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Temporal-to-spatial dynamic mapping, flexible recognition, and temporal correlations in an olfactory cortex model

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Abstract. This paper proposes temporal-to-spatial dynamic mapping inspired by neural dynamics of the olfactory cortex. In our model the temporal structure of olfactory-bulb patterns is mapped to the spatial dynamics of the ensemble of cortical neurons. This mapping is based on the following biological mechanism: while anterior part of piriform cortex can be excited by the afferent input alone, the posterior areas require both afferent and association signals, which are temporally correlated in a specific way. One of the functional types of the neurons in our model corresponds to the cortical spatial dynamics and encodes odor components, and another represents temporal activity of association-fiber signals, which, we suggest, may be relevant to the encoding of odor concentrations. The temporal-to-spatial mapping and distributed representation of the model enable simultaneous rough cluster classification and fine recognition of patterns within a cluster as parts of the same dynamic process. The model is able to extract and segment the components of complex odor patterns which are spatiotemporal sequences of neural activity.

1 Introduction

Flexible object recognition, feature binding and segmentation, attention focusing, and other pattern processing tasks are hardly handled by computational techniques based on stationary principles. On the other hand, they are successfully resolved by biological neural systems, where not only spatial, but also different kinds of temporal dynamics and correlation are believed to be the underlying principles of the brain's abilities (Fujii et al. 1996; Malsburg 1992).

Olfaction is an example of such a system in which spatiotemporal dynamics has been the subject of both numerous experimental studies (Duchamp-Viret et al. 1996; Joerges et al. 1997; Ressler et al. 1994; Scarda and Freeman 1987; Wehr and Laurent 1996) and theoretical modeling (Haberly and Bower 1989; Hendin et al. 1998; Hoshino et al. 1998; Wilson and Bower 1992). However, most odor recognition techniques do not make use of temporal encoding and processing. In static systems patterns are recognized by the stationary pattern recognition methods, which do not appear to be linked to biological temporal dynamics. The lack of such dynamics and dynamic processing principles in pattern recognition systems is one of the reasons for their poor computational abilities in comparison to biological neural circuits.

On the other hand, there are a number of olfactory cortex models which are based strictly on the system's neurobiological description and produce spatiotemporal dynamics similar to the experimental data (Ballain et al. 1998; Wilson and Bower 1992). Although such models do not clarify the functional significance of this dynamics, they provide insights about its possible role in cortical information processing.

Indeed, biological data demonstrate that pyramidal cells are principal neurons of olfactory cortex that receive and integrate four major types of input signals: from the olfactory bulb (OB) through afferent fibers, and also from three functional cortical areas via association fibers. These four signals are delayed differently by different branches of fibers, and arrive to the area of convergence at different times. Moreover, their signals need different times to propagate through the dendrites and reach the cell body. Temporal correlation of incoming afferent and associative signals proved to be crucial for the signal integration by a pyramidal cell (see Sect. 6.1 for details) (Haberly 1998). We explore this type of temporal correlation in our model and suggest that it could give some cues to understand how a recognition of multicomponent odors and their mixtures is realized in the olfactory cortex.

In the ensemble of spiking neurons described in Sect. 3, the neurons at different layers have different functional properties. The dynamics of the neurons

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which are sensitive to the odor components represents the activity of the neural pool corresponding to the spatial pattern of activity induced by this component (Haberly 1998). Although another type of neuron, sensitive to the concentrations of the odor components, also proved to have its biological analog in the frog olfactory cortex (Duchamp-Viret et al. 1996), its function can be interpreted more generally. The activity of this neuron delivers OB signals to the cortical neurons with different delays, so it may correspond to the dynamics of association fibers.

This ensemble's architecture, due to its distributed and dynamical representation of memory, provides the basis for solution of the coarseness-sensitivity flexibility problem. A coarse-enough system cannot distinguish fine variations of the patterns within a cluster. On the other hand, a sensitive-enough system is not able to detect what cluster these slightly different patterns belong to. The temporal-to-spatial mapping and distributed representation of the model enable simultaneous rough cluster classification and fine recognition of patterns within a cluster as parts of the same dynamic process.

Another group of tasks handled by biological systems includes feature binding, segmentation, attention focusing, and other multipattern recognition problems. There are experimental data that suggest that in the brain these tasks are solved with temporal processing (Fujii et al. 1996; Jinks and Laing 1999), and there are models that propose possible mechanisms (Ambros-Ingerson et al. 1990; Campbell and Wang 1998; Grossberg 1999; Hendin et al. 1998; Lysetskiy et al. 2001; Malsburg 1992). In Sect. 4 we show that the temporal structure of our model allows us to realize this multipattern processing.

In Sect. 2 we introduce the biological olfactory system and its functional properties. Sect. 3 describes the basic block layout of the model and its spatiotemporal dynamics which ensures the recognition flexibility. An example of temporal segmentation of odor patterns in a mixture is presented in Sect. 4. Methods and parameters of the simulation are shown in Sect. 5, which is followed by discussion and conclusions in Sect. 6.

2 Olfactory system

2.1 Olfactory bulb

An odor identity is defined by a group of physical and chemical parameters of the odor's constituent molecules and their relative concentrations. However, these parameters are not clearly determined, nor is the correlation between their candidates and the odor properties (Wise et al. 2000). For the sake of simplicity we assume that one constituent molecule possesses one of these crucial parameters and corresponds to one of the odor components. The odors can therefore be presented by the concentration vector $\boldsymbol{C} = \{c_1, c_2, \ldots, c_n\}$, where c_j is the concentration of jth molecule.

In the olfactory system, odors are first perceived in the olfactory epithelium by different types of receptor neurons. These neurons are sensitive to different kinds of molecules and respond selectively to their presence with oscillatory firing. An odor is further encoded into a quasiperiodic temporal sequence of spatial patterns of synchronized oscillatory neural activity of the olfactory bulb or antennal lobe (Hoshino et al. 1998; Laurent 1996; Scarda and Freeman 1987; Wehr and Laurent 1996).

The spatial patterns of the olfactory bulb/antennal lobe have been proved to be correlated with the odor components (Joerges et al. 1997; Laurent 1996; Ressler et al. 1994), but the functional significance of their temporal structure is unclear. There are two major hypotheses of its possible role. Experiments such as these of Laurent et al. (1996) and Wehr and Laurent (1996) show that the temporal structure of firing of different ensembles contributes to encoding of odor identity in a certain combinatorial way. Another idea is that temporal dynamics of the olfactory bulb encodes the concentrations of the odor components. According to the concept that the odor components are encoded as dynamic attractors of neural activity (Scarda and Freeman 1987), the order in which the state of the system visits these attractors and the time the state spends wandering around them could be correlated with the concentrations of the odor components (Hoshino et al. 1998). There is also experimental and theoretical support for the idea that a component's concentrations can be encoded by precise timing of a spike, a burst, or the phase of the periodic firing of corresponding neuron or ensemble (Duchamp-Viret et al. 1996; Hopfield 1995). These hypothesis do not necessarily contradict each other; they could coexist and complement one another or be the parts of a more complicated neural coding scheme.

Our model realizes a mapping of the temporal relations of input patterns into spatiotemporal dynamics of the output activity. We follow the idea proposed by Hopfield (1995) and assume that the precise time advance of a pattern's firing encodes the concentration of an odor, though it is a simplification of the real olfactory code that is yet to be discovered. However, the idea of the temporal-to-spatial mapping could still be applicable if the temporal structure carried some other functional significance.

We assume that spatiotemporal patterns in the olfactory bulb are formed in the following way: the greater the concentration of the odor component applied, the earlier the correspondent neural ensemble synchronizes its activity and fires (Hoshino et al. 1998), and the greater is the time φ_j that the jth ensemble fires in advance of the moment of the maximum of its subthreshold activation, which serves as a reference time (Hopfield 1995).

According to the Hopfield's (1995) hypothesis, the corresponding concentrations c_j of n constituent molecules are encoded as time advances $\varphi_1, \varphi_2, \ldots, \varphi_n$ of the ensemble's firing:

$$\varphi_j = t_j - t^{(r)} \tag{1}$$

where t_j is the time of the ensemble's spike and $t^{(r)}$ is the reference time mentioned above. The functional relation

between stimulus intensity and time advance of the spikes has been proposed by Hopfield:

$$\varphi_j = \alpha \ln(c_j/\delta) \quad (2)$$

where each time advance is assumed to be proportional to the logarithm of the corresponding concentration, α is a coefficient, and δ is a scale factor (Hopfield 1995).

Such logarithmic scaling makes the relative time advances of spatial patterns invariant to different concentrations of the same odor. The changing of the concentration of a multicomponent odor results in a time advance of the whole pattern, while the relative time advances remain constant.

2.2 Olfactory cortex

2.2.1 Synaptic organization. The piriform cortex (PC), the part of the olfactory cortex we focus on, is divided in three functional areas: ventral and dorsal parts of the anterior PC (APCv and APCd), and the posterior PC (PPC).

The input (spatial activation patterns) from the OB is delivered directly to the APCv by the lateral olfactory tract (LOT), and via LOT collaterals further to the PPC. The conduction velocities along the LOT (7.0 m/s) are greater than along its collaterals (1.6 m/s) (Wilson and Bower 1992). Thus, there is a time delay of about 5–7 ms between the arrivals of the OB signal to anterior and posterior parts of the PC, as measured by Ketchum and Haberly (1993a,b).

In addition to afferent input from the OB, pyramidal cells also receive association projections from each other, which are distinguished by the area they come from: APCv, APCd, and PPC. The striking feature of the PC is the spatiotemporal organization of its afferent and association connections: four major fiber systems, afferent input from OB, and association projections from APCv, APCd, and PPC make synapses in distinct sublayers of the PC.

The closer the source of the signal is to the LOT, the further from the cell body corresponding fibers synapse and the greater is the time of the signal's propagation along the dendritic tree to the cell body. Afferent axons synapse on the dendrites of pyramidal cells in layer Ia (the closest one to the cortical surface). Association axons from the APCv and the APCd synapse, respectively, in superficial (sup Ib) and deep (deep Ib) parts of layer Ib. Association axons from the PPC excite the same dendrites deeper in layer deep Ib and in layer III.

2.2.2 Spatiotemporal dynamics. The temporal dynamics of the dendritic trees in response to LOT activation is also strictly structured. It includes four peaks of inward currents: excitatory postsynaptic current (EPSC) in layer Ia (caused by the signals of afferent fibers), disynaptic EPSC in layer sup Ib (mediated by association fibers from the APCv), small EPSC in deep Ib (which is due, in part, to the APCd's signals), and inhibitory PSC in layer II.

The structure of this temporal sequence of the dendritic inward currents proved to be crucial for their integration at the cell body. In order to produce maximum activity, the cell body needs not only for both afferent and association signals to be applied, but also for them to be temporally correlated in a specific way (Ketchum and Haberly 1993a,c). This idea is also supported by the results of Wilson et al. (1992) (see Sect. 6.1). We explore this integration mechanism in our model and suggest that it could be employed by the olfactory cortex for the recognition of complex odors.

Another question we focus on in this paper is: how is the concentration of odor components encoded in the cortex? The experimental data of Duchamp-Viret et al. (1996) show that in a frog olfactory cortex there is a special class of neurons which do not discriminate well between different odors, but instead seem to encode odor concentration. The latency of their bursting was found to be correlated to the odor concentration: the greater the concentration, the smaller is the latency. This data is in accordance with the idea of Hopfield (1995), and suggests that odor components and odor concentrations may be encoded by different populations of neurons.

However, such "concentration neurons" were not found in other olfactory systems, where intensity encoding may be different. In various olfactory systems odor concentrations influence the temporal structure of OB activity patterns. When they are injected to the PC, the resulting temporal patterns of incoming signals to different PC regions invoke corresponding sequences of inward dendritic currents at the dendritic trees. As well as the integration of EPSCs in the cell body depending crucially on this pattern of inward currents (Haberly 1998; Ketchum and Haberly 1993b,c), we conclude that the dynamics of association-fiber signals could be correlated with the concentrations of odor components. We explore these ideas in our model, where there is a special type of neurons sensitive to different concentrations.

3 The model

Let an odor be a mixture of two components A and B. For recognition of this mixture as a whole, some kind of AND logic gate ODOR = A AND B has to be realized at some level of a recognition system: in our model this AND function is performed by integration of afferent and association signals by an integrate- and-fire neuron, which fires if these signals arrive within a close-enough time window.

We define an odor as a cluster of odor patterns that have identical components with different relative concentrations. An odor recognition system has to be rough enough to be able to recognize that different patterns may belong to the same cluster. On the other hand, it has to be sensitive enough to distinguish slightly different odors within a cluster.

In our model the recognition of an odor is represented by the firing of the neurons of a specific ensemble in a specific sequence. Cluster recognition and fine

recognition are represented by activation of different neural subensembles.

Our network consists of a layer of leaky integrate-and-fire neurons u_j, interconnected via arrays of intermediate-delay neurons d_k^{ji} (Fig. 1). The neurons u_j are also connected with the layer of temporal inputs $s_j(t)$. These inputs simulate activity of the OB and the neural layer functionally corresponds to the olfactory cortex that receives and processes those patterns.

The periodic inputs $s_j(t)$, $j = 1, \ldots, n$, represent n spatial patterns which correspond to n components of odor concentration vector $\boldsymbol{C} = \{c_1, c_2, \ldots, c_n\}$. The inputs are presented as follows:

$$s_j(t) = s \sum_{k=1}^{\infty} \delta(t + \varphi_j - kT) \tag{3}$$

where $\delta(t)$ is Dirac delta function, T is the signal's oscillation period, s is a spike's amplitude, and the time advances φ_j encode concentrations of constituent molecules according to (2). An example of input pattern is shown in Fig. 1.

There are three types of neurons in the layer. Each neuron is characterized by its state, that is the neuron's membrane potential: $u_j(t)$ for the principal neurons, $d_k^{ji}(t)$ for the delay neurons, and $x_k^{ji}(t)$ for the selective neurons. The neurons and inputs are connected with weights $w^{(\mathrm{neur})}$, $w^{(\mathrm{del})}$, and $w^{(\mathrm{sup})}$ (Fig. 1).

As described below in (4), a neuron u_j receives corresponding input signal $s_j(t)$ from the jth input and lateral signals $l_k^{ji}(t) = L[d_k^{ji}(t)]$ (operator L is defined below) from the activated neuron u_i, which are propagated and delayed by the delay neurons d_k^{ji}.

The operator L used above maps the functions of a neuron membrane potential to the function of the spikes $l(t)$ which this neuron produces. So, for example, $L[u_j(t)] = l_j(t)$ where $l_j(t)$ is equal to $\sum_k s\delta(t - t_{\mathrm{thresh}}^k)$, and where t_{thresh}^k are the times when the value of membrane potential u_j reaches its threshold.

If a neuron receives a spike at time t_s, its potential $u_j(t)$ is increased by the weighted value

$$w^{(\mathrm{neur})} \int s_j(t)\mathrm{d}t = w^{(\mathrm{neur})} s \ ,$$

if it is a spike from the input level, or

$$w^{(\mathrm{neur})} \int l_k^{ji}(t)\mathrm{d}t = w^{(\mathrm{neur})} \int L[d_k^{ji}(t)]\mathrm{d}t = w^{(\mathrm{neur})} S \ ,$$

if it is a spike propagated though a delayneuron d_k^{ji}. If the potential of a neuron reaches its threshold value u_{thresh}, the neuron fires. Its output signal $l_j(t) = L[u_j(t)]$ produces a spike which is propagated to the array of delayneurons that transfer the spike to all other neurons in the layer. At the same time its potential u_j is instantly reset to 0, as shown in (5). Additionally, the potential u_j is constantly decreasing with decay coefficient k. These mechanisms are employed by all the neurons in the model:

$$\frac{\mathrm{d}u_j(t)}{\mathrm{d}t} = -ku_j(t) + w^{(\mathrm{neur})} s_j(t) + \sum_{i:i\neq j}^{n} \sum_{k=1}^{m} w^{(\mathrm{neur})} L[d_k^{ji}(t)] \tag{4}$$

$$u_i(t^-) = u_{\mathrm{thresh}} \Rightarrow u_i(t^+) = 0 \tag{5}$$

The parameters of the equation are set in such a way that in order for a neuron u_j to fire it needs to receive two spikes in the narrow time window $\Delta t^{(u)}$: one spike, $s_j(t)$, from the corresponding input; and another, $l(t) = L[d_k^{ji}(t)]$, from one of the delay neurons (see details in Sect. 5). An exception is made for the very first input spike in the first cycle, which alone is able to activate the corresponding neuron. This adds to the model the functional property of the networks like the so-called LEGION, where the global inhibition of the neurons depends on the number of the activated neurons (Campbell and Wang 1998). Such inhibition

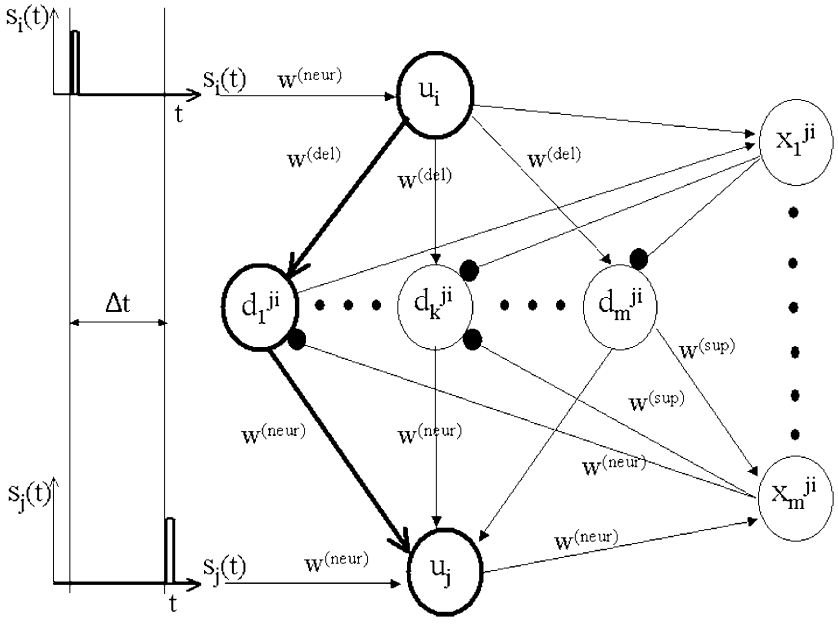

Fig. 1. Network architecture. The neurons of activated sub-ensemble $\{u_i, d_1^{ji}, u_j\}$ are shown in *bold*. *Arrows* and *black circles* represent excitatory and inhibitory connections, respectively

ensures that when fewer neurons are activated, the greater is the probability for a neuron to fire. In our model the neurons are made more sensitive to the very first input spike, because there is no activation yet in the neuron layer. The biological correspondence of this assumption is discussed in Sect. 6.1.

Delay neurons in the arrays are integrate-and-fire neurons with added inherent propagation delays D_k, $k = 1, \ldots, m$, defined as

$$\frac{\mathrm{d}d_k^{ji}(t)}{\mathrm{d}t} = -kd_k^{ji}(t) + w^{(\mathrm{del})}L[u_i(t - D_k)] + \sum_{q:q\neq k}^{m} w^{(\mathrm{sup})}L[x_k^{ji}(t)] \quad (6)$$

The parameters of the equation make the delay neuron work as a delay operator (details in Sect. 5). When d_k^{ji} receives a spike at time t it fires at $t + D_k$. Functionally, d_k^{ji} are equivalent to the ordinary integrate-and-fire neurons as in (4), connected to the principal neuron u_i via corresponding delay D_k. The values of delays D_k change gradually across the array as follows:

$$D_k = \frac{T(k - 1/2)}{m}, \quad k = 1, \ldots, m \quad (7)$$

where T is the oscillation period (3), and m is the number of the delay neurons in the array. This specific delay distribution ensures recognition properties of the system which are discussed below.

As a pattern processing example we consider a simple case where an odor with two components $\{0, \ldots, c_I, c_J, \ldots, 0\}$ is applied with $c_I > c_J$. For convenience we will be presenting this as $\{c_I, c_J\}$. When this odor is applied, the neuron u_I receives the input spike $s_I(t)$ first, at the moment t_1, and then u_J receives $s_J(t)$ at t_2.

The single spike s_I is enough for u_I to fire because of the exception mentioned above. The neuron u_I fires at the moment t_1 and sends spikes $L[u_I(t)]$ to all other neurons u_j, $j = 1, \ldots, n$, $j \neq I$ via delay arrays d_k^{ji}. The neurons u_j receive the delayed signals from d_k^{ji} at times $t + D_k$, $k = 1, \ldots, m$. However, this is not enough for them to fire because a spike from the input level is also needed. Although all of them show subthreshold activation, only the neuron u_J which will receive the input spike s_J will actually reach the threshold and fire. Finally, the neurons that fire are u_I, u_J, and all intermediate neurons d_k^{JI} in the array which connects them.

The values of D_k set by (7) ensure that one and only one of the delay neurons fires and sends a spike to the neuron u_J within the time window $\Delta t^{(x)}$. Thus, although all of the delay neurons in the array fired, only one of them actually contributes to the firing of the neuron u_J. To distinguish this contributing delay neuron from others, an additional layer of selective neurons x_k^{ji} is added (Fig. 1).

Selective neurons x_k^{ji} are functionally equivalent to the principal neurons u_j. They work as coincident time detectors and fire if spikes from neurons u_j and d_k^{ji} arrive at x_k^{ji} within time window Δt:

$$\frac{\mathrm{d}x_k^{ji}(t)}{\mathrm{d}t} = -kx_i(t) + w^{(\mathrm{neur})}L[d_k^{(ji)}] + w^{(\mathrm{neur})}L[u_j(t)] \quad (8)$$

Selective neurons provide negative feedback $\sum_{q:q\neq k}^{m} w^{(\mathrm{sup})}L[x_k^{ji}(t)]$ to the delay neurons $d_k^{(JI)}$ that did not contribute to the firing of u_J (6). Because of this selective feedback, neurons d_k^{JI} which contributed to the firing of u_J stay unchanged, while the rest of the delay neurons are suppressed and will not be sensitive to the spikes from u_i during suppression time T_S, defined as follows:

$$T_S = \frac{1}{k}\ln\left(\frac{w^{(\mathrm{sup})}s}{d_{\mathrm{thresh}}/s - w^{(\mathrm{del})}}\right) \quad (9)$$

At the output level there is now a sequence of firing of neurons u_I, d_K^{JI}, and u_I one after another. Firing of the neurons u_I and u_J indicates that an odor of the cluster $\{c_I, c_J\}$ is recognized. The firing of the specific delay neuron d_K^{JI} defines the relative concentration of two components, the logarithm of which lays in the vicinity of the delay D_K of the corresponding delay neuron:

$$D_K - \frac{T}{2m} < \alpha \ln\left[\frac{c_I}{c_J}\right] < D_K + \frac{T}{2m} \quad (10)$$

An example of the system's dynamics is shown in Figs. 2 and 3. During the first cycle ($0 < t < T$), neurons d_k^{JI} are activated by u_I and fire consequently in the order of their inherent delays D_K, starting from the one with the smallest D_K, until d_3^{JI} gets activated, which fires within time window Δt with u_J. The correlated firing of u_J and d_3^{JI} makes x_3^{JI} fire. Selective neuron x_3^{JI} suppresses the remaining delay neurons for the suppression time T_S, which is equal to the oscillation period $T = 20$. After time T, selective neuron x_3^{JI} will suppress them again. So, the only delay neuron that will fire during the second and following cycles is d_3^{JI}. The parameters used in the simulation are described in Sect. 5.

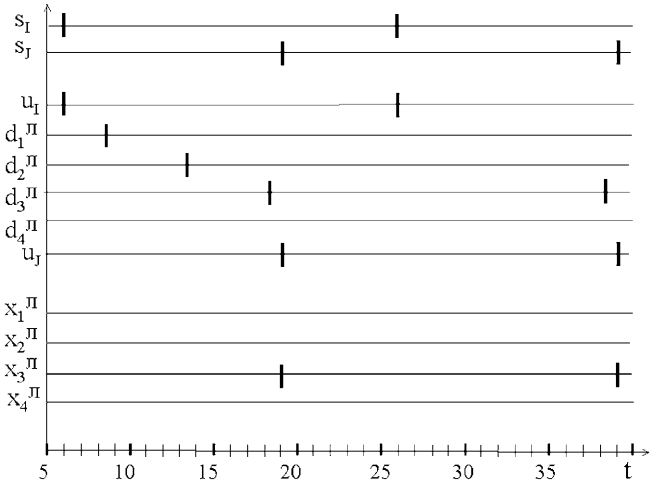

Fig. 2. Dynamics of the neural ensemble during the recognition process. The *bars* represent the spikes of the corresponding neurons

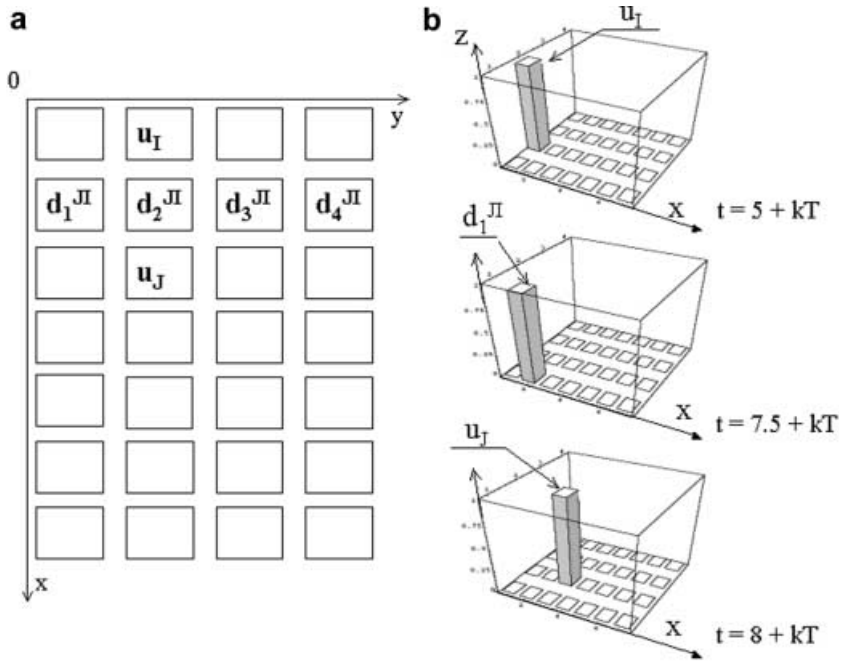

Fig. 3a,b. Simulation of spatiotemporal dynamics of the ensemble: **a** distribution of the neurons in the layer; **b** spatiotemporal neural dynamics. Axis z corresponds to the membrane potentials $u(t)$ or $d(t)$: $k = 1, 2, \ldots, N$; and T is the period of the oscillations

4 Temporal segmentation

According to Hopfield's (1985) mechanism of formation of the input temporal sequence, if a mixture of several odors is applied, the corresponding spatiotemporal sequences are superimposed and the resulting input sequence contains patterns of all components of each odor. The stronger the component, the earlier its pattern fires, no matter which odor the component belongs to.

In order to segregate the odor patterns in time, one of the ensembles should win and hence suppress the others for a period of several cycles. After that, due to the neural fatigue, the winning ensemble stops firing and the second-strongest ensemble wins and fires during the next several cycles (Campbell and Wang 1998; Hoshino et al. 1998; Malsburg 1992). To realize such pattern segmentation, the modified network from Sect. 2 with additional neural interaction and neural fatigue function $F(p)$ is used:

$$\frac{\mathrm{d}u_j(t)}{\mathrm{d}t} = -ku_j(t) + \{w^{(\mathrm{neur})}s_j(t) + \sum_{i:i\neq j}^{n}\sum_{k=1}^{m} w^{(\mathrm{neur})}L[d_k^{ji}(t)] + \sum_{i:\forall z, u_i\cup u_j\notin E_z}^{n} w_{ji}^{(\mathrm{inter})}L[u_i(t)]\}F(p) \tag{11}$$

where $F(p)$ is defined as a step function, with $F(p) = 1$ if $2kp_f < p < (2k+1)p_f$, and $F(p) = 0$ if $(2k+1)p_f < p < (2k+2)p_f$; $\forall k : k = 1, 2, \ldots, K$. The variable p is the number of times the potential of neuron u_j reached its threshold, and p_f is the number of firings after which the neuron becomes insensitive to the inputs and stays silent for another p_f cycles.

Neural ensemble E_z, $z = 1, \ldots, Z$, is a group of neurons that correspond to the components of the same odor. All neurons which are not members of the same ensemble are interconnected with negative weights $w_{ji}^{(\mathrm{inter})}$. When a neuron u_i fires, it sends inhibitory signals $w_{ji}^{(\mathrm{inter})}L[u_i(t)]$ to the neurons that do not belong to any of the ensembles E_z in which the neuron u_i participates. The membrane potentials of those neurons are decreased by $w_{ji}^{(\mathrm{inter})}L[u_i(t)]$. They stay suppressed for the refractory period T_R during which they cannot fire regardless of the input signals received. T_R is determined as follows:

$$T_\mathrm{R} = \frac{1}{k}\ln\left(\frac{w^{(\mathrm{inter})}s}{u_{\mathrm{thresh}} - 2w^{(\mathrm{neur})}s}\right) \tag{12}$$

The dynamics of the competition between ensembles is quite a complicated process (Campbell and Wang 1998; Hoshino et al. 1998), because for a neuron in the ensemble, its probability of being suppressed depends on the statistical value of the difference of received inhibitory and excitatory spikes.

In our model, according to (11) and the exception for the first spike in the input sequence (Sect. 3), the first activated neuron suppresses the others which are not in its ensemble, and does not allow them to fire with 100% probability. So, the ensemble which contains the winning neuron, or, in other words, the odor with the strongest component, always wins the competition first.

As an example we consider the case where two odors $\{c_I, c_J\}$ and $\{c_P, c_Q\}$ are applied to the network with the following order of the concentrations of their components: $c_I > c_P > c_J > c_Q$. The temporal sequence of input spikes is the same, $\{s_I(t), s_P(t), s_J(t), s_Q(t)\}$, as shown in Fig. 4. The first of them, $s_I(t)$, activates neuron u_I, which sends inhibitory signals to u_P and u_Q, and excitatory signal

to u_J via an array of the delay neurons. When input spike $s_P(t)$ appears, the corresponding output neuron u_P is suppressed and will not respond to the impulse. Then input s_J activates neuron u_J, which already received an excitatory signal from u_I. After that $s_Q(t)$ fails to activate neuron u_Q. Finally the neurons u_I and u_J fire, while u_P and u_Q remain silent. In this way the odor $\{u_I, u_J\}$ is segmented from the background and attention is focused on it for the period of $p_f = 2$ cycles (Fig. 3). Then, due to the neural fatigue $F[p]$, the neurons u_I and u_J stop firing and u_P and u_Q become activated, so the attention is now refocused on this odor. So, the odor patterns are temporally segregated and processed one at a time, as is shown in Figs. 4 and 5. The parameters used in the simulation are specified in Sect. 5.

5 Simulation

The neurons described by (4) and (8) work as coincident time detectors. They fire if two spikes arrive at a neuron within time window Δt, the size of which is defined by the parameters of the integrate-and-fire neurons as follows:

$$\Delta t^{(u)} = -\frac{1}{k}\ln\left(\frac{u_{\text{thresh}}}{w^{(\text{neur})}s} - 1\right)$$
$$\Delta t^{(x)} = -\frac{1}{k}\ln\left(\frac{x_{\text{thresh}}}{w^{(\text{neur})}s} - 1\right) \tag{13}$$

where $\Delta t^{(u)}$ and $\Delta t^{(x)}$ are the time windows of neurons u_j and x_k^{ji}, respectively. In our simulation $u_{\text{thresh}} = x_{\text{thresh}}$, so $\Delta t^{(u)} = \Delta t^{(x)}$, and we will represent them both as Δt.

Since this is essentially the property of the neurons used in the model, there was no need to implement them by the actual integrate-and-fire neurons. The neurons u_j were replaced by logic units u_j^*, characterized by its state $u_j^*(t)$ that has the following properties. Without inputs, $u^*(t)$ is equal to 0. If u_j^* receives two spikes with weights $w^{(\text{neur})}$ at the moments t_1 and t_2 with $t_2 > t_1$, then

$$\text{if } \left|t^2 - t^1\right| < \Delta t$$
$$\text{then } u^*(t_2^+) = u_{\text{thresh}}$$
$$\text{else } u^*(t) = 0 \tag{14}$$

If the state $u_j^*(t)$ of logic unit u_j^* reaches its threshhold value u_{thresh}^* at time t_{thresh}, it behaves in the same way as neurons u_j do. The value of $u_j^*(t)$ is reset to 0 and the output function of the unit, $L[u_j^*(t)]$, is equal to $\Delta(t - t_{\text{thresh}})$. The rules for units x_k^{*ji} are analogous to the rules of u_j^*. The state of d_k^{*ji} is defined as $d_k^{*ji}(t) = d_k^{ji}(t) = L[u_i(t)]$.

The focus of the model is the computational abilities of spatiotemporal integration and temporal dynamics discussed in Sect. 3. For this reason, temporal parameters have been assigned biologically realistic values, such as the period of oscillations, $T = 20$ ms, which corresponds to 50-Hz oscillations observed in the olfactory cortex. This also makes the values of time delays D_K, defined by (7), comparable with the delays of 5–7 ms, related to different association fibers (see Sect. 6.1 for details).

The values of the following parameters were chosen arbitrarily: $T = T_{\text{R}} = T_{\text{S}} = 20$, $\Delta t = 5$, $\alpha = 4$, $\delta = 1$, $s = 1$, $u_{\text{thresh}} = x_{\text{thresh}} = d_{\text{thresh}} = 1$, $p_f = 2$, $n = 4$, and $m = 4$.

The weights $w^{(\text{del})} = 1.1$ were assigned their values in order to make a single weighted spike $sw^{(\text{del})}$ be enough to fire a delay neuron. The values of weights $w^{(\text{neur})} = 0.75$ were defined so as to ensure that not one, but two weighted spikes $sw^{(\text{neur})}$ (and in a small-enough time window) are needed to activate a principal neuron. The parameters $w^{(\text{sup})} = -8.0963$, $w^{(\text{int})} = -39.91$, and $k = 0.2197$ were defined by (9), (12), and (13), respectively.

The dynamics of an example simulation is shown in Fig. 5, where the mixture of odors $\{u_I, u_J\} = \{100, 50\}$

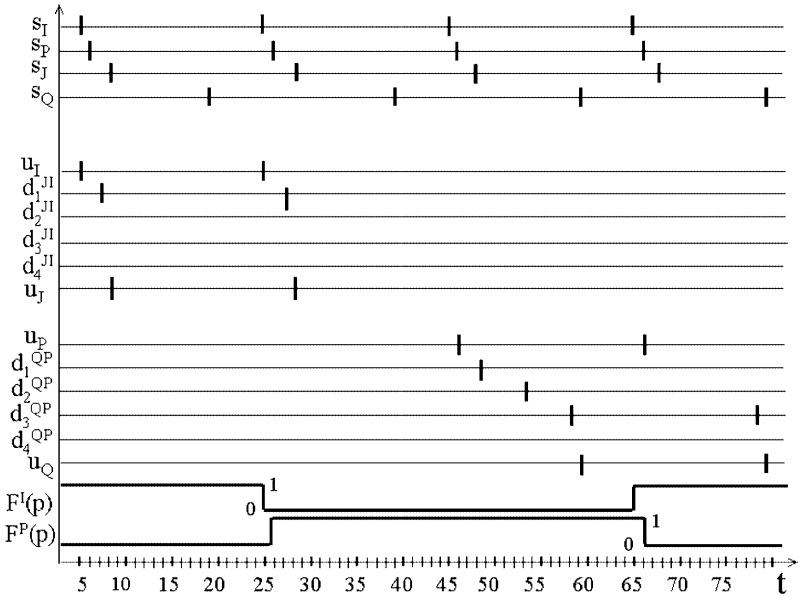

Fig. 4. Dynamics of two neural ensembles during processes of temporal binding, segmentation, and attention

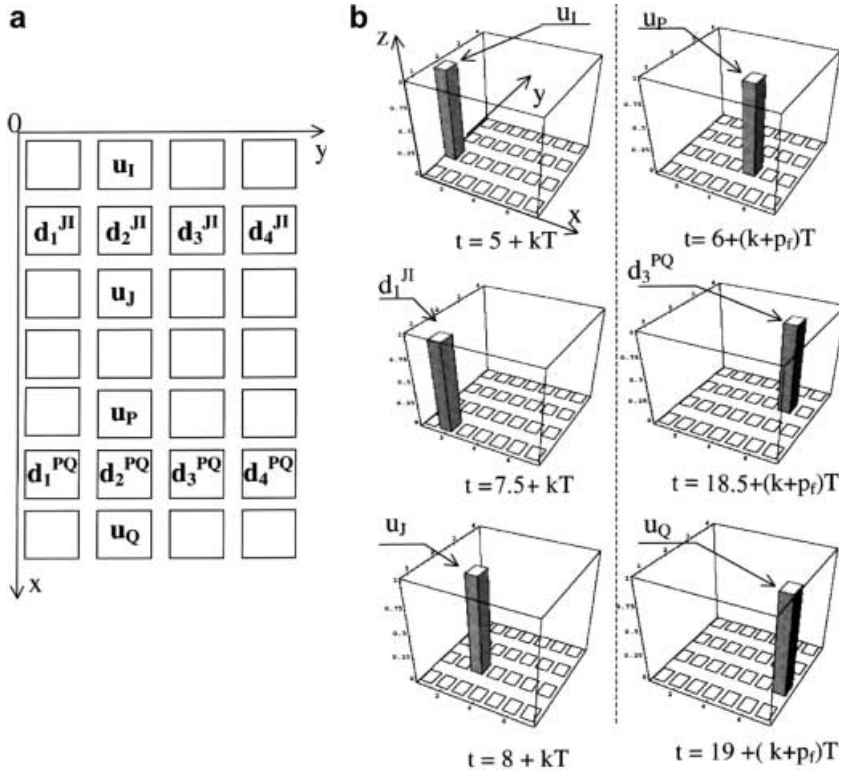

Fig. 5a,b. Simulation of the neural dynamics of pattern segmentation and attention focusing: **a** distribution of the neurons in the layer; **b** spatiotemporal neural dynamics during the first p_f (*left column*) and second p_f (*right column*) cycles. Axis z corresponds to the membrane potentials $u(t)$ or $d(t)$: $k = 1, \ldots, p_f$; and T is the period of the oscillation

and $\{u_P, u_Q\} = \{80, 3\}$ is applied. During the first three cycles the neurons of the first odor fire in the following sequence: u_I, d_1^{JI}, and u_J (Fig. 5b, left column). This indicates that the odor $\{u_I, u_J\}$ is recognized with the relative concentrations of its components defined by (9) as $0 < \ln[\frac{c_I}{c_J}] < 1.25$. After three cycles $\{u_P, d_3^{JI}, u_Q\}$ becomes activated and suppresses in its turn the first ensemble (Fig. 5b, right column). So, the ratio of the concentrations of the components of this odor is $2.5 < \ln[\frac{c_P}{c_Q}] < 3.75$.

6 Discussion

6.1 Biological correspondence

We argue that the dynamics of our model reflects certain aspects of olfactory cortex activity related to information processing. The key principles of mixture recognition in our system are that a single input spike from the OB is enough to activate a certain neuron (e.g., u_i, in the model) while the others (e.g., u_j) need signals both from the OB and from another principal neuron, propagated by the delay neurons.

Experimental results (Wilson and Bower 1992) indeed suggest that while anterior areas of the cortex may be activated by afferent input only, the posterior parts require both afferent and association signals. This mechanism rises from the properties of the relative density of association and afferent terminals, defined by the association-to-afferent dominance ratio (AADR). The AADR increases along the distance from the LOT: in the APCv (the closest area to the LOT), afferent fibers prevail over the association ones, and the opposite is true for the PPC (Haberly 1998). The results of Wilson and Bower (1992) show that when the afferent activity is not strong enough, it can only activate the APC, where the AADR is low. Activation of the posterior cortex (with a high AADR) results mostly from delayed arrival of association-fiber activity. These results suggest that the areas with medium AADRs, such as the APCd, may need equally both afferent and association inputs to be activated.

In Sect. 2.2.2 we described the spatiotemporal sequence of the dendritic currents, produced by afferent and association signals. Its correspondence with the dynamics of our model is the following: neuron u_j receives the spikes $s_j(t)$ from the OB, and $L[d_k^{ji}]$ from the principal neurons, differently delayed by delay neurons (or association fibers, as in the real PC), as shown in Fig. 2. Each of the incoming signals increases the state of the neuron (i.e., produces a peak of inward current). u_j is activated only if afferent input $s_j(t)$, and one of the association inputs $L[d_k^{ji}]$, arrive in a small-enough time window (in terms of the PC, the induced EPSCs are close enough in time).

This mechanism is supported by experimental results described in Ketchum and Haberly (1993b,c) and Haberly (1998), which show that the optimal temporal correlation of inward currents is the one which ensures their roughly synchronous arrival at the cell body. In these experiments, when three EPSCs were presented in their natural sequence (with interpeak latencies of several milliseconds), the induced potential at the cell body was 50% greater than the one caused by the same EPSCs applied simultaneously.

Moreover, the delays produced by propagation along the dendritic tree could synchronize the incoming signals, as did delay neurons in our model. Indeed, different fibers synapse at distinct distances from the cell body, and thus require different times for a postsynaptic spike to propagate to it via the dendritic tree. The latency between peak depolarization in afferent input in layer Ia and the peak depolarization of the cell body is approximately 6 ms (Haberly 1998).

The repetitive temporal dynamics in our model is also related to the one of the real PC, where the temporal sequence of dendritic postsynaptic currents evolves in each cycle of 50-Hz cortical oscillations. Odor components are also segregated temporally, with each of them processed during different oscillation cycles. Thus, the temporal sequence of EPSCs, whatever functional role it plays, participates repetitively in the processing of each odor component.

Selective suppression of the delay neurons in our model, which corresponds to the suppression of association-fiber signals, also has its prototype in the PC. As shown in Ketchum and Haberly (1993a), when two successive shocks are applied to the LOT, the first one induces the full sequence of the peaks of inward currents, but the second one produces only an isolated monosynaptic EPSC coming from the APCv. The association-fiber signals are blocked by inhibitory postsynaptic currents evoked by the first shock. However, there is not enough biological evidence yet to specify functional significance of this suppression and compare it to the one of our model, where all delay neurons are active at the first cycle and get selectively suppressed at the second one (Fig. 2).

In our model, activity of a delay neuron represents corresponding concentration of the odor component. Such behavior, although detected in the frog olfactory cortex (Duchamp-Viret et al. 1996), was not observed in other olfactory systems. We argue that the dynamics of delay neuron in our model can be seen as differently delayed activity of association fibers coming from different cortical areas: APCv, APCd, and PPC. They also are of the same range: the time of signal propagation along the cortex – from anterior to posterior parts – is 5–7 ms.

6.2 Olfactory system models

The general idea behind most of the odor recognition models is that an odor pattern is temporally segregated in the patterns of its components, which are processed in the order of their significance or intensity (the strongest one is processed first). However, it is not absolutely clear which parts of the olfactory system are involved in this process, and to what degree.

In the model of Ambros-Ingerson et al. (1990), temporal segmentation of the bulbar activation patterns is realized by the selective inhibitory cortical feedback. During each cycle, OB activity is projected to the cortex where the pattern of its strongest component suppress the other ones (the winner-takes-all mechanism) and activates inhibitory feedback to the bulb. This feedback suppresses the part of the bulbar activity which corresponds to this strongest component. During the following cycles, the normalized remainder of the input is presented to the cortex and the same process occurs repetitively. During different cycles, input is classified as a part of a cluster of the corresponding hierarchical level. Processing during the first cycle corresponds to the first level clusters (rough recognition), subcluster recognition is realized at the second cycle, and so on.

Input segmentation in this model is due to the corticobulbar interaction. However, it may be also realized in the OB without corticobulbar interplay. In the model of Hoshino et al. (1998) the winner-takes-all competition occurs in the OB itself. The winning pattern suppresses the others, stays active during several cycles, and then stops firing due to the neural fatigue. The second-strongest pattern then wins, and the process repeats. Chaotic dynamics, which is believed to be crucial for bulbar information processing, is also taken into account in this system.

The models discussed above deal with odors which have distinct components. If, instead, complex odors with the same components but in different concentrations are ideally mixed, the information about them is lost, and their separation is impossible. An odor mixture {4A, 7B} may be composed of an infinite number of odor combinations, such as {2A, B} + {2A, 6B} or {A, 3B} + {3A, 4B}. However, the problem becomes solvable if temporal fluctuations of the odors are independent. This is the case when, for example, the sources of odors are spatially distinct and there is enough turbulence in the airflow. This idea was explored in the models of Hendin et al. (1994, 1998), where temporal segmentations of the bulbar activity is based on the temporal fluctuations of input odors.

In our model we focus on the recognition of the odor mixtures which are already segmented into spatiotemporal patterns of OB activity, after the temporal fluctuations of odors, if any, were employed by the OB. We propose a new possible functional role of temporal correlation of association-fiber signals, activity of which is influenced by the temporal structure of the OB signals, which, in turn, is assumed to be correlated with the odor concentrations.

The advantage of the distributed representation of our model is its flexible recognition ability. Speaking of the olfactory system, where the number of odors and their mixtures the brain can possibly perceive is enormous, one of the computational problems is how to preserve the hierarchy and similarity in the representation of odor memory. In our system the neural ensemble which corresponds to the odor of coffee would be a part of a bigger ensemble that represents more complicated odors of a coffee house. The dynamics of the smaller ensemble also would be part of the bigger ensemble's dynamics. On the other hand, two similar odors (odors with some common components) would activate two similar neural ensembles with close spatial dynamics. This would happen because common components and their relative concentrations would

activate the same spatial dynamics of the same ensemble. The neural processing of spatiotemporal patterns is one of the key principles for the brain's fast flexible pattern recognition that is still beyond the reach of modern computational techniques. In this paper we present an attempt to understand the principles of how the brain could use its spatiotemporal dynamics for recognition tasks.

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