

Coherent oscillations as a neural code in a model of the olfactory system

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Abstract-This paper presents an investigation of two odor coding mechanisms in Freeman's KIII neurodynamics model. Motivated by experimental evidence that supports the existence of a neural code based on synchronous oscillations, we propose an analogy between synchronization in neural populations and phase locking in KIII channels. The information carried by the phase is compared against the conventional amplitude code in terms of pattern-recovery capabilities. First, the scalar invariance of the KIII with respect to phase information is established. Symmetries and redundancies in the associative memory matrices are then exploited to perform an exhaustive evaluation of patterns on an 8-channel model. Simulation results show that phase information outperforms amplitude information in the recovery of odor patterns from incomplete or corrupted sensory stimulus.

I. INTRODUCTION

Neural coding schemes based on firing synchrony are the most compelling hypothesis for a temporal code spatially distributed across large neural populations. These types of codes have been found experimentally in different neocortical areas [1], and play an important role in the integration of visual information [2] and the codification of odors [3,4]. The objective of this paper is to ascertain whether this coding mechanism can be exploited in the KIII model of Freeman et al. [5,6], arguably the most complete neurodynamics model of the olfactory system.

The long term goal of this work is to develop biologically-plausible computational models to process data from chemical sensor arrays, commonly referred to as the electronic nose. An e-nose consists of (1) an array of chemical sensors with broad and overlapping selectivities and (2) a pattern recognition engine capable of associating sensor patterns with the corresponding odor labels [7]. Biologically-inspired approaches have been the focus of attention in recent years [8] as an alternative to the statistical pattern recognition procedures commonly employed in electronic-nose data processing [9].

Along these lines, our experience with the KIII model [10,11] shows that the information provided by the amplitude of the channels tends to degrade when the input patterns have a significant level of overlap, as is oftentimes the case in electronic nose data due to the cross-selectivity of the chemical sensors. This raises the question whether additional

robust information can be extracted from the output of the model. In particular, we have observed that the KIII has a tendency to display similar phases in channels that encode for the same odor. This observation, along with experimental evidence for a neural code based on coherent oscillations in neural populations, motivates the study presented in this paper.

II. TEMPORAL CODING AND COHERENT OSCILLATIONS

Work by Adrian [12,13] more than 75 years ago showed that the firing rate of stretch receptor neurons is related to the force being applied to the muscles. This seminal contribution led to the widespread belief that firing rate was the code used by neural systems to transmit information. As a consequence, early neural network models interpreted the output of artificial neurons as an abstraction of the neural firing rate in their biological counterparts. In recent years, this view has been challenged with ample experimental evidence showing the need to take into consideration the temporal dimension in neural information processing.

Undisputable evidence for a temporal code is best illustrated by the work of Thorpe et al. [14,15], who have shown that humans and monkeys are able to respond to a visual categorization problem in a very short period of time. In their experiments, an image is briefly flashed and the subject has to decide if it belongs to a target category or not. Considering (i) the pathway of the visual signal as it propagates through the brain, (ii) the minimum time required for a neuron to generate an action potential and (iii) the response time of the subjects in these experiments, it is possible to determine that there is time for only one spike to be generated at every relay station in the visual pathway. This result clashes with a frequency-rate coding hypothesis, and clearly points to the existence of a temporal dimension.

A number of possible temporal coding mechanisms have been proposed, including inter-spike interval codes, time of arrival (latency) codes and synchrony codes [16]. Among these, the synchronous oscillation of ensembles presents the most empirical evidence. Synchronization has been proposed as a potential mechanism to correlate information from different senses or different parts of the brain [1]. It has also been found to play a role in visual feature integration [2]. Of particular interest to our work, Laurent et al. [3,4] have found that synchronous oscillations of neuron populations in insects is used as an odor encoding mechanism. Their work has shown that different odors evoke coherent oscillations in different but usually overlapping ensembles of neurons in the olfactory system.

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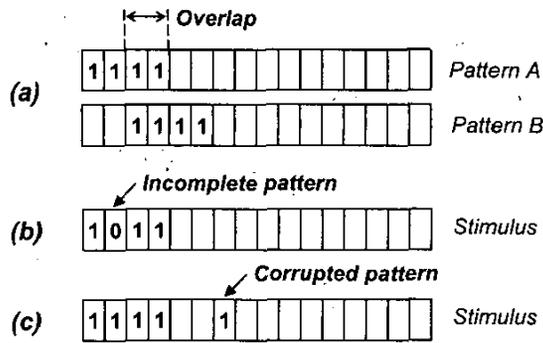


Fig. 3. Overlap between input patterns for a 16-channel KIII (a). Simulating an incomplete (b) and a corrupted (c) input pattern.

The KIII model with matrix formulation described in [6] was employed in this work. The model was implemented in MATLAB using fourth-order Runge-Kutta ODE integration with a time step of 1.0 ms. Initial conditions for all variables and their derivatives were set to zero. KIII parameter settings were borrowed from [18].

IV. SCALING INVARIANCE

Invariance of the KIII model with respect to the number of channels has been empirically established by Yao and Freeman [5] in terms of the amplitude and general shape of the oscillations observed at each channel. To determine if these results can be generalized to phase information, we present a thorough study on three KIII models with 16, 32 and 64 channels. The study simulates a two-odor classification problem with varying levels of complexity in terms of (1) the degree of overlap between the two stored patterns and (2) the number of missing or corrupted channels that are presented at the input.

Fig. 3 illustrates the two input patterns for the 16-channel case. Each pattern consists of four active channels, represented by a 1, and 12 inactive channels, represented by a blank bit. Due to the symmetry of the problem, in what follows the KIII model is always excited with a stimulus from Pattern A. To incorporate different degrees of overlap, three patterns sets are considered having 0, 1 and 2 bits of overlap. Each one of these three sets leads to a unique Hebbian associative matrix and, therefore, a separate KIII model. Fig. 3(a) illustrates the situation where the patterns have an overlap of 2 bits. To simulate incomplete patterns (e.g. caused by sensor degradation), 0, 1 or 2 of the active bits in the stimulus may be set to zero. Fig. 3(b) illustrates the case where the stimulus for pattern A is incomplete by one bit. Finally, to simulate corrupted patterns (e.g. to due to background odors), 0, 1 and 2 bits not belonging to either pattern may be set to one. Fig. 3(c) shows a stimulus for Pattern A with one corrupted bit. All these different combinations lead to $3 \cdot 3 \cdot 3 = 27$ possible scenarios for a 16-channel KIII model. Data for the 32- and 64-channel models is obtained by scaling the stored patterns and input stimuli by a factor of 2 and 4, respectively.

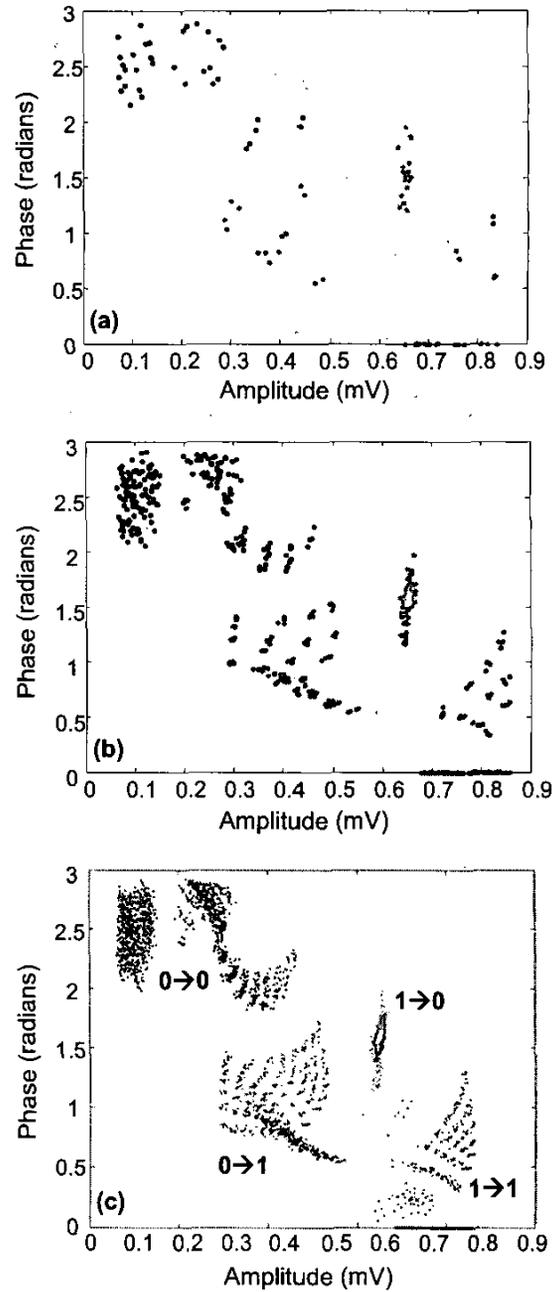


Fig. 4. Scatter plot of amplitude vs. phase codes for different input-stimulus \rightarrow desired-response cases

Simulation results are presented in Fig. 4 in the form of bivariate scatter plots. Each point in the scatter plots represents the output of one KIII channel for one stimulus. The abscissa axis is the RMS amplitude of the channel, whereas the ordinate axis is the phase relative to channel 0, which is consistently activated and used as a reference. In this work the G1 signals are not band-pass filtered in the gamma band (20-80 Hz) as suggested in [19]. Comparable results, however, were obtained on the gamma-band filtered signals.

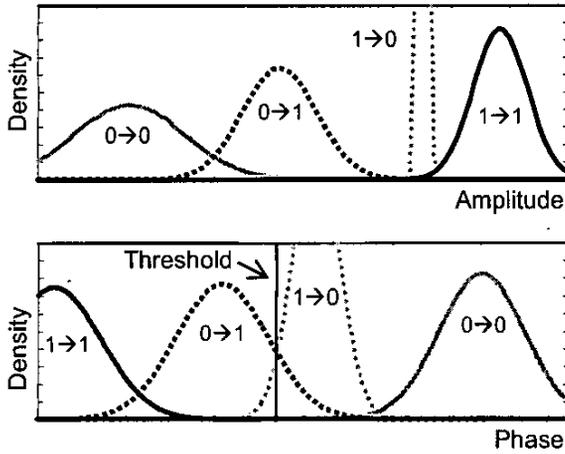


Fig. 5. Univariate density functions for the amplitude and phase codes

Four different cases of input-stimulus→desired-response are considered in the study, which correspond to two correct and two erroneous input stimuli:

- 1→1 (no error): stimulus in a channel that encodes for pattern A
- 0→0 (no error): no stimulus in a channel that does not encode for pattern A
- 0→1 (incomplete pattern): missing stimulus in channel that encodes for pattern A
- 1→0 (corrupted pattern): noisy stimulus in a channel that does not encode for pattern A

The results in Fig. 4 show that, although a higher number of channels yields a more detailed structure of the amplitude/phase clusters, these scatter plots have a similar structure regardless of the number of channels. This result leads to the conclusion that the KIII model is not only scale invariant with respect to amplitudes, a result previously established by Yao and Freeman [5], but also with respect to phase information.

A. Pattern recovery: preliminary results

An important conclusion can also be extracted from these scatter plots. Fig. 5 shows the univariate distribution of the amplitude and phase codes in the 64-channel model for each of the four input-stimulus→desired-response cases. A Gaussian distribution has been assumed for visualization purposes. It can be observed that the amplitude code is able to recover either incomplete or corrupted bits, but not both, since the 0→1 and 1→0 densities lie on opposite sides of their desired response. This result indicates that the amplitude of a particular channel tends to be driven primarily by the input stimulus rather than by the lateral connections in the Hebbian matrix. In the case of a phase code, a simple threshold can be obtained to correct the majority of the incomplete or corrupted bits, indicating a higher sensitivity to lateral connections. Pattern recovery is, therefore, more reliable using phase information. This key result is further explored in the next section.

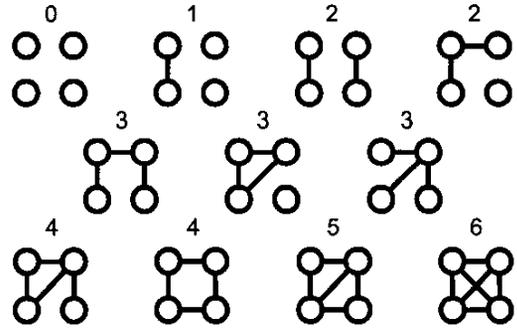


Fig. 6. Reduction of a 4-channel model to 11 non-isomorphic graphs. The index above each graph denotes the number of active Hebbian connections.

V. SYMMETRY OF THE ASSOCIATIVE MEMORY MATRIX

Once the scale invariance of the KIII model with respect to phase information has been validated, the study can now be focused on a lower dimensional model where an exhaustive evaluation of every possible combination of input stimulus and pattern sets is computationally feasible. Although 2- and 4-channel models could be used to this effect, the results in Fig. 4 show that more channels lead to higher resolution. For this reason, an 8-channel model is chosen for the final study.

In order to avoid exploring redundant combinations, the symmetries in the KIII associative-memory matrix will be exploited. Following [5], the mitral-mitral lateral connections can be computed as:

$$W_{MI} = \sum_{v_i} f(p_i p_i^T) \quad (1)$$

where p_i is the correct input pattern for the i -th odor class, and $f(\cdot)$ is a threshold function so that the elements in W_{MI} are binary, either HIGH or LOW (diagonal elements in the matrix are set to zero.) Thus, a HIGH element in the Hebbian matrix represents two KIII channels that are simultaneously active for *at least* one odor pattern. Since different pattern sets can lead to the same Hebbian matrix, an exhaustive evaluation of every possible pattern set can be reduced to the study of all possible matrix configurations.

A representation of the Hebbian matrix as an undirected graph will be used to illustrate the existing symmetries. For simplicity, assume a 4-channel model with only one connection between channels. Since the channels are symmetric, the behavior of the system will be the same regardless of where this connection is located. Generalizing this idea, graphs with the same number of connections and the same topology (i.e. isomorphic graphs) have to be considered just once. As a result, a 4-channel model with $2^6 = 64$ possible configurations is reduced to the 11 non-isomorphic graphs in Fig. 6. Similarly, an 8-channel model can be reduced from $2^{28} = 2.7 \cdot 10^8$ to 1,192 cases, for a significant savings in CPU time.

VI. PATTERN RECOVERY: FINAL RESULTS

The final comparison of the two coding schemes will be performed on an 8-channel KIII model, for a total of 1,192

non-isomorphic cases. As opposed to the preliminary study in section IV.A, where performance was studied as a function of degrees of overlap in the pattern set and distortions in the input stimulus, the pattern recovery capabilities in this final study can only be evaluated in terms of the properties of each graph since the relationship between pattern sets and graphs is many-to-one. Two observations will greatly simplify this analysis. First, any two neighboring nodes (those that are connected directly by an edge) represent channels that are simultaneously active for at least one stored pattern. Conversely, any two nodes that are more than one edge away represent channels where two or more patterns overlap. Therefore, it is possible to analyze the across-fiber pattern-recovery performance of the phase and amplitude codes by comparing the activation between nodes connected by a single edge (which represents a true pattern) against the activation between nodes connected by a multi-edge path (which represents an undesirable overlap).

This idea is illustrated in Fig. 7(a). For a given graph, a single input stimulus is applied to the channel with the highest number of lateral connections (d_0 in the figure), and the activity on the remaining channels is analyzed. Nodes within one edge from d_0 (denoted by d_1) are part of a pattern. Nodes two edges away (denoted by d_2) are the effect of an overlap between two or more patterns. The remaining nodes (d_3 through d_∞) can be neglected since they involve higher-order overlaps between patterns. Fig. 7(b) illustrates the situation where the response of d_0 and d_1 nodes is linearly separable from the rest, indicating that a simple threshold function could be used to recover an incomplete pattern from an input stimulus having a single active channel. Fig. 7(c) illustrates the opposite situation, where the response of d_0 and d_1 nodes is not linearly separable from the rest and, as a result, the incomplete pattern cannot be recovered.

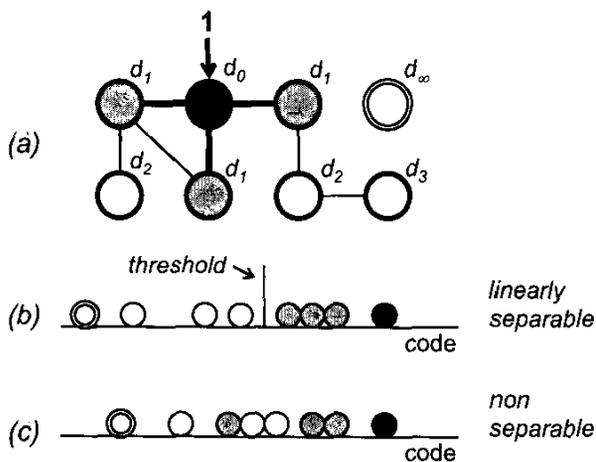


Fig. 7. (a) Pattern and overlap bits for a given Hebbian graph. (b, c) Pattern recovery as a linear separability problem

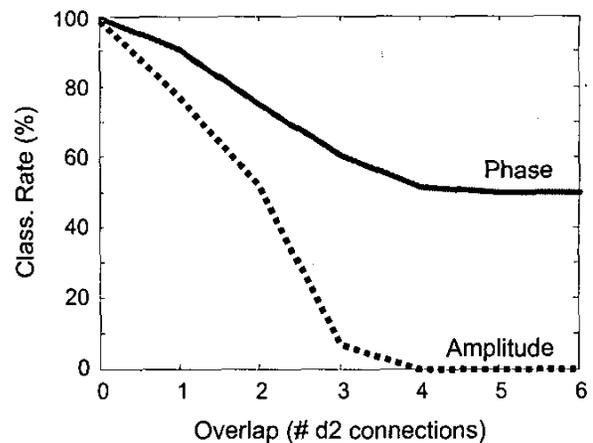


Fig. 8. Overall performance of the phase and amplitude codes as a function of pattern overlap

The procedure outlined in Fig. 7 is repeated individually for each of the 1,192 non-isomorphic cases in the 8-channel KIII in order to measure the pattern recovery capabilities of the amplitude and phase codes. The results are presented in Fig. 8 as a function of the number of d_2 connections in each graph, which can be related to the overlap (e.g. the complexity) of the corresponding pattern sets. Each point in the plot represents the percentage of graphs where the linear separability in Fig. 7(b) is achieved, relative to the total number of graphs. This result shows that the performance of the amplitude code decreases dramatically as the degree of overlap increases, whereas the phase code degrades in a more graceful manner and always provides higher classification rates. Along with the preliminary data presented in Fig. 5, this result clearly demonstrates the remarkable superiority of the phase code over the amplitude code.

VII. CONCLUSIONS

This article has proposed an analogy between coherent oscillations in neural populations and phase locking in the KIII model. We have shown that phase information between two channels can be efficiently captured by treating the state-space trajectory as a two-dimensional distribution and computing its correlation coefficient. Scale invariance of the KIII with respect to this phase information has been empirically validated on three models with 16, 32 and 64 channels.

An exhaustive comparison of the pattern recovery capabilities of the proposed phase coding and the conventional amplitude coding has been presented on an 8-channel model. In order to avoid the combinatorial explosion, redundant pattern and stimulus combinations have been eliminated by means of graph isomorphism. Experimental results show that information embedded in the phase of the KIII channels clearly outperforms the amplitude code.

The present study has focused on binary stimuli, but the KIII has also been shown [19] to work efficiently with

continuous inputs. Thus, a natural extension of the work presented in this article is to consider continuous amplitude and phase representations. Additional information other than correlation coefficients (which relate to phase for sinusoidal waveforms) could also be extracted from the KIII dynamic attractors in two- or higher-dimensional state spaces. These areas constitute promising directions for future work.

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