathbb{P}(r_1|s)$ and $\mathbb{P}(r_2|s)$. $\mathbb{P}(r_1|s)\mathbb{P}(r_2|s)$ to estimate the probability of a stimulus given a response. As $\mathbb{P}(r_1|s)\mathbb{P}(r_2|s)$ is not quite the true distribution, using it should lead to a loss of information.

Therefore, the amount of independent information is given by

$$I_{IND} = - \sum_{r_1, r_2} \mathbb{P}(r_1, r_2|s) \log_2 \mathbb{P}(r_1|s)\mathbb{P}(r_2|s) \quad (6)$$

$$+ \sum_s \mathbb{P}(s) \sum_{r_1, r_2} \mathbb{P}(r_1, r_2|s) \log_2 \mathbb{P}(r_1|s)\mathbb{P}(r_2|s) \quad (7)$$

The amount of information in bits lost, ΔI , is given by

$$\Delta I = I - I_{IND} \quad (8)$$

$$= \sum_s \mathbb{P}(s) \sum_{r_1, r_2} \mathbb{P}(r_1, r_2|s) \log_2 \frac{\mathbb{P}(r_1, r_2|s)}{\mathbb{P}(r_1|s)\mathbb{P}(r_2|s)} \quad (9)$$

$$- \sum_{r_1, r_2} \mathbb{P}(r_1, r_2) \log_2 \frac{\mathbb{P}(r_1, r_2)}{\sum_s \mathbb{P}(r_1|s)\mathbb{P}(r_2|s)\mathbb{P}(s)} \quad (10)$$

ΔI is very small, as most pairs lost less than 10% of information. If there were pairs of ganglion cells with higher degrees of correlation than the maximum 34% observed, more information loss could have occurred. This finding means that strategies used to decode ganglion cell activity, which treat the cells as independent

encoders are reasonable, as they can capture more than 90% of the information the cells carry. Furthermore, the activity of any given ganglion cell can be evaluated separately from other cells, without accounting for other cells in the population. This allows the problem of decoding population activity to be significantly simplified, as much less data is needed to analyze the uncorrelated case as opposed to the correlated case.

Several concerns with the study are that capturing more than 90% in ganglion cell activity may not be enough to fully understand its activity. Also, perhaps correlation should not be ignored for the activity of a larger population of cells than just pairs of cells studied here.

IV. A SIMPLE CODING PROCEDURE ENHANCES A NEURON'S INFORMATION CAPACITY

This study by Laughlin 1981 validates Barlow 1961's suggestion that redundancy reduction is an important principle in neural coding. Laughlin that the receptors of large monopolar cells (LMCs), the first order interneurons of the insect compound eye, have a compressive intensity-response function corresponding to the background intensity. Instead of absolute intensity, the LMC's contrast-response function matches the range of contrasts encountered in natural scenes, which increases the efficiency.

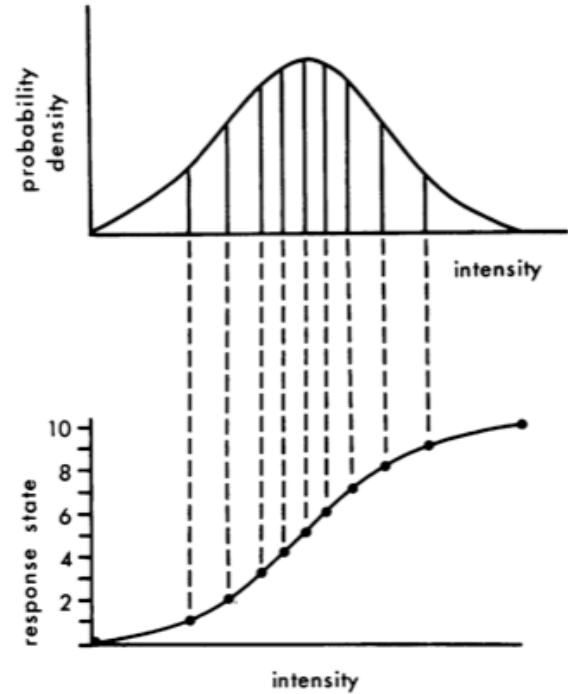
A neuron has a limited range of responses that can represent the states of its inputs. If its sensitivities are too high, inputs would saturate the response, and input outside the response range would be lost. If sensitivities are too low, the response range would correspond to very large ranges of input, and many parts of it would therefore be underutilized. Information theory suggests that the most efficient way to apportion the neuron's limited response range is to maximize entropy by encoding inputs so that all response levels are used with equal frequency.

In the simplest case, shown in Figure 1, a neuron represents a single input parameter with a single output parameter. Maximum entropy is achieved when inputs are amplified in proportion to their expected frequency of occurrence. Larger portions of the response range are used for better resolution of common events, and smaller portions for improbable events.

Figure 1: UPPER DIAGRAM: Probability density function for stimulus intensities.

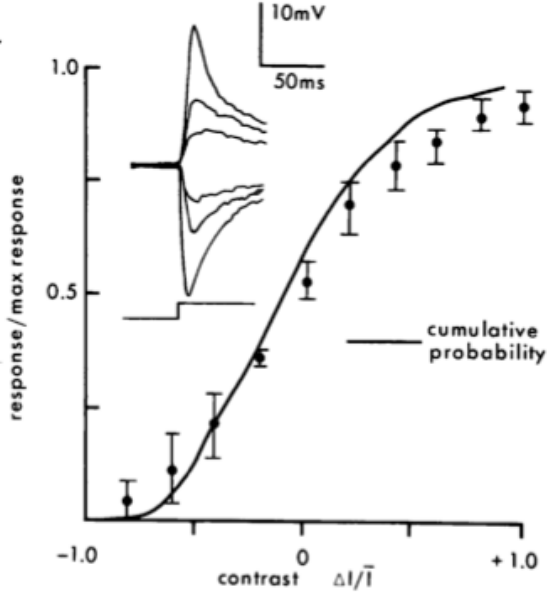
LOWER DIAGRAM: Intensity-response function that implements the strategy.

Maximizing a neuron's information capacity by ensuring that all response levels are used with equal frequency. Intervals between each response level encompasses an equal area under the intensity distribution, so each state is used with equal frequency.



To test this hypothesis, Laughlin compared contrast-response functions with contrast levels measured in natural scenes, such as lakeside vegetation in LMCs. Relative intensities were measured across the scenes with a detector with spectral sensitivity similar to a fly monopolar cell. Contrast values were obtained by dividing each scan into intervals. Within each interval, the intensity \bar{I} was found, and for each data point the fluctuation about the mean $\delta I = I - \bar{I}$ was computed. Finally, the contrast $\frac{\Delta I}{\bar{I}}$ was found. The contrast-response function approximates the form of the cumulative distribution function for contrast levels in natural scenes ??, indicating that the neurons uses the strategy for efficient coding suggested by information theory. Therefore, there is little redundancy associated with the LMC response to natural scenes.

Figure 2: *The contrast-response function of light adapted fly LMCs compared to the cumulative probability function for natural contrasts (50° interval).*



V. VISION AND THE STATISTICS OF THE VISUAL ENVIRONMENT

In his paper Simoncelli has several criticisms about articles relating to the Efficient Coding Hypothesis that were published in the last several years. He argues some misconceptions about the theory behind Efficient Coding Hypothesis, and also criticizes some experimental results.

I. Criticisms of hypothesis

The purpose of Vision

Firstly, Simoncelli suggests that the efficient coding of visual information is not important, as the purpose of vision is not to encode and reconstruct the visual world. The hypothesis does not take into account how the information that has been extracted is to be used, which could be an advantage as one does not need to specify what is being represented, or a limitation as goals are relevant for visual processing. There are other, more complete theories such as Bayesian estimation which take the statistical structure of the environment and goal into account.

Relevance of Information Theory

The Efficient Coding Hypothesis is not important because brain does not work with bits as an unit of information. However, the definition of information is relevant to the brain; bits are merely a standard choice of unit for information.

Experimentall Observed Dependency

Some experimental data from multi-neuron recordings show correlation, synchronization, or other forms of statistical dependency between neurons.

However, most of these data came from experiments that did not use naturalistic stimuli. Also, other studies suggest that responses to natural stimuli in the primary visual cortex (V1) are relatively independent. Even if one were to observe dependencies in neural responses under natural stimulus conditions, the hypothesis states only that the system strives for independence; the constraints of neural processing may prevent this being achieved. Taking this into account, a more realistic expectation might be that successive stages of processing (e.g. steps along an ascending sensory pathway) should reduce statistical dependence.

Simonelli also suggests that the brain increases redundancy. Assuming that the coding capacity of all neurons is the same, since the number of neurons used to process sensory information increases as the information goes deeper into the brain, his suggestion follows. However, we point out that increased number of neurons does not always yield redundancy as different neurons have different properties. For instance, cortical neurons have slower firing rates and tend to have more complex temporal dynamic properties. The redundancy for retinal and V1 neurons has not yet been experimentally compared a similar comparison in auditory system demonstrated the reduction of redundancy.

The Efficient Coding Hypothesis is strongly dependent on the assumptions that the distribution of inputs is represented with a collection of calibrated images, and the definition of the neural response used. The accuracy of various studies which ignore noise and other simplistic physical constraints is therefore questionable. Although this criticism is valid, it is not fatal in the application of the Efficient Coding Hypothesis to neuroscience.

II. Testing the Efficient Coding Hypothesis

Although the Efficient Coding Hypothesis is already 50 years old, it is only now being more widely explored today, due to better information on neural signal processing, and better mathematical and engineering tools to process large amounts of experimental data.

The two basic approaches for testing the Efficient Coding Hypothesis are:

- Focus on examining statistical properties of neural responses under natural stimuli, and
- Using statistical properties of natural images to constrain and derive a model for the early sensory processing.

In the last few years researchers have been able to measure the efficiency in several different ways. Results of those studies vary — some studies confirm the Efficient Coding Hypothesis while the others seem to be highly inconsistent with the proposed hypothesis. In example, a study conducted on cats and monkeys has shown that firing rate distributions of cat's visual V1 and monkey's inferotemporal (IT) neurons is exponential under naturalistic conditions and this yields optimal information transmission for a fixed average rate of firing. Furthermore, another study with monkey's IT neurons found that only minority could be described with an exponential firing distribution. Later, it was mentioned that exponential distribution is a correct solution only in noise-free cases.

In a study presented in Meister *et al.* it was shown that retinal ganglion cells show strong firing correlations and that the observed patterns could provide useful information. Article by (cite 23) adds that retinal ganglion cells act as an independent encoders. Similar result for V1 neurons was found by Reich *et al.* where it was stated that V1 neurons are almost independent under non-natural stimuli. Results mentioned so far can seem not in line with the Efficient Coding Hypothesis as one would expect the level of independence to degrade for non-natural stimuli.

Lewen *et al.* and Kern *et al.* suggest that visual system shows better performance while input is a naturalistic stimulant.

Even though the connection has not yet been completely established, Efficient Coding Hypothesis sug-

gests that optimal characterization of neural system will be while using natural stimuli.

The other method of testing the Efficient Coding Hypothesis is to derive a model for efficient coding of the environment and afterwards to compare it with the observed psychological data. This model is highly constrained with linear filtering and second order statistical modeling. In the last few years, a couple of authors have established a connection between higher order statistical model and linear filtering.

Finally, it is worth mentioning that several authors successfully applied Efficient Coding Hypothesis to adaptive processes.

The recent interest in Efficient Coding Hypothesis has given interesting theoretical and experimental results. After all this being said it does seem improbable that Efficient Coding Hypothesis will be sufficient and the only principle for the understanding of sensory system design but it is clear that this hypothesis will play an important role.

REFERENCES

- [Barlow 1961] Barlow, H. B. (1961). Possible Principles Underlying the Transformations of Sensory Messages. *Sensory communication*, (1961):217-234.
- [Laughlin, 1981] Laughlin, S. (1981). A Simple Coding Procedure Enhances a Neuron's Information Capacity. *Z. Naturforsch*, 36.910-912 (1981): 51.
- [Nirenberg et. al., 2001] Nirenberg, S., Carcieri, S. M., Jacobs, A. L., & Latham, P. E. (2001). Retinal ganglion cells act largely as independent encoders. *Nature*, 411(6838), 698-701.
- [Simoncelli 2003] Simoncelli, E. P. (2003). Vision and the statistics of the visual environment. *Current opinion in neurobiology*, 13(2), 144-149.
- [Meister et. al., 1995] Meister M., Lagnado L., Baylor D. A. (1995). Concerted signaling by retinal ganglion cells. *Science* 1995, 270:1207-1210.
- [Vinje 2000] Vinje W. E., Gallant J. L. (2000). Sparse coding and decorrelation in primary visual cortex during natural vision *Science* 2000, 287:1273-1276.