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Odor recognition and segmentation by coupled olfactory bulb and cortical networks

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Abstract

We present a model of a coupled system of the olfactory bulb and cortex. Odor inputs to the epithelium are transformed to oscillatory bulbar activities. The cortex recognizes the odor by resonating to the bulbar oscillating pattern when the amplitude and phase patterns from the bulb match an odor memory stored in the intracortical synapses. We assume a cortical structure which transforms the odor information in the oscillatory pattern to a slow DC feedback signal to the bulb. This feedback suppresses the bulbar response to the pre-existing odor, allowing subsequent odor objects to be segmented out for recognition.

Key words: olfaction; detection; recognition; segmentation; adaptation

1 Introduction

There is a great deal of current interest in how neural systems, both artificial and natural, can use top-down feedback to modulate input processing. Here we propose a minimal model for an olfactory system in which feedback enables it to perform an essential task – olfactory segmentation. Most olfactory systems need to detect, recognize, and segment odor objects. Segmentation is necessary because different odors give overlapping activity patterns on odor receptor neurons, of which there are hundreds of types (1), and each has a broad spectrum of response to different odor molecules (2). Different odor objects seldom enter the environment in the same sniff cycle, but they often stay together in the environment afterwards. Humans usually can not identify

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the individual odor objects in mixtures (3), although they easily perceive an incoming odor superposed on pre-existing ones. Our model performs odor segmentation temporally: First one odor is detected and encoded by the olfactory bulb and recognized by the associative memory circuits of the olfactory cortex. Then the cortex gives an odor-specific feedback to the bulb to inhibit the response or adapt to this odor, so that a superposed second odor arriving later can be detected and recognized with undiminished sensitivity while the sensitivity to the pre-existing odor is reduced, as observed psychophysically(3). The stimulus-specific feedback makes odor adaptation an intelligent computational strategy, unlike simple fatigue, which is not sufficient for odor segmentation. Our model displays the oscillatory neural activities in the bulb and cortex as observed physiologically(4). Furthermore, odor cross-adaptation — the suppression and distortion of odor perception immediately after an exposure to another odor — as observed psychophysically(3), is a consequence of this model.

2 The Model

Our model (Fig. 1) describes the essential elements of primary olfactory neural circuitry: the olfactory bulb, the olfactory cortex, and feedforward and feedback coupling between them. The formal neurons in our system model the collective activity of local populations of real neurons. The synaptic architecture is consistent with the known physiology and anatomy of the olfactory system in most mammalian species (5).

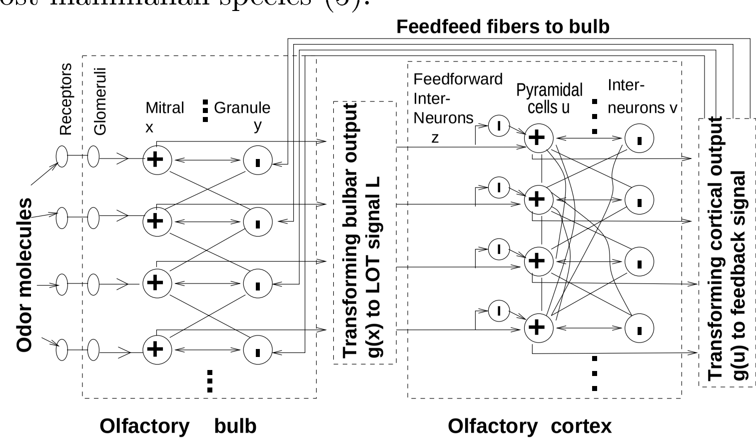


Fig. 1. The olfactory system in the model.

Our bulb model contains interacting excitatory mitral and inhibitory granule cells, with membrane potentials x_i and y_i respectively, and firing rates $g_x(x_i)$ and $g_y(y_i)$ respectively (see (6) and (7) for details). The odortials

$\dot{x}_i = -\alpha x_i - \sum_j H^0_{ij} g_y(y_j) + I_i \qquad \dot{y}_i = -\alpha y_j + \sum_j W^0_{ij} g_x(x_j) + I^c_i,$

where $-\alpha x_i$ and $-\alpha y_i$ model the decays to resting potentials, $\mathsf{H}^0_{ij} > 0$ and $\mathsf{W}^0_{ij} > 0$ the synaptic connections from the granule to mitral cells and vice versa, and vector $\mathbf{I}^c$ (components I^c_i) the feedback signal from the cortex to the granule cells. Slowly varying input $\mathbf{I}$ and $\mathbf{I}^c$ adiabatically determine the fixed or equilibrium point $\bar{\mathbf{x}}$ and $\bar{\mathbf{y}}$ of the equations. Neural activities oscillates around this equilibrium as $\mathbf{x} = \bar{\mathbf{x}} + \sum_k c_k \mathbf{X}_k e^{-\alpha t \pm \mathrm{i}(\sqrt{\lambda_k} t + \phi_k)}$, where $\mathbf{X}_k$ is an eigenvector of $\mathsf{A} = \mathsf{HW}$ with eigenvalue λ_k, and $H_{ij} = H^0_{ij} g'_y(\bar{y}_j)$ and $W_{ij} = W^0_{ij} g'_x(\bar{x}_j)$. Spontaneous oscillation occurs if $\mathrm{Re}(-\alpha \pm i\sqrt{\lambda_k}) > 0$; then the fastest-growing mode, call it $\mathbf{X}_1$, dominates the output and the entire bulb oscillates with a single frequency $\omega_1 \equiv \mathrm{Re}(\sqrt{\lambda_1})$, and the oscillation amplitudes and phases is approximately the complex vector X_1. Thus, the bulb encodes the input via the steps: (1) the input $\mathbf{I}$ determines $(\bar{\mathbf{x}}, \bar{\mathbf{y}})$, which in turn (2) determines the matrix A, which then (3) determines whether the bulb will give spontanous oscillatory outputs and, if it does, the oscillation pattern $\mathbf{X}_1$ and frequency ω_1.

The mitral cell outputs $g_x(x_i)$ are transformed to an effective input I^b_i to the excitatory (pyramidal) cells of the cortex by (1) a convergent-divergent bulbar-cortex connection matrix and (2) an effective high-pass filtering via feedforward interneurons in the cortex. Our cortical model is structurally similar to that of the bulb. We focus only on the upper layer pyramidal cells and feedback interneurons:

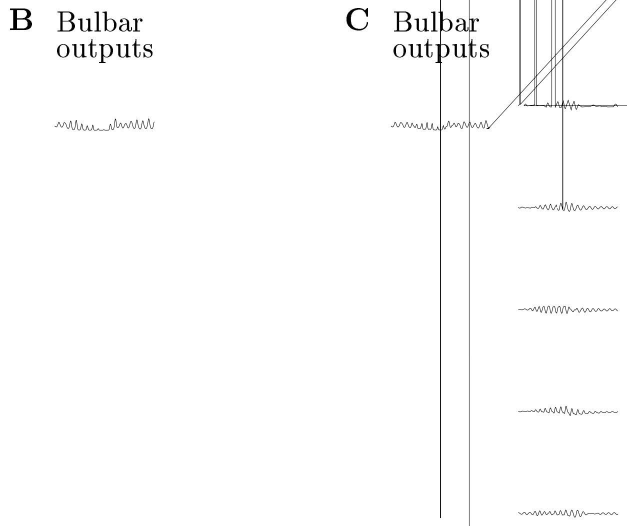
$$\dot{u}_i = -\alpha u_i - \beta^0 g_v(v_i) + \sum_j J^0_{ij} g_u(u_j) + I^b_i, \quad \dot{v}_i = -\alpha v_i + \gamma^0 g_u(u_i) + \sum_j \tilde{W}^0_{ij} g_u(u_j),$$

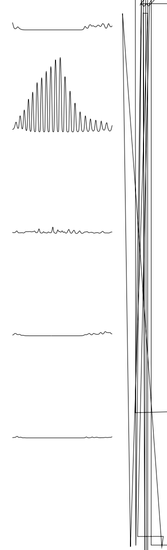
where $\mathbf{u}$, $\mathbf{v}$, and $\tilde{\mathsf{W}}^0$ correspond to $\mathbf{x}$, $\mathbf{y}$, and W^0 for the bulb. J^0 is global excitatory-to-excitatory connections, β^0 and γ^0 are local synaptic couplings.

Carrying out the same kind of linearization around the fixed point $(\bar{\mathbf{u}}, \bar{\mathbf{v}})$ as in the bulb, we obtain a system of driven coupled oscillators. With appropriate cell nonlinearities and overall scale of the synaptic connections, the system does not oscillate spontaneously, nor does it respond much to random or irrelevant inputs. However, the cortex will resonate vigorously when the driving oscillatory force $\mathbf{I}^b$ matches one of intrinsic oscillatory modes $\vec{\xi}^\mu$ in frequency and patterns amplitudes and phases. These intrinsic modes $\vec{\xi}^\mu$ for $\mu = 1, 2, ...P$, are memory items in an associative memory system (8; 9; 10), and can be stored in the synapses J^0 and $\tilde{\mathsf{W}}^0$ in a generalized Hebb-Hopfield fashion

$$J^0_{ij} - \frac{\mathrm{i}}{\omega}(\beta \tilde{W}^0_{ij} - \alpha J^0_{ij}) = J \sum_\mu \xi^\mu_i \xi^{\mu *}_j / g'_u(\bar{u}_j).$$

Fig. 2 shows that 3 odors A, B, and C all evoke bulbar oscillatory responses. However only odor A and B are stored in the in the cortical synapses; hence the cortical oscillatory response to odor C is almost nonexistent.





C: Crossadapting B by A
Bulbar outputs
Cortical outputs

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