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Temporal binding of non-uniform objects

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Abstract

Gestalt-based feature binding becomes problematic if different objects overlap in their positional configuration and/or feature space, or if features vary over the spatial extent of an object. If synchronization is to be a viable mechanism for binding the responses of disparate feature selective neurons in the brain, it must cope with resulting ambiguities. In this article the synchronization properties of an oscillator network for multidimensional feature binding are investigated. For non-uniform feature distributions in a stimulus, its components are adequately represented by the eigenmodes of the oscillatory dynamics. The significance of the eigenmodes corresponds to the salience of different stimulus interpretations.

Keywords: Binding; Oscillations; Eigenmodes; Representations; Ambiguity

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1. Introduction

The temporal properties of neuronal responses constitute a coding dimension for dynamic relations between these neurons. Synchronized neuronal activity has been used to explain a mechanism that binds the responses of feature specific neurons, if these features are instantiated by the same object [10]. This integration of distributed responses is necessary for perceiving an object as a single entity. Neuronal synchrony has been observed in numerous cell recording experiments (reviewed by Singer [7]) and experiments related to attention [8], perception [2], expectation [5] and mental representations [11]. In experiments on the perception of plaid stimuli [9] and temporally structured displays [1] synchronization was not relevant.

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The question arises, which elements of a visual scene should be bound during the process of perception. According to two of the Gestalt principles of perception, spatially proximal elements with similar feature values will be grouped. Most real-world objects, however, are non-uniform in one or more of their feature dimensions, e.g., within one object illumination, edge orientation and/or color can vary. On the other hand, two distinct objects that are overlapping and are possibly similar in one or more feature dimensions, could generate the same retinal activation pattern like a single object with non-uniform properties. How, then, can the brain distinguish both percepts?

In [6], the synchronization properties of an oscillator network has been investigated for a stimulus that was uniform in one feature dimension (orientation), but differed in two others (features were orientation, disparity and color). It turned out that the oscillators receiving input from the same object synchronized with each other, while the oscillatory functions of oscillators receiving input from two distinct objects differed by a phase shift. This corresponds to the perception of two distinct objects.

For an even number of feature dimensions or varying feature values within the object, the binding task can become ambiguous. A possible solution is the simultaneous representation of candidate binding solutions for later selection. In a preceding article [3] it has been shown that the dynamics of an oscillator network can simultaneously represent multiple binding solutions. In the next section the extension of the model to multiple feature dimensions will be introduced. Section 3 shows the results that were obtained from ambiguous stimuli. The paper concludes with a semantic interpretation of the results obtained.

2. Oscillator network for multidimensional feature binding

A network of coupled oscillators was used to implement Gestalt-based feature binding in the temporal domain. The subnetwork for binding a single feature has been detailed in [3], but the general structure will be shortly reproduced.

A single oscillator consists of an excitatory and inhibitory neuron with recurrent synaptic connections. Each model neuron is considered a representative of a larger group (100 to 200) of spatially proximal and physiologically similar biological neurons. Oscillators are arranged on a three-dimensional grid. Two dimensions represent the retinotopic mapping of the spatial domain, while the third dimension represents discrete values of a single feature. If a specific feature (value) is present in the receptive field, the corresponding oscillator will be activated by an input signal. The oscillators are locally connected by synchronizing and desynchronizing connections. This network exhibits binding of a single feature and will be called a “feature module” in accordance with [6]. A mathematical analysis of a single oscillator as well as of the network was carried out in [4].

The current work extends this model to multiple features. Here, the network consists of several feature modules, one for each feature dimension. For the qualitative design of the coupling between the feature modules, two criteria were relevant:

1. The distinctive features of a single object should synchronize the activity of oscillators activated by this object in the respective feature modules. For this

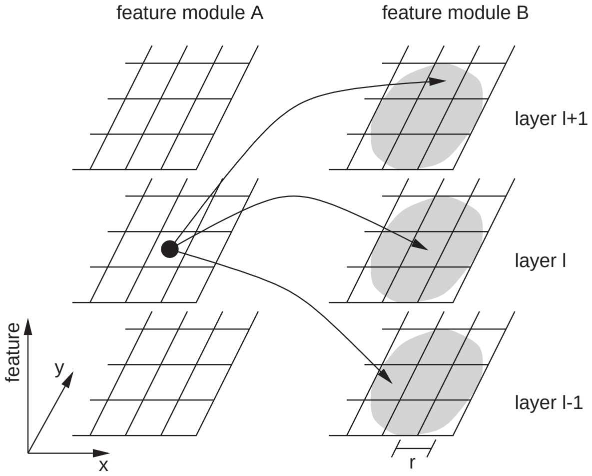

Fig. 1. Schematic of the coupling between two feature modules. Only three connections are drawn out. The single oscillator in module A has connections to all oscillators in the shaded region of module B. This schema is applied to all other oscillators and feature modules.

reason, feature modules are coupled by synchronizing connections that preserve topology.

2. No particular relations are specified between the magnitudes in each feature channel of a single object. Therefore, couplings between feature modules are unspecific in the feature dimensions.

Fig. 1 illustrates a subset of the network. In order to synchronize different feature modules, the excitatory neurons of oscillators were coupled. Quantitatively, the coupling strength $L^{AB}(i,j)$ between oscillator i in feature module A and oscillator j in feature module B is given by

$$L^{AB}(i,j) = \begin{cases} \dfrac{L_0}{\sqrt{2\pi\sigma^2}} \mathrm{e}^{-(d(i,j)/2\sigma)^2} & \text{if } d(i,j) < r, \\ 0 & \text{else.} \end{cases} \tag{1}$$

The distance in geometric space between the receptive fields of both oscillators is denoted by $d(i,j)$ and the weight parameter is L_0. Connections emanating from oscillator i are allowed to contact oscillators in a surround of size r from the target oscillator j.

3. Results

For the experiments two feature dimensions were used: color and orientation. In order to investigate the binding capabilities of the network, two types of stimuli were tested (Figs. 2a–d). The first contained a horizontal and vertical bar that overlapped in the center. When both bars share the same color, this is usually perceived as a cross. This stimulus is uniform in the color dimension, but non-uniform in the orientation

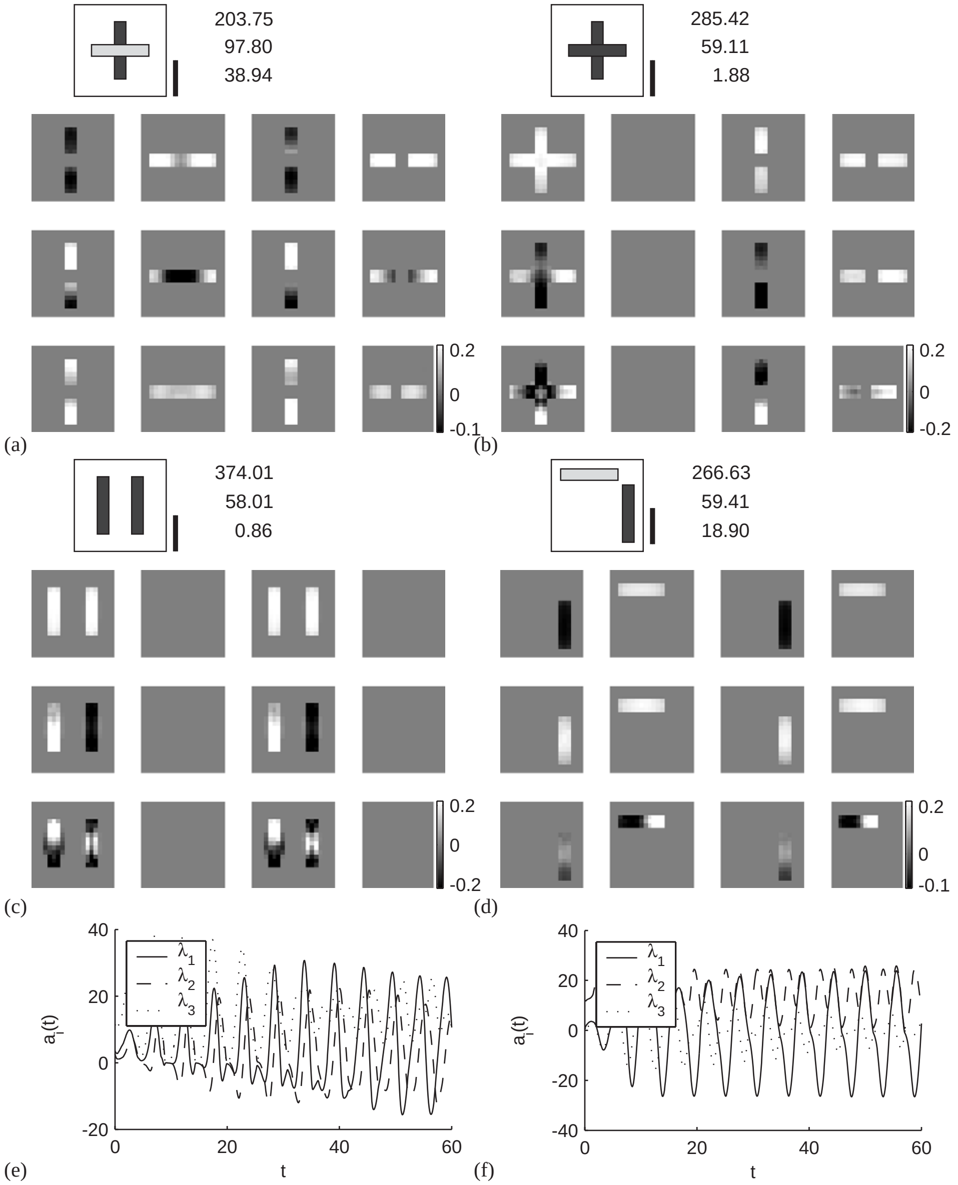

Fig. 2. (a)–(d) The top figure shows the stimulus. The small bar to the right depicts the diameter of couplings within a feature module. Shown below are the eigenmodes with the three largest eigenvalues arranged from top to bottom. The magnitudes of the eigenvalues are given to the right of the stimulus. Each eigenmode was split into the components for each active layer in every module. From left to right each row displays the mode for color 1 and color 2 of the color module and vertical and horizontal orientation of the orientation module. (e, f) Time course of the magnitude of the order parameters for stimulus c (e) and b (f). The coupling parameters were $L_0 = 0.1$, $r = 2$ and the module parameters $\tau_x = \tau_y = 1$, $m_x = m_y = 2$, $\theta_x = 2$, $\theta_y = 1$, $I_0 = 2$, $L_0^{xx} = 0.6$, $J_0 = 0.5$, $W_0 = 0.1$, $r_x = r_y = 4$.

dimension. If the bars have different colors, they are non-uniform in both feature dimensions. In the other type of stimulus there was no overlap between the two bars.

The input to the network was computed from these stimuli. Since the feature values are binary in each dimension (2 colors, 2 orientations), at most two layers of each feature module received input.

The dynamic equations (given in [3]) were then solved numerically by a fourth-order Runge–Kutta method. The activity of all excitatory neurons at each integration step constituted a vector $\mathbf{x}(t)$. The eigenvectors $\mathbf{e}_i$ of the covariance matrix $\mathbf{C} = \langle \mathbf{x}\mathbf{x}^{\mathrm{T}} \rangle$ were computed. In the eigenspace the dynamics take the form

$$\mathbf{x}(t) = \sum_i a_i(t)\mathbf{e}_i,$$

where the $a_i(t)$ denote superposition coefficients that are determined by projecting the activity $\mathbf{x}(t)$ into the eigenspace. In [4], it was shown that the eigenvectors approximate the eigenmodes of the solution of the system of ODEs describing the network dynamics, if the time course of the superposition coefficients is sinusoidal and there are strong differences in the variances of each principal direction (expressed by the magnitude of the corresponding eigenvalues). Under these conditions the superposition coefficients associated with each eigenvector correspond to the order parameters associated with each eigenmode. Order parameters are shown in Figs. 2e and f and eigenvalues in Figs. 2a–d.

For display purposes the eigenvectors were split into the contributions from each activated layer and reshaped to a matrix. To analyze the eigenmodes, the sign of the components of each mode (visualized by light and dark shades of grey) are taken into account. Regions with the same sign are activated together, while regions with opposite signs are activated alternately. This shows which parts of the stimulus are bound by correlated activity of the oscillators.

When considering the eigenmode with the highest eigenvalue (the first row in Figs. 2a–d), a number of interesting observations can be made. To begin with, only oscillators that are stimulated by input in their receptive field become activated. The activity of spatially proximal oscillators is synchronized. The activity of oscillators in different feature modules activated by the same bar is synchronized as well. Finally, if the bars have different colors, the oscillations are desynchronized. The most prominent mode therefore exhibits the binding expected according to the theory of dynamic binding.

When the same analysis is applied to the eigenmodes with the second largest eigenvalue (second row), alternative interpretations emerge. This is most obvious in the stimulus in Fig. 2b. The orientation components of this mode (the two rightmost subplots) display the difference in orientation of the two bars constituting a (monochromatic) cross. The result for stimulus 2c has been analyzed in [3]. There, only the color domain was used. Taking the orientation domain additionally into account does not change the interpretation obtained. The second eigenmode of stimulus 2d represents an interpretation in which the two bars are bound together. This is an alternative to the first mode which represents two separate bars. The same interpretation is displayed by the third eigenmode for stimulus 2a.

The eigenvalues and the time-course of the order parameters show that the conditions under which eigenvectors of the covariance matrix can be considered an approximation of the eigenmodes of the underlying system of differential equations are fulfilled.

4. Discussion

The dynamics of the network can be understood in semantic terms. We are allowed to regard oscillation functions as internal representations of individual objects. They may be assigned as meanings of some of the individual terms of a first-order predicate language with identity. Let *Ind* be the set of individual terms, then the partial function

$$\alpha : Ind \to Osc \tag{2}$$

is a constant individual assignment of the language into the set of oscillation functions *Osc*. The sentence $b = c (b, c \in Ind)$ expresses a representational state of the system to the degree the oscillation functions $\alpha(b)$ and $\alpha(c)$ of the system are synchronous. Provided that *Cls* is the set of sentences, the degree to which a sentence expresses a representational state of the system, for any eigenmode **e**, can be measured by the function

$$v_{\mathbf{e}} : Cls \to [-1, +1]. \tag{3}$$

In case of identity sentences we have

$$v_{\mathbf{e}}(b = c) = \Delta(\alpha(b), \alpha(c)), \tag{4}$$

where Δ measures the synchrony of oscillation function by rendering a value between -1 and $+1$ as defined by [12]. Most vector components of a given eigenmode are exactly zero, while few in some cases are positive and few in some cases are negative. Since the contribution of an eigenmode **e** to the entire network state temporally evolves according to a function $a(t)$, any positive eigenmode component $e^j = +|e^j|$ contributes to the activity of the jth oscillator with $+|e^j|a(t)$, while any negative component $e^l = -|e^l|$ contributes with $-|e^l|a(t)$ to the activity of the lth oscillator. Since the Δ-function is normalized, only the signs of the constants matter to determine that the activities of the jth and the lth oscillator, contributed by an eigenmode, are exactly anti-parallel, while any two with $a(t)$ temporally evolving components of equal signs contribute mutually parallel activity. We may interpret this by saying that each eigenmode represents maximally two objects as different from one another. The representation of the first object is the positive function $+a(t)$ and the representation of the second object is the negative function $-a(t)$. Both positive and the negative functions can be assigned to individual constants, b and c, respectively. These considerations, for every eigenmode **e**, justify the following evaluation of non-identity:

$$v_{\mathbf{e}}(\neg b = c) = \begin{cases} +1 & \text{if } v_{\mathbf{e}}(b = c) = -1, \\ -1 & \text{if } v_{\mathbf{e}}(b = c) > -1. \end{cases} \tag{5}$$

Feature clusters function as representations of properties. They can be expressed by monadic predicates. We will assume that our language has a set of monadic predicates *Pred* such that each predicate denotes a property featured by some feature cluster. To every predicate $F \in Pred$ we now assign a diagonal matrix $\beta(F) \in \{0,1\}^{k\times k}$ that, by multiplication with any eigenmode $\mathbf{e}$, renders the sub-vector of those components that belong to the feature cluster expressed by F, i.e., its neuronal intension (k the number of oscillators):

$$\beta : Pred \to \{0,1\}^{k\times k}. \tag{6}$$

The neuronal intension of a predicate, for every eigenmode, determines its neuronal extension, i.e., the set of those oscillations that the neurons on the assigned feature layer, per eigenmode, contribute to the dynamics of the network. Hence, for every predicate F its *neuronal extension* in the eigenmode $\mathbf{e}$ comes to the set of activity functions $\{f_j | \mathbf{f} = \beta(F)\mathbf{e}a(t)\}$. To determine to which degree an oscillation function assigned to an individual constant b is in the neuronal extension of a predicate F, we have to compute how synchronous it maximally is with one of the oscillation functions in the neuronal extension:

$$v_{\mathbf{e}}(Fb) = \max\{\Delta(\alpha(b), f_j) | \mathbf{f} = \beta(F)\mathbf{e}a(t)\}. \tag{7}$$

[12] extends this semantics to all truth-functional connectives. The network generates a multitude of eigenmodes. Eigenmodes seem to represent different epistemic possibilities and play a similar role for neuronal representation, as possible worlds play for semantics.

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