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Temporal coding: The relevance of classical activity, its relation to pattern frequency bands, and a remark on recoding of excitatory drive into phase shifts

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ABSTRACT

We consider an oscillatory network model that is obtained as complex-valued generalization of the classical Cohen–Grossberg–Hopfield (CGH) model. Apart from a synchronizing mechanism, a stronger and/or more coherent input to a unit in the network implies a higher phase velocity of this unit. This constitutes the desynchronizing mechanism, referred to as acceleration. The units' activity of the classical model translates into the amplitudes of the phase model oscillators. This allows to associate classical and temporal coding with amplitude and phase dynamics, respectively. We discuss how the two dynamics act together to achieve the unambiguous pattern recognition that avoids the superposition problem. With respect to coherence, dominating patterns may take coherent states also if only a subset of its units is on-state. The competition for coherence, introduced by acceleration, realizes a kind of feature counting that identifies the dominating pattern as the pattern with the most on-state units. This dominating but possibly only partially active pattern may take a coherent state with a frequency level that is related to the number of on-state units. We also speculate on neurophysiological findings, related to observed phase differences between optimally and suboptimally activated neurons, that may indicate the presence of acceleration.

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1. Introduction

Specifying states of neural networks by assigning on- and offstates to its units, thereby describing their state of activity, is an approach that goes back at least to the earliest work of McCulloch and Pitts (1943). In 1949, based on this picture of on- and off-state neurons, Donald Hebb proposed that mental objects are represented as sets of on-state units, referred to as assemblies (Hebb, 1949). In the 1960s, instead of using only the binary on- and off-values for neural units, the sigmoid firing characteristic was introduced, given by

$$V_k = g(u_k) = \frac{1}{2}(1 + \tanh(u_k)),$$
(1)

where V_k describes the firing rate of the unit k of a network with N units, k = 1, ..., N, and u_k describes the input to this unit (Cowan, 1967). On- and off-state units are then characterized through, correspondingly, $V_k \simeq 1$ and $V_k \simeq 0$. This continuous generalization allowed for smooth transitions between these states, making the continuous dynamical system models possible that generated a

number of new approaches. For example, this continuous version is used with the Cohen-Grossberg-Hopfield (CGH) model that identifies assemblies with patterns that are stored according to the rules of Hebbian memory (Cohen and Grossberg, 1983; Hopfield, 1984). In the following, we refer to the paradigm that identifies assemblies with sets of on-state neural units as classical coding. Today, there are doubts whether classical coding may describe the complete picture. Already in 1961, Rosenblatt observed that classical coding has to deal with a severe problem when applied to the simultaneous formation of several assemblies. This problem is the so-called superposition catastrophe (Rosenblatt, 1961). In the 1980s, it motivated von der Malsburg (1981) to propose the temporal correlation hypothesis. This is based on using also some temporal structure of the units' activity. According to the temporal correlation hypothesis, a set of on-state neural units constitutes an assembly only if the units are grouped together based on temporal correlation of these activities. Different assemblies may then be simultaneously active but still be separable with regard to different temporal correlations. For reviews of the superposition problem and temporal coding, as well experimental confirmations in the context of brain dynamics, see von der Malsburg (1999) and Singer (2003).

The modeling of temporal coding is still an open problem. It may be expected that some oscillatory network model is appropriate (see Section 2.4 and Burwick (2006) for a list of references



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to models based on oscillatory networks). Using such an approach, the formation of assemblies based on temporal correlation requires synchronizing as well as desynchronizing mechanisms. Without a desynchronizing mechanism, global synchronization would reintroduce the superposition catastrophe. The model that we use in this paper is based on a desynchronizing mechanism that is referred to as acceleration. It implies that the phase velocities of neural units are increased in case that the input from the other units is stronger and/or more coherent. Recently, it was demonstrated that such a desynchronizing mechanism has a profound and favorable effect on segmenting overlapping patterns (Burwick, 2007, 2008a, b). Thereby, it provides a new perspective on solving a central problem of classical neural networks.

The model that we use may be formulated as complex-valued generalization of the classical (real-valued) CGH model that was mentioned above. Thus, it is an oscillatory network model that is particularly close to the classical case. In consequence, it allows to integrate and compare the roles of classical and temporal coding. The classical activation, representing on- and off-states of the neural units, translates into large and small amplitude oscillations, respectively. Classical coding is therefore related to the amplitude dynamics, while the phase dynamics is related to temporal coding.

In this paper, our focus is on the role that on- and off-states may have in the context of temporal coding. Moreover, we speculate on neurophysiological findings that could indicate the presence of acceleration. We go beyond the discussions in Burwick (2007, 2008a, b, in press) in three respects. First, we demonstrate with an example the attracting character of the on- and off-states and the presence of the corresponding boundary between the two basins of attraction (compare Fig. 4, panels A and C). Second, we extend the pattern-frequency correspondence that was introduced in Burwick (2008a). The described complementarity of classical and temporal coding motivates that we introduce different frequency levels for each of these patterns, related to different numbers of onstate units. The presence of such frequency levels is demonstrated with an example (see Eq. (20) and Fig. 7). Third, we speculate that (analogs of) the neurophysiologically observed recoding of excitatory drive into phase shifts (see references in Section 5.1) may be related to the presence of acceleration couplings. Thereby, we discuss a proposal that was given at the end of Burwick (in press).

In Section 2, we review the model. In Section 3, the patternfrequency correspondence that was introduced in Burwick (2008a) is extended to different frequency levels for each pattern. Each of these levels is specified by the number of on-state units, as mentioned above. Section 4 gives two examples. The first example demonstrates the pattern segmenting interplay of synchronization and acceleration. The second example uses the same network architecture but different initial values. Then, in contrast to the first example, only part of the network becomes active. This allows to demonstrate the interplay of amplitude and phase dynamics, reflecting the complementary roles of classical and temporal coding. Moreover, it illustrates the relevance of the number of on-state units for the pattern frequency level. The comments on possible neurophysiological findings may be found in Section 5. Section 6 contains the summary.

2. The Model: Oscillatory Networks with Synchronization and Acceleration

2.1. Real Coordinates

Consider a network with *N* units, where each unit *k* is described in terms of amplitude V_k and phase θ_k , k = 1, ..., N. Using the

activation function g that was described with Eq. (1), the oscillatory system that we study is a generalization of the classical Cohen–Grossberg–Hopfield (CGH) model:

$$\tilde{\tau}(u_k)\frac{\mathrm{d}u_k}{\mathrm{d}t} = I_k - u_k + \frac{1}{N}\sum_{l=1}^N w_{kl}(\theta_l - \theta_k)V_l$$
(2a)

$$\frac{\mathrm{d}\theta_k}{\mathrm{d}t} = \omega_k\left(u,\theta\right) + \underbrace{\frac{1}{N}\sum_{l=1}^N s_{kl}(\theta_l - \theta_k)V_l}_{\text{synchronization terms}}$$
(2b)

with

$$\omega_{k} = \omega_{1,k} + \omega_{2,k}V_{k} + \underbrace{\frac{1}{N}\sum_{l=1}^{N}\Delta\omega_{kl}(\theta_{l} - \theta_{k})V_{l}}_{\text{acceleration terms}}$$
(3)

Here, *t* is the time, I_k is an external input, the $\omega_{1,k}$ are the eigenfrequencies of the oscillators, and the $\omega_{2,k}$ parameterize the shear terms. A comparison of Eq. (2) with the CGH model (Cohen and Grossberg, 1983; Hopfield, 1984) shows that the amplitude is the analog of the classical activity.

In Burwick (2007), Eq. (2) is described as complex-valued gradient system. This form implies the phase-dependent couplings

$$w_{kl}(\theta) = h_{kl} \left(a + \frac{\sigma}{2} \cos\left(\theta\right) - \frac{\tau \omega_3}{2} \sin\left(\theta\right) \right), \tag{4}$$

$$s_{kl}(\theta) = h_{kl} \sigma \sin\left(\theta\right),\tag{5}$$

$$\Delta \omega_{kl}(\theta) = h_{kl} \,\omega_3 \cos\left(\theta\right),\tag{6}$$

where a > 0, $\sigma > 0$, $\omega_3 > 0$ are real parameters, and the scaling factor,

$$\tilde{\tau}(u_k) = (1 - V_k)\tau,\tag{7}$$

uses a time-scale $\tau > 0$. Notice, $\tilde{\tau}(u_k) > 0$ due to Eq. (1). The h_{kl} describe Hebbian couplings (see Section 2.3). The more general system with all-order mode couplings was given in Burwick (2007). In this paper, we only discuss the simple form with first-mode couplings as given in Eqs. (2)–(7).

2.2. Complex-valued Gradient System

As mentioned above, Eq. (2) was derived from a complex-valued gradient system,

$$\tau \frac{dz_k}{dt} = -\left|z_k\right| \frac{\partial \mathcal{L}}{\partial \bar{z}_k},\tag{8}$$

where \mathcal{L} is a complex-valued potential function and the complex coordinates are given by

$$z_k = V_k \exp(i\theta_k), \bar{z}_k = V_k \exp(-i\theta_k).$$
(9)

Due to Eq. (1), the dynamics is restricted to the punctured unit disk,

$$0 < |z_k| = V_k = g(u_k) < 1.$$
⁽¹⁰⁾

In the following, we will frequently refer to the complex coordinates formulation, in particular by describing the dynamics on the (punctured) complex unit disk, given by Eq. (10). The explicit form of \mathcal{L} may be found in Burwick (2007).

2.3. Hebbian Memory

According to Hebbian memory, the storage of *P* patterns ξ_k^p (related to the assemblies that were mentioned in Section 1),

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