Efficient Coding Hypothesis and an introduction to information Theory

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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 than an internal model of the environment causing the pst sensory inputs ins built up, while the current sensory situation is represented in a way that simplified the task of the parts of the nervours ssystem responsible for learning and conditioning. To investigate animals' sensory mechanisms, Barlow 1961 suggests that one 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

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II. Possible Principles Underlying the Transformations of Sensory Messages

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:

$$I = - \sum_{r_1, r_2} \mathbb{P}(r_1, r_2) \log_2 \mathbb{P}(r_1, r_2) \tag{1}$$

$$+ \sum_s \mathbb{P}(s) \sum_{r_1, r_2} \mathbb{P}(r_1, r_2 | s) \log_2 \mathbb{P}(r_1, r_2 | s) \tag{2}$$

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 occured.

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 $\mathbb{P}(r_2|s)$. $\mathbb{P}(r_1|s)\mathbb{P}(r_1|s)$ to estimate the probability of a stimulus given a response. As $\mathbb{P}(r_1|s)\mathbb{P}(r_1|s)$ is not quite the true distribution, using it should lead to a loss of information.

Therefore, the amount of independent information is given by

$$I_{IND} = -\sum_{r_1, r_2} \mathbb{P}(r_1, r_2|s) \log_2 \mathbb{P}(r_1|s)\mathbb{P}(r_2|s) \quad (3)$$

$$+ \sum_s \mathbb{P}(s) \sum_{r_1, r_2} \mathbb{P}(r_1, r_2|s) \log_2 \mathbb{P}(r_1|s)\mathbb{P}(r_2|s) \quad (4)$$

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

$$\Delta I = I - I_{IND} \quad (5)$$

$$= \sum_s \mathbb{P}(s) \sum_{r_1, r_2} \mathbb{P}(r_1, r_2|s) \log_2 \frac{\mathbb{P}(r_1, r_2|s)}{\mathbb{P}(r_1|s)\mathbb{P}(r_2|s)} \quad (6)$$

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

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 occured. 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.
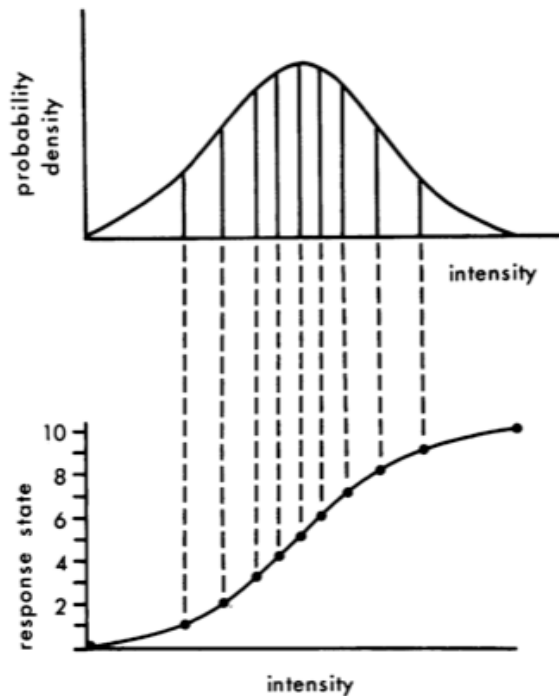
A neuron has a limited range of responses that can represent the states of its inputs. If its sensitivities are too high, inputs would saturate the response, and input outside the response range would be lost. If sensitivities are too low, the response range would correspond to very large ranges of input, 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 frequeny of occurence. 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.*
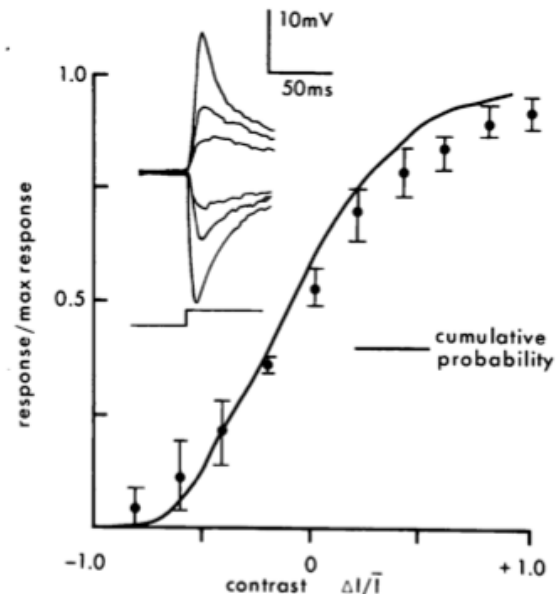Lower diagram: *Intensity-response function that implements the strategy.*
Maxmimizing a neuron's information capacity by ensuring that all response levels are used with equal frequency. Intervals between each response level encompasses an equal area under the intensity distribution, so each state is used with equal frequency.

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

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 accross 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 2, indicating that the neurons uses the strategy for efficient coding suggested by information theory. Therefore, there is little redundancy associated

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