

Phase and Amplitude Modulation in a Neural Oscillatory Model of the Orientation Map

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Abstract. The traditional approach to characterization of orientation maps as they were expounded by Hubel and Wiesel treats them as static representations. Only the magnitude of a neuron’s firing response to orientation is considered and the neuron with the highest response is said to be “tuned” to that response. But the neuronal response to orientation is a time-varying spike train and, if the response of an entire cortical area that potentially responds to orientations in a given part of the visual field is considered, the response must be considered as a spatio-temporal wave. We propose a neural field model consisting of FitzHugh-Nagumo neurons, that generates such a wave. Reflecting the dynamics of a single FitzHugh-Nagumo neuron, the neural field also exhibits excitatory and oscillatory regimes as an offset parameter is increased. We consider the question of the manner in which the input orientation is coded in the response of the neural field and discovered that two different codes – Amplitude Modulation and Phase Modulation – are present. Whereas for smaller offset values, when the model is in excitatory regime the orientation is coded in terms of amplitude, for larger offset values when the model is in the oscillatory regime, the orientation is coded in terms of phase.

Keywords: NFM, Oscillator, Amplitude, Phase, FN

1 Introduction

In their seminal studies on mammalian visual cortex Hubel and Wiesel found neurons that respond to oriented bars [14]. This discovery was significant in that neurons at lower levels of the visual hierarchy – retinal layers, Lateral Geniculate Nucleus etc – showed responses to simple dot-like patterns, while the visual cortical neurons showed no response to dots, but responded to linear oriented patterns. Furthermore, neurons are tuned to bars of specific orientation, θ . The mapping of the orientation, on the two dimensional surface of the primary visual cortex, $\theta(x,y)$ is known as the orientation map. Among neurons that exhibit orientation tuning, there are the simple cells that respond to an

oriented line present in the center of their Receptive Field (RF) and complex cells that respond to an oriented line present almost anywhere in their RF. Orientation tuning changes continuously as a function of cortical location except at isolated points: these points, mathematically speaking, are singularities and are commonly referred to as “pinwheels” [2]. An extensive amount of computational modelling effort has been invested in understanding these intriguing features of orientation maps (see Chapter 5 of Miikkulainen et al (2006) [22] for an extensive review of both biological and computational aspects of orientation maps). There are spectral models that show how to compute maps that resemble visual orientation maps without invoking neurons or learning [13],[26]. These models are based on the insight that orientation map like patterns can be produced simply by filtering random dot images. Then there are correlation-based learning models in which there are neurons with lateral and afferent connections. In these models, the afferent connections are trained while the lateral connections are fixed [23],[32],[36]. A particularly elegant map model of this category was the one proposed by Obermayer et al [27]. This model, which was based on the Self-organizing Map (SOM) model proposed by Kohonen [18], was able to account for several key features of orientation maps like pinwheels and fractures. Another line of models of orientation maps that involved trainable lateral connections was the Laterally Interconnected Synergistically Self-Organizing Map (LISSOM) proposed by Miikkulainen and colleagues [21]. The LISSOM was later used to model a wide variety of topographical maps in the visual cortex.

But the visual cortical “maps” denote static representations of visual stimuli. They embody a static notion of the kind of information processing performed by the visual cortex. There is an entire perspective of cortical processing that posits that the fundamental building block of cortical computation is not a single neuron but a neuronal ensemble [5][28][11][19] and the collective activity of such an ensemble is not a spike train but a Local Field Potential (LFP) [25],[15]. Unlike spike trains, the LFP is usually resolved into a small number of oscillatory components described in terms of amplitude, frequency and phase. Information transfer between two such ensembles can be achieved by mechanisms like entrainment and synchronization [8][29][31][16]. There is a growing body of experimental literature that describes cortical responses to stimuli and learning in terms of LFP oscillations [34][12][20][33][7]. Theta oscillations in visual cortical LFPs show adaptation to stimulus and the ability to predict time of reward prediction [37]. Klimesh et al (2011)[17] proposed that the visual alpha waves play a key role in encoding the visual stimulus in the early post stimulus interval (< 150 ms). The varied roles of all the Electroencephalogram (EEG) waves not just in visual perception but in cognitive processes in general have been extensively reviewed [1]. In view of the extensive literature on the roles of oscillatory neural activity in cortical processing, we propose that the notion of cortical “maps” is slightly outmoded. There must be a more expanded notion of cortical representations in terms of oscillatory activity. With such a motivation we set out to construct an oscillatory neural model of orientation sensitivity. The model consists of a two-dimensional array – a “neural field” – of FitzHugh-

Nagumo neurons with afferent and lateral connections. The network is trained to respond to oriented bar stimuli. An analysis of the network responses shows that orientation is coded in two forms: Amplitude Modulated (AM) form and Phase Modulated (PM) form. The network is operated in two modes: 1) excitatory mode and 2) oscillatory mode. Whereas the AM code dominates in the excitatory mode, PM is predominantly found in the oscillatory mode. The paper is outlined as follows. Section 2 presents the model architecture and learning equations. Section 3 describes the simulation results and the emergence of AM and FM codes of orientation sensitivity. The modeling results and future work is discussed in the last section

2 Methods

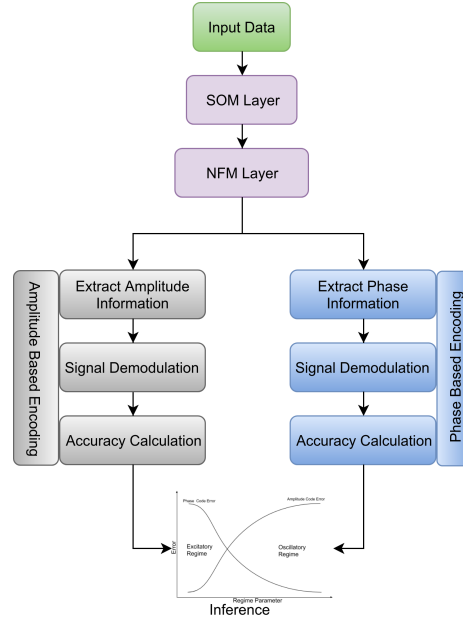


Fig. 1: The above figure shows flow of the data, modulation and demodulation strategies followed in our method

The architecture of the proposed model of oscillatory orientation maps consists of a cascade of two components: the Self-organizing Map (SOM) and a Neural Field Model (NFM) consisting of the FitzHugh-Nagumo (FN) neurons. The SOM represents a traditional and one of the simplest models of orientation selectivity. The output of the SOM is presented to the NFM which encodes the input oriented bar in terms of its oscillations. The architecture is shown in figure 1

2.1 The network architecture

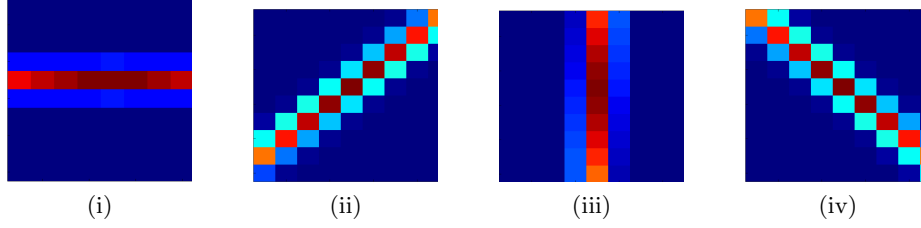


Fig. 2: Gaussian bars at different orientations which are used as input stimulus for the experiment

The SOM layer is trained using orientation bars shown in figure 2. The output of the SOM network is given as a one to one projection to the oscillatory neural network called Neural Field Model (NFM). Each element of the NFM is a Fitzhugh Nagumo (FN) oscillator. Each FN oscillator is connected among the neighbors by means of a fixed Mexican Hat connectivity (M) to form the NFM. The strength of the lateral connections can be made strong or weak depending on the variable β . The input influences the neuron both in an additive and multiplicative manner. The NFM layer can exist in two states and behaves as an excitatory network or as an oscillatory network depending on the parameter C . It is observed that the information is encoded by the NFM either by amplitude modulation or by phase modulation depending on the state in which it exists. For example, in the oscillatory regime, unless the input is presented, all of the neurons oscillate in synchrony; but once the input is presented, neural oscillations attain phase relationships that are uniquely related to the input orientation. The FN oscillator is a dynamical system defined using two variables, V (fast variable) and W (recovery variable) as shown in equation(1),(2) and (3).

$$\dot{V}_{i,j} = \frac{f(V_{i,j}) - W_{i,j} + I_{i,j}}{\varepsilon_{i,j}} \quad (1)$$

$$\dot{W}_{i,j} = bV_{i,j} - \gamma W_{i,j} \quad (2)$$

$$f(V) = V(a - V)(V - 1) \quad (3)$$

where b, γ and a are constants. I is the total external current felt by the neuron, and ε is the time scale variable, defined by equations (4) and (6) respectively. The external current, I is taken as a sum of afferent input(A), current from lateral connections and also the offset parameter (C) with appropriate scaling parameters as shown in equation (4).

$$I_{i,j} = C + A_{i,j} + \beta \sum_{k,l} M_{kl,ij} (V_{k,l} - V_{i,j}) \quad (4)$$

where, M denotes the fixed mexican hat weight connection among the neighbouring neurons, β is a scaling parameter and A is the afferent input given by:

$$A_{i,j} = g \times SOM \quad (5)$$

where SOM is the output of the self orientation map layer and g is a scaling parameter. The factor g ensures that the input does not override the lateral connections.

The time scale variable ε is given by the equation (6)

$$\varepsilon_{i,j} = 1 - SOM_{i,j} + p \quad (6)$$

where p is a constant. The value of p is chosen to ensure the stability of the oscillator such that a stable limit cycle exists for all values of SOM outputs ranging between 0 and 1. Considering the facts that the value of ε is ensured to lie between $p(p \rightarrow 0^+)$ and 1, the parameters b and γ are constants and the afferent and lateral inputs are bounded (absolute normalization of lateral weights), the model complies with the classic Fitzhugh Nagumo model and is hence stable at both excitatory and inhibitory regimes. The values of the parameters used are given in table 1.

Table 1: Table of Parameters

Parameter	Value Chosen
a	0.5
b	0.1
γ	0.1
β	0.6
g	0.05
p	0.01

2.2 Oscillatory neural response demodulation

The response of each oscillatory neuron is observed for 50 time units. Two different methods of data processing, phase demodulation and amplitude demodulation is done to extract the phase and amplitude information respectively from the response waveforms.

2.3 Phase Demodulation

In order to extract the phase information from the NFM response, the relative phase difference (RP) of each neural response is calculated by taking the phase of

first neuron - the neuron at the location (1,1) of the NFM as reference. Instantaneous phase of the output of a neuron $V_{i,j}$ is calculated using Hilbert transform of a signal and Mean of the Relative Phases (MRP) is used to train the logistic regression model.

$$RP_{i,j}(t) = \angle H\{V_{i,j}(t)\} - \angle H\{V_{1,1}(t)\} \quad (7)$$

where $H\{X\}$ defines hilbert transform of X and $\angle H\{X\}$ calculates the instantaneous angle of $H\{X\}$

$$MRP_{i,j} = \frac{1}{T} \left(\sum_{t=0}^T RP_{i,j}(t) \right) \quad (8)$$

Using the data generated from 20 different trials for each orientation, and 4 different Orientations (figure.2), a multi-nomial logistic regression model was trained with the $n^2 - 1$ dimensional input data with corresponding K dimensional one hot vectors as labels, where K is the number of classes (In this case, $K = 4$). The classification accuracy was calculated on held out test data.

2.4 Amplitude Demodulation

The amplitude demodulation was done by simply averaging the output, $V_{i,j}$, of the NFM across time. The averaged NFM response (A) is given by.

$$A_{i,j} = \frac{1}{T} \left(\sum_{t=0}^T V_{i,j}(t) \right) \quad (9)$$

Similar to Phase demodulation, the data was generated from 20 different trials for each orientation and 4 different orientations. The data was used to train a multi-nomial logistic regression model with n^2 dimensional input data with corresponding K dimensional one hot vectors as labels. The classification accuracy was calculated on held out test data.

3 Results and Discussion

The response of the neural sheet is observed for 50 time units and the waveform is analyzed for each network characteristics. By varying the value of offset parameter, C , between 0 to 0.8, the NFM shifts from excitatory regime to oscillatory regime. The response of the network in both regimes, while presented with a SOM input is shown in plot (a) in figure 3 and figure 5.

In figure 3 (i) and (ii), plot(b) shows the relative phase of each neuron with respect to the phase first neuron and plot (c) shows the mean relative phase vector of all neurons across time (MRP). As can be seen, the phase difference during excitatory regime (figure 3: i.b and i.c) is almost zero everywhere, carrying no information, while the phase difference plot in oscillatory regime (figure 3:ii.b

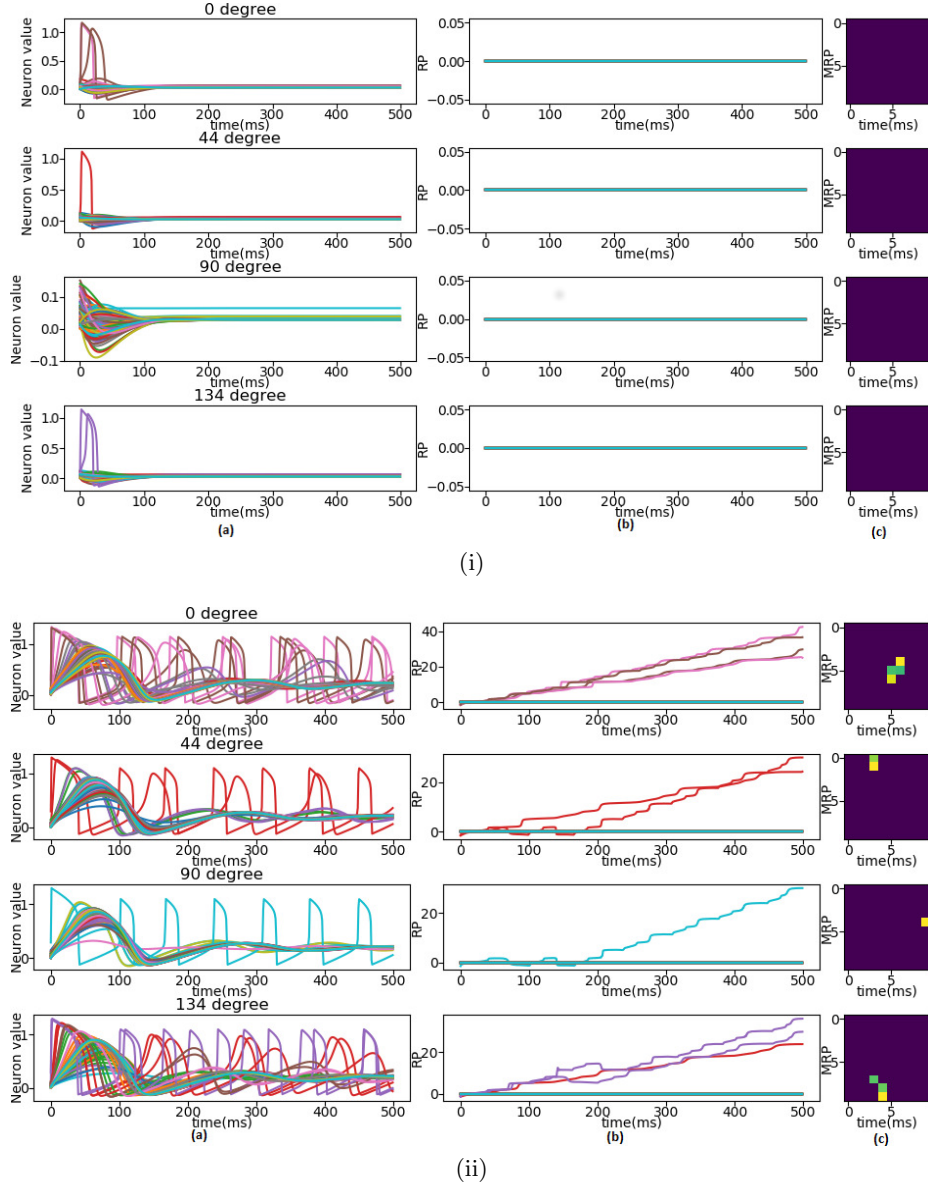


Fig. 3: (a) The wave forms of individual neurons, (b) Unwrapped phase difference across time, (c) Mean relative phase, during (i) excitatory regime and (ii) oscillatory regime.

and ii.c) shows a unique pattern. As seen in figure 3:ii.a, in the oscillatory regime, most of the background neurons oscillate in phase and the neurons encoding the input oscillate at a higher frequency. This indicates the encoding of information in phase during oscillatory regime. This is further verified by calculating classification accuracy using the MRP vectors by means of logistic regression. The results are shown in figure 4 where the classification accuracy increases once the network enters the oscillatory regime.

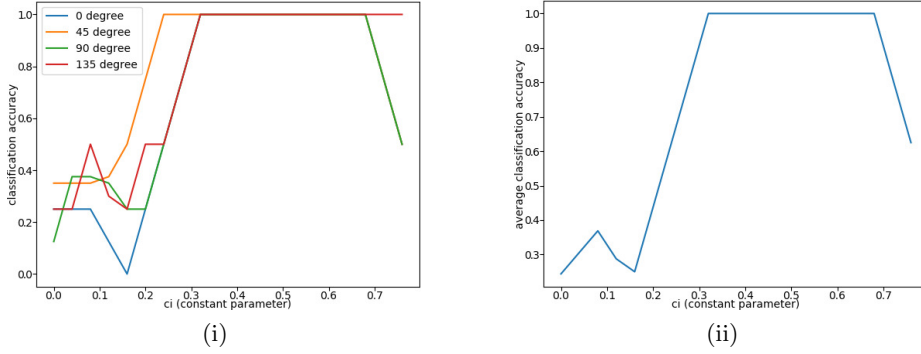


Fig. 4: (i) Classification accuracy on new test data, and figure (ii) Average classification accuracy for all the test angles (obtained by Phase demodulation).

In the figure 5(i.b and ii.b), the average sheet response across time is observed for both excitatory regime and oscillatory regime. Though the average sheet resembles the SOM response in both regimes, the variance (noise) in the average sheet responses is zero in the excitatory regime (figure 3 i.b) and it increases once the neuron enters the oscillatory regime as shown in figure 3(ii.b). This suggests a stronger amplitude coding in the excitatory regime than in the oscillatory regime which is further confirmed by computing average classification accuracy using logistic regression as shown in figure 6 where the classification accuracy decreases once the network enters the oscillatory regime.

4 Conclusion

We proposed a neural field model ($n \times n$) of an orientation map in which the orientation information is encoded in the spatio-temporal response of the neural field. The model consists of a laterally connected 2D layer of FN neurons. Oriented bar patterns are used to train a SOM ($n \times n$), whose output is presented to the NFM in a one-to-one fashion. The neural field model was shown to exist in two regimes: in the excitatory regime for lower values of the offset parameter, and in the oscillatory regime for higher values of the offset parameter. The classical orientation map which presents a static picture of orientation responses of

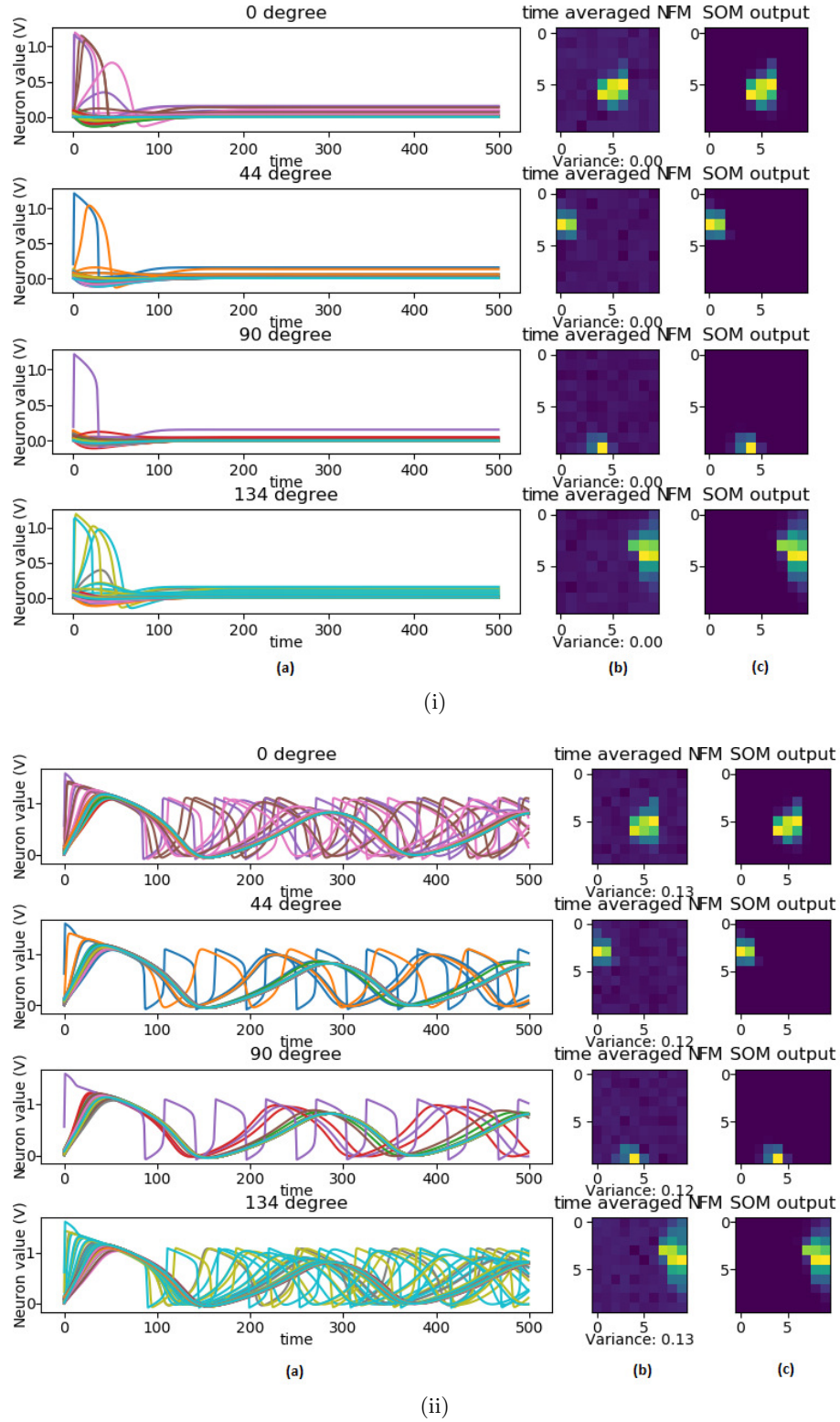


Fig. 5: (a) The wave forms of individual neurons, (b) average responses of NFM across time, (c) SOM output, during (i) excitatory regime and (ii) oscillatory regime.

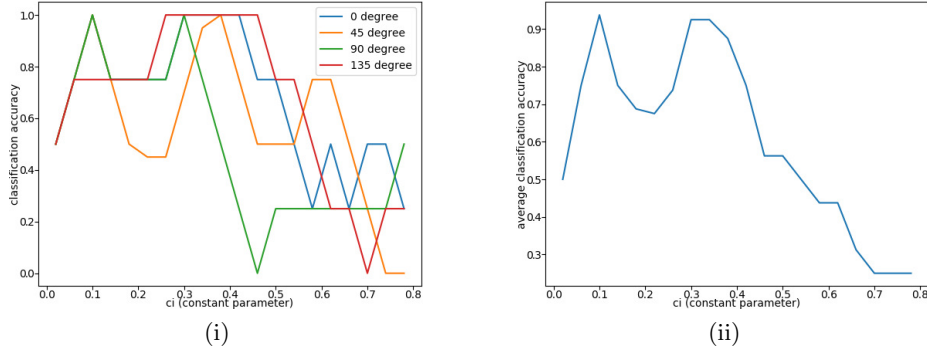


Fig. 6: (i) Classification accuracy on new test data, and figure (ii) Average classification accuracy for all the test angles (obtained by Amplitude demodulation).

the visual cortical neurons, can be reinterpreted in terms of neural oscillations. The proposed NFM model encoded the input orientation information primarily using amplitude modulation while in excitatory regime and using phase modulation while in the oscillatory regime. The classical depictions of orientation maps, or for that matter any topographic map of the brain, present the impression that information is encoded in static forms in the cortical surface. However the brain is a dynamical system and cortical responses to stimuli are more ideally considered as spatio-temporal responses. A primary instance of such a characterization of neural responses to sensory stimuli, is the study of the responses of the olfactory bulb by Freeman and colleagues [9]. In these studies Electroencephalogram (EEG) recordings were made by grid electrodes from the rabbit's olfactory bulb. The responses of the bulb to odors showed stable and repeatable spatio-temporal patterns.

But the aforementioned recordings in the olfactory bulb are Local Field Potentials (LFPs) and not spike patterns. A prominent perspective of neural computations posits that the fundamental unit of computations in the brain is not a single neuron but a neural ensemble. The activity of a neural ensemble is captured by a LFP, often described in terms of a small number of oscillatory components. Neural models often fall under two broad categories: rate coded or spiking neuron models. But a large number of cerebral phenomena can be best described in terms of oscillatory activity [4]. For example, gamma rhythm is thought to have a key role in information transfer between brain regions [35][6][10][3]. Synchronized gamma oscillations are thought to underlie feature binding, a temporal mechanism by which the diverse features of an object are integrated in a unified representation [24],[30]. The growing effort to describe brain function in terms of dynamics and oscillations points to the need to rethink static notions of neural information processing like the topographic maps. The proposed model is a small step in that direction.

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