Group Redundancy Measures Reveal Redundancy Reduction in the Auditory Pathway

Gal Chechik, Amir Globerson, Naftali Tishby
School of Computer Science and Engineering
and The Interdisciplinary Center for Neural Computation
Hebrew University of Jerusalem, Israel

ggal@cs.huji.ac.il

Michael J. Anderson, Eric D. Young
Department of Biomedical Engineering
Johns Hopkins University, Baltimore, MD, USA

Israel Nelken
Department of Physiology, Hadassah Medical School
and The Interdisciplinary Center for Neural Computation
Hebrew University of Jerusalem, Israel

Abstract

The way groups of auditory neurons interact to code acoustic information is investigated using an information theoretic approach. We develop measures of redundancy among groups of neurons, and apply them to the study of collaborative coding efficiency in two processing stations in the auditory pathway: the inferior colliculus (IC) and the primary auditory cortex (A1). Under two schemes for the coding of the acoustic content, acoustic segments coding and stimulus identity coding, we show differences both in information content and group redundancies between IC and A1 neurons. These results provide for the first time a direct evidence for redundancy reduction along the ascending auditory pathway, as has been hypothesized for theoretical considerations [Barlow 1969, 2001]. The redundancy effects under the single-spikes coding scheme are significant only for groups larger than ten cells, and cannot be revealed with the redundancy measures that use only pairs of cells. The results suggest that the auditory system transforms low level representations that contain redundancies due to the statistical structure of natural stimuli, into a representation in which cortical neurons extract rare and independent component of complex acoustic signals, that are useful for auditory scene analysis.
1 Introduction

How do groups of sensory neurons interact to code information and how do these interactions change along the ascending sensory pathways? According to the common view, sensory systems are composed of a series of processing stations, representing more and more complex aspects of sensory inputs. The changes in representations of stimuli along the sensory pathway reflect the information processing performed by the system. Several computational principles that govern these changes were suggested, such as information maximization and redundancy reduction [2, 3, 11]. In order to investigate such changes in practice, it is necessary to develop methods to quantify information content and redundancies among groups of neurons, and trace these measures along the sensory pathway.

Interactions and high order correlations between neurons were mostly investigated within single brain areas on the level of pairs of cells (but also for larger groups of cells [9]) showing both synergistic and redundant interactions [8, 10, 21, 6, 7, 13]. The current study develops information theoretic redundancy measures for larger groups of neurons, focusing on the case of stimulus-conditioned independence. We then compare these measures in electro-physiological recordings from two auditory stations: the auditory mid-brain and the primary auditory cortex.

2 Redundancy measures for groups of neurons

To investigate high order correlations and interactions within groups of neurons we start by defining information measures for groups of cells and then develop information redundancy measures for such groups. The properties of these measures are then further discussed for the specific case of stimulus-conditioned independence.

Formally, the level of independence of two variables $X$ and $Y$ is commonly quantified by their mutual information (MI) [17, 5]. This well known quantity, now widely used in analysis of neural data, is defined by

$$I(X; Y) = D_{KL}[P(X, Y)||P(X)P(Y)] = \sum_{x,y} p(x, y) \log \left( \frac{p(x, y)}{p(x)p(y)} \right)$$

and measures how close the joint distribution $P(X, Y)$ is to the factorization by the marginal distributions $P(X)P(Y)$ ($D_{KL}$ is the Kullback-Leibler divergence [5]).

For larger groups of cells, an important generalized measure quantifies the information that several variables provide about each other. This multi information measure [18] is defined by

$$I(X_1; \ldots; X_n) = D_{KL}[P(X_1, \ldots, X_n)||P(X_1)\ldots P(X_n)] = \sum_{x_1, \ldots, x_n} p(x_1, \ldots, x_n) \log \left( \frac{p(x_1, \ldots, x_n)}{p(x_1)\ldots p(x_n)} \right)$$

Similar to the mutual information case, the multi information measures how close the joint distribution is to the factorization by the marginals. It thus vanishes when variables are independent and is otherwise positive.

We now turn to develop measures for group redundancies. Consider first the simple case of a pair of neurons $(X_1, X_2)$ conveying information about the stimulus $S$. In this case, the redundancy-synergy index ([4, 7]) is defined by

$$RS_{pair}(X_1, X_2, S) = I(X_1, X_2; S) - [I(X_1; S) + I(X_2; S)]$$

(3)
Intuitively, \( RS_{pairs} \) measures the amount of information on the stimulus \( S \) gained by observing the joint distribution of both \( X_1 \) and \( X_2 \), as compared with observing the two cells independently. In the extreme case where \( X_1 = X_2 \), the two cells are completely redundant and provide the same information about the stimulus, yielding \( RS_{pairs} = I(X_1, X_2; S) = I(X_1; S) = -I(X_1; S) \), which is always non-positive. On the other hand, positive \( RS_{pairs} \) values testify for synergistic interaction between \( X_1 \) and \( X_2 \) [8, 7, 4].

For larger groups of neurons, several different measures of redundancy-synergy may be considered, that encompass different levels of interactions. For example, one can quantify the residual information obtained from a group of \( N \) neurons compared to all its \( N-1 \) subgroups. As with inclusion-exclusion calculations this measure takes the form of a telescopic sum: \( RS_{N|N-1} = I(X^N; S) - \sum_{i=1}^{N} I(X_i; S) + \cdots + (-1)^{N-1} \sum_{i \in \{X^k\}} I(X_i; S) \), where \( \{X^k\} \) are all the subgroups of size \( k \) out of the \( N \) available neurons. Unfortunately, this measure involves \( 2^N \) information terms, making its calculation infeasible even for moderate \( N \) values.

A different \( RS \) measure quantifies the information embodied in the joint distribution of \( N \) neurons compared to that provided by \( N \) single independent neurons, and is defined by

\[
RS_{N|1} = I(X_1, ..., X_N; S) - \sum_{i=1}^{N} I(X_i; S)
\]  

Interestingly, this synergy-redundancy measure may be rewritten as the difference between two multi-information terms

\[
RS_{N|1} = I(X_1, ..., X_N; S) - \sum_{i=1}^{N} I(X_i; S) = H(X_1, ..., X_N) - H(X_1, ..., X_N|S) - \sum_{i=1}^{N} H(X_i) - H(X_i|S) = I(X_1; ..., X_N|S) - I(X_1; ..., X_N)
\]

where \( H(X) = -\sum_x p(x) \log(p(x)) \) is the entropy of \( X \). We conclude that the index \( RS_{N|1} \) can be separated into two terms: one that is always non-negative, and measures the coding synergy, and the second which is always non-positive and quantifies the redundancy. These two terms correspond to two types of interactions between neurons: The first type are within-stimulus correlations (sometimes termed noise correlations) that emerge from functional connections between neurons and contribute to synergy. The second type are between stimulus correlations (or across stimulus correlations) that reflect the fact that the cells have similar responses per stimulus, and contribute to redundancy. Being interested in the latter type of correlations, we limit the discussion to the redundancy term \(-I(X_1; ..., X_N)\).

Formulating \( RS_{N|1} \) as in equation 5 proves highly useful when neural activities are independent given the stimulus \( P(\vec{X}|S) = \prod_{i=1}^{N} P(X_i|S) \). In this case, the first (synergy) term vanishes, thus limiting neural interactions to the redundant

\[^1\]Our results below suggest that some redundancy effects become significant only for groups larger than 10-15 cells.

\[^2\]When comparing redundancy in different processing stations, one must consider the effects of the baseline information conveyed by single neurons. We thus use the normalized redundancy (compare with [15] p.315 and [4]) defined by \( RS_{N|1} = RS_{N|1}/I(X_1; ..., X_N; S) \).