Bulbocortical interplay in olfactory information processing via synchronous oscillations

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Abstract. Emergence of synchronous oscillatory activity is an inherent feature of the olfactory systems of insects, mollusks and mammals. A class of simple computational models of the mammalian olfactory system consisting of olfactory bulb and olfactory cortex is constructed to explore possible roles of the related neural circuitry in olfactory information processing via synchronous oscillations. In the models, the bulbar neural circuitry is represented by a chain of oscillators and that of cortex is analogous to an associative memory network with horizontal synaptic connections. The models incorporate the backprojection from cortical units to the bulbar oscillators in particular ways. They exhibit rapid and robust synchronous oscillations in the presence of odorant stimuli, while they show either nonsynchronous states or propagating waves in the absence of stimuli, depending on the values of model parameters. In both models, the backprojection is shown to enhance the establishment of large-scale synchrony. The results suggest that the modulation of neural activity through centrifugal inputs may play an important role at the early stage of cortical information processing.

1 Introduction

Olfactory cortex is considered one of the evolutionarily older parts of mammalian cerebral cortex and is known to have various morphological, physiological and pharmacological similarities in neural circuitry with that in hippocampal cortex and neocortex (Haberly 1990). Therefore exploring emergent computational abilities and perceptual functions of the neural circuitry of the olfactory system from the viewpoint of dynamical system analysis is expected to reveal many aspects of the basic mechanism of biological information processing. Despite this potential importance of olfactory systems, less theoretical work relative to that on visual information processing has been conducted to study the mechanism of olfactory memory learning and storage (Freeman 1987; Li and Hopfield 1989; Bower 1990; Taylor and Keverne 1991; Erdi et al. 1993; Barkai et al. 1994). This may be due partially to the difficulties in gaining a clear insight into the link between observed neuronal activity and psychological-level perceptual functions in olfaction. On the other hand, odor perception seems to require less complex modalities than does visual perception, which requires multimodal analysis of visual stimuli for colors, contrast, motion, shapes and so on. This aspect of olfactory information processing may allow us to achieve a good insight into the physiological functions of the related neural circuitry. In the present paper, I propose computational models of the olfactory bulb and olfactory cortex in order to discuss their functional roles, which are inferred from the organization of the related neural circuitry, in olfactory information processing.

Molecular biological studies have revealed (Buck and Axel 1991) that mammals have in general about a thousand types of odorant receptor genes. Each olfactory receptor neuron has been suggested to express one or a small number of receptor genes (Ressler et al. 1993) and sends an axon to one of the glomeruli in the olfactory bulb where it makes excitatory synaptic connections with bulbar cells (Mori 1987, 1995). It was recently suggested that neurons expressing a given receptor segregate within one of four broad zones in the olfactory epithelium (Ressler et al. 1993) and converge on a single, or at most a few glomeruli (Ressler et al. 1994; Vassar et al. 1994), while retaining the zonal organization in the olfactory bulb. Thus it is likely that olfactory information is divided into four large sets by this topographic organization. Neurons expressing a particular receptor type, however, are distributed throughout a nasal zone and the axonal projection to the bulb is highly distributed within each zone. Furthermore, a single odorant stimulates a large number of spatially distributed glomeruli, which implies that it is recognized by a large number of different receptor types. These findings seem to indicate that the code for an odorant is represented by an odor-dependent spatial pattern of glomerular activity in the olfactory bulb.

The activity within a glomerulus is transmitted to about a hundred mitral/tufted cells belonging to the
glomerulus and they in turn project axons to be pyramidal cells in the olfactory cortex through the lateral olfactory tract (LOT). Anatomical and physiological studies revealed that the LOT is highly distributed in nature and shows no apparent topographic organization (Shepherd 1990). Furthermore, the olfactory cortex is known to possess a long-range sparse horizontal fiber system which makes the neural circuitry of the cortex rather resemble neural network models of associative memory (Haberly and Bower 1989). These facts suggest that olfactory information related to a particular odorant is encoded as a spatial (and possibly temporal) activity pattern of an enormous number of neurons in both olfactory bulb and cortex.

In fact, studies of mammalian olfactory bulb (Adrian 1942; Freeman 1975) with electroencephalographic brain wave recordings revealed that odorant stimuli give rise to burst oscillatory activities which are synchronous over broad regions of those olfactory systems with frequencies ranging from 40 to 80 Hz. (Throughout this paper, I use the term, 'synchronous oscillations' to imply phase-locked oscillations with vanishing phase differences.) Moreover, clear emergence of stimulus-induced synchronous oscillation was recently observed in the olfactory systems of lower animals such as insects (Laurent and Naraghi 1994) and the terrestrial mollusk Limax (Delaney et al. 1994; Kleinfield et al. 1994). By measuring both evoked local field potential and intracellular current in the mushroom body of the insect brain, which is the counterpart of the piriform cortex of the mammalian brain, the authors of the former report showed the occurrence of synchronous oscillations with frequency of 20 Hz in the presence of odorant stimuli. In the latter experiment, an optical recording method was employed to observe simultaneously the neuronal activity over broad regions of the procerebral lobe of Limax, and revealed the presence of oscillations of a slightly different type. When there was no odorant stimulus, the lobe exhibited a constant oscillatory activity propagating along the long axis of the lobe. Odorant stimuli then caused a rapid collapse of phase differences in the propagating waves and consequently gave rise to synchronous oscillations which lasted for the entire duration of the stimuli over broad regions of the lobe. After the removal of the stimuli, the lobe again returned to the states with propagating waves. These experimental findings suggest that the synchronization and desynchronization of oscillations are essential features of olfactory information processing and play a key role in the primary analysis of olfactory stimuli.

In this paper I construct two similar, but slightly different, models of an olfactory system that consists of olfactory bulb and cortex by taking account of known anatomical and physiological data on the related neural circuits. Both models involve backprojection from the olfactory cortex to the olfactory bulb, but in slightly different manners. Information on odorants is assumed to be embedded into the cortical horizontal fiber system. It is shown that the cortex-to-bulb backprojection enables the models to establish rapid and robust synchrony among oscillators encoding information on an odorant. Interesting phenomena of stimulus-induced transitions between propagating waves, rather than nonoscillatory states, and synchronous oscillations are found for certain values of model parameters, suggesting a possible relationship of the present models with the olfactory systems of lower animals.

2 Models of bulbarcortical neural circuitry

The olfactory bulb receives its main input from olfactory receptor neurons of the olfactory epithelium. Mitral/tufted cells and granule cells are the principal cells and inhibitory interneurons, respectively, of the olfactory bulb. They interact with each other mainly through local dendrodendritic synaptic connections. A granule cell inhibits the mitral/tufted cells which activated it and such successive activation and inactivation of mitral/tufted and granule cells can be the source of oscillations observed experimentally (Freeman 1975; Bressler 1987).

Since olfactory information from neurons expressing a receptor type is mapped onto one or a few glomeruli, it is reasonable to assume that the mitral/tufted cells belonging to a glomerulus and the granule cells making synaptic contacts primarily with these mitral/tufted cells constitute a basic oscillator. Anatomical studies of the bulbar neural circuitry (Shepherd 1990) suggest that such an oscillator consists of roughly 100 mitral/tufted cells and 10000 granule cells. For simplicity, a pair of excitatory and inhibitory units are assumed to approximate the population oscillatory activity of this cell pool. To be specific, the Wilson-Cowan oscillator (Wilson and Cowan 1972) is employed as the model bulbar oscillator. The bulbar neural circuit is viewed as a network of many such oscillators coupled predominantly through short-range reciprocal synaptic connections.

The mitral/tufted cells send an afferent projection through the LOT to the pyramidal cells in the olfactory cortex. The axonal terminals of this projection are broadly distributed in the cortex and each mitral/tufted cell seems to have synaptic connections with more than ten pyramidal cells (Shepherd 1990). To make the models as simple as possible, a pyramidal cell in the cortex is assumed to be innervated by a single mitral/tufted cell pool in the bulb. This may imply that the pyramidal cells which receive axonal terminals of the same mitral/tufted cell pool and hence are coactivated by the same afferent input should exhibit synchronous neuronal activities. In the present study, such a population of pyramidal cells is represented simply by a single processing unit. Note that the abovementioned assumption concerning the afferent fiber system does not imply the existence of topographic organization in it.

Other important fiber systems in the olfactory pathway besides the afferent projection include the centrifugal fibers from the cortical pyramidal cells to the bulbar granule cells. It is known that the cortex-to-bulb backprojection terminates on the deep dendrites and cell bodies of the granule cells. These centrifugal inputs have been suggested to produce inhibitory effects on mitral/tufted cell activity (Shepherd 1990). Since the details of
the topographic organization of the centrifugal fiber system are unknown, the backward input from a cortical unit is assumed to project back to the bulbar oscillator which drives the unit (Fig. 1). The alternative possibility that the input projects back to the neighbors of this oscillator will not be discussed in this paper.

2.1 Type I model

The type I model suggested by the anatomical organization of the olfactory pathway is of primary importance in this study and is defined by the following set of equations:

\[
\frac{dM_i}{dt} = -M_i + f(aM_i - bG_i - KG_i - KG_{i-1} - \theta^{(M)} + I_i) \tag{1}
\]

\[
\frac{dG_i}{dt} = -G_i + f(cM_i - dG_i + KM_i - KM_i - KM_{i-1} + KM_{i+1} + \theta^{(G)}) + wP_i - \theta^{(G)} \tag{2}
\]

\[
\frac{dP_i}{dt} = -P_i + f(M_i + \sum_{j \neq i} J_{ij}P_j - \theta^{(P)}) \tag{3}
\]

where \(M_i, G_i\) and \(P_i\) express the activities of the ith mitral/tufted, granule and pyramidal cells, respectively, and \(f(x)\) is a sigmoid function representing the (normalized) mean firing rate of a population of each cell type. Note that \(M_0 = G_0 = M_{N+1} = G_{N+1} = 0\). The external inputs to the olfactory bulb are represented by the \(I_i\) terms. In modeling the bulbar neural network, I assumed a simple case where only the nearest-neighbor oscillators are mutually coupled. Therefore the bulbar neural network represents a one-dimensional chain of oscillators having a uniform coupling of strength \(K\). The assumption that the bulbar neural circuitry can be regarded as a homogeneous one-dimensional oscillator chain may be an extreme one. In particular, the likely presence of long-range connections in the bulb (Shepherd 1990), which are not incorporated into the present model, may give nontrivial features to its dynamic properties. For simplicity, however, the local connections are employed in the present model.

The long-range fiber system in the cortical neural network is represented by the mutual coupling terms in (3) and is used in the present model for the storage of odorant information. The weights \(J_{ij}\) are defined later in conducting numerical simulations.

2.2 Type II model

In the type I model, backprojection was assumed to increase the activity of the granule cells. In the type II model, on the other hand, backprojection is assumed to modulate the bulbar activity in a slightly indirect way: its effect is a short-lasting reinforcement of the granule-to-mitral/tufted cell contacts. The model is defined as:

\[
\frac{dM_i}{dt} = -M_i + f(aM_i - (b + b'P_i)G_i - KG_i - KG_{i-1} - \theta^{(M)} + I_i) \tag{4}
\]

\[
\frac{dG_i}{dt} = -G_i + f(cM_i - dG_i + KM_i - KM_{i-1} + KM_{i+1} - \theta^{(G)}) \tag{5}
\]

\[
\frac{dP_i}{dt} = -P_i + f(M_i + \sum_{j \neq i} J_{ij}P_j - \theta^{(P)}) \tag{6}
\]

Note that the temporal values of weight \(b + b'P_i\) of the granule-to-mitral/tufted synaptic connections are changed in a cortical-activity-dependent manner. The anatomical organization of the olfactory system may suggest that the type I model is more probable than the type II model. In the present study, I include the type II model to show an alternative mechanism for achieving synchronous oscillations by means of backprojection, since the mechanism might be involved in other modalities of cortical information processing.

3 Mechanism of synchronization

I will examine how the cortex-to-bulb backprojection promotes the establishment of rapid and robust synchronization. The dynamic behavior of the bulbar neural oscillator is essentially determined by two nullclines, \(M = 0\) and \(G = 0\), in the \(M-G\) plane. Assume that two nullclines of the type I model are located in such a way as to ensure almost no activity, i.e., \((u_0, v_0) \approx (0,0)\), when \(I = 0\) (Fig. 2a). Now sufficiently large positive \(I\) shifts \(M = 0\) upward (the dashed curve in Fig. 2a) so that it intersects \(\dot{G} = 0\) at \((M_{\sigma}, G_{\sigma})\) denoted by a filled circle. Linear stability analysis shows that the new intersection point is unstable and the oscillator starts to oscillate if

\[
1 + \beta(dq - ap) < 0
\]

\[
1 + 2\beta(dq - ap) + 4\beta^2(bc - ad)pq > 0
\]
where \( p = M_x(1 - M_x) \) and \( q = G_x(1 - G_x) \). The above conditions imply that the intersection point can be a stable fixed point when \( I \) is sufficiently large. In this case, the temporary state of the oscillator is attracted by the fixed point. As the state approaches it, \( M(t) \) increases and so does \( P(t) \) because of an increasing input from \( M \). This increase of \( P \) shifts nullcline \( G = 0 \) leftward (the dotted curve in Fig. 2a). If the amount of this shift is not small, i.e., the strength of backprojection is sufficiently large, the fixed point becomes unstable. The network state thus continues to move on a periodic orbit since the attracting force of the fixed point disappears.

In the type II model, similar temporal generation of a fixed point can occur in a slightly different manner. Consider the case such as shown in Fig. 2b. Sufficiently large positive \( I \) shifts \( M = 0 \) upward (the dashed curve in Fig. 2b) so that it intersects \( G = 0 \) in the upper right region of the \( M-G \) plane. One of the intersection points (the filled circle in Fig. 2b) becomes an attracting fixed point. As the state of the oscillator approaches it, the value of \( P \) and accordingly the weight of \( G \)-to-\( M \) feedback inhibition are increased. Then two nullclines can be again separated and the attracting fixed point disappears.

Now consider the system of two oscillators (either type I or type II) coupled to each other. The motion of a leading oscillator approaching its fixed point slows down in the neighborhood of the attractors. While the leading oscillator is trapped near the fixed point, the other oscillator can rapidly catch up with the leading one, being attracted by its own fixed point. As a result, the phase difference between two oscillators is rapidly reduced if the leading oscillator stays at the fixed point for a sufficiently long time before it is released from the trap owing to the effect of the backprojection. This temporal freeze of motion of leading oscillators is the major cause of synchronization in the proposed neural networks.

A similar mechanism was first discussed by Campbell and Wang (1996) for a network of Wilson–Cowan-type oscillators (without \( P \)-unit). In their model, an inhibitory unit (\( G \)) of each oscillator sends an excitatory synaptic connection to its excitatory partner (\( M \)) for generating an appropriate fixed point needed for synchronization. Furthermore, a particular type of interaction, which may be classified as 'electronic' coupling rather than 'synaptic' according to Kopell and Ermentrout (1986), was used to generate and annihilate the fixed point. Physiologically the excitatory synaptic action may occur if disinhibition exists between the inhibitory and excitatory cells. In the present model, the generation and annihilation of fixed points are controlled by the cortex-to-bulb backprojection, whose existence is experimentally known.

To investigate whether the presence of backprojection indeed enhances the establishment of synchrony, minimal models with \( N = 2 \) of both types were studied numerically. Typical results are presented for the type I model in Fig. 3a and 3b in the presence (\( w \neq 0 \)) and absence (\( w = 0 \)) of backprojection effects, respectively. It is seen that two oscillators rapidly synchronize in the presence of backprojection, whereas they cannot achieve synchrony in its absence. Similar results were obtained.
for the type II model with certain values of the parameters (see the caption to Fig. 3) and both models were found to be equally suitable for present purposes.

### 4 Stimulus-dependent synchronization in the model olfactory systems

The finding that backprojection from the P cells to the M-G oscillators significantly enhances synchronization of two oscillators suggests the occurrence of a similar phenomenon in larger systems. In the preceding section, two models were proposed since the method for establishing synchronous oscillations by means of backprojection in biological neural networks is not necessarily unique. In the following, however, only the results for the type I model, which is of primary interest in this study, are shown in order to avoid duplicating similar results.

In the numerical simulations it is assumed that a particular odor memory is represented by a synchronous cortical activity pattern which is determined by weights $J_{ij}$ of the horizontal connections. In olfactory perceptual process, these activity patterns may be retrieved by the presentation of appropriate stimuli associated with the odorants. Let $\{\xi^p_i\}_{i=1, \ldots, P} = \{0, 1\}$ be those memory patterns with $\xi^p_i = 1(0)$ implying that cell $i$ is activated (inaactive) in the $\mu$th memory pattern. Each memory pattern is fixed according to the following probability distribution:

$$P(\xi^p_i) = r\delta(\xi^p_i - 1) + (1 - r)\delta(\xi^p_i)$$

which implies that a pattern consists of $rN$ '1's and $(1 - r)N$ '0's. Then the synaptic connections in the cortical neural network are assumed to be given by

$$J_{ij} = \eta \sum_{\mu=1}^P \xi^p_i (\xi^p_j - r)$$

where $p$ is the total number of memory patterns stored by the network and $\eta$ is a positive constant. This connection matrix basically describes the mutual excitation among the P cells encoding each memory pattern and allows the network to exhibit a synchronous oscillation representing a memory pattern if the related oscillators are activated by suitableafferent inputs (Fukai 1994).

The degree of synchrony between two $M$ cells both showing oscillations can be most conveniently measured with the following correlation:

$$C_{12}(t) = \frac{\langle M_1(t) M_2(t) \rangle - \langle M_1(t) \rangle \langle M_2(t) \rangle}{\sqrt{\langle M_1^2(t) \rangle - \langle M_1(t) \rangle^2} \sqrt{\langle M_2^2(t) \rangle - \langle M_2(t) \rangle^2}}$$

where $\langle x(t) \rangle$ stands for

$$\langle x(t) \rangle = \frac{1}{T} \int_{t-T}^{t} dx(t)$$

with time duration $T \approx$ the period of oscillation.

$|C_{12}(t)| \leq 1$ and two oscillators oscillating in complete synchrony yield $C_{12}(t) = 1$. We now define order parameters $Q_d(t)$ and $\overline{Q}_d(t)$ in terms of the correlations as follows:

$$Q_d(t) = \frac{1}{N} \sum_{j=1}^{N} \xi_j^d C_{i,j}(t)$$

$$\overline{Q}_d(t) = \frac{1}{N(1 - r)} \sum_{j=1}^{N} (1 - \xi_j^d) C_{i,j}(t)$$

where any $i$ giving $\xi_i^d = 1$ may be chosen as a reference site. $Q_d(t)$ measures the degree of synchrony among cells encoding the $\mu$th memory pattern: $Q_d(t) = 1$ when complete synchrony, i.e., $C_{i,j}(t) = 1$ for any $j$ satisfying $\xi_j^d = 1$, takes place. On the other hand, $\overline{Q}_d(t)$ measures the mean correlation between a cell encoding $\{\xi^d\}$ and those not engaged in the encoding.

Numerical simulations were conducted for two types of the networks. Values of some intrinsic parameters of oscillators were distributed within certain ranges to examine whether synchrony is robust against possible small nonhomogeneities in biological networks. The results showing typical dynamic behavior of the models are illustrated for the type I model in Fig. 4 in terms of $\langle M_1(t) \rangle$ values, $Q_d(t)$ and $\overline{Q}_d(t)$. During time interval $30 \leq t \leq 80$, afferent input $I_i(t) = \sigma \xi^p_i$ was delivered to the network, where $\mu \in \{1, \ldots, p + 1\}$ and $\sigma (> 0)$ determines the magnitude of the input.

![Fig. 4. Results of simulations for the type I model with a stimulus given by a a memory pattern or b a non-memory pattern in time interval $30 \leq t \leq 80$. $N = 400$ and $p = 10$. In each case, $M_1(t)$ values were shown only for a subset of oscillators activated by the stimulus. The time courses of the correlations $Q_d(t)$ (continuous curves) and $\overline{Q}_d(t)$ (dashed curves) are given respectively in c and d for the cases of a and b. The parameters used are $r = 0.3$, $w = 1.2$, $\eta^{(M)} = 0.13$, $\eta^{(C)} = 0.18$, $\eta = 0.7$, $K = 0.05$ and $\sigma = 0.4$. a, b, c, d and (b) have about 5% fluctuations around their central values of 0.45, 1.5, 0.1, 0.9 and 0.75, respectively.](image-url)
strength of the input. The \((p+1)\)th pattern, which was also fixed according to (8), was not embedded into \(J_0\), and thus may represent an unfamiliar odor stimulus. In Fig 4a and 4b, \(M_i(t)\) values were plotted only for (a subset of) oscillators receiving nonzero inputs. Other oscillators may exhibit oscillations, but their amplitudes are very small.

From Fig 4a for \(\mu \in \{1, \ldots, p\}\), we can see that synchronous oscillations are established immediately after the onset of the stimulus. If identical oscillators are employed, an almost complete synchrony can be established (not shown). In Fig 4b for \(\mu = p + 1\), although instantaneous synchronization is observed at the onset of the input due to rapid coactivation of the oscillators, the synchronous oscillations are not stable. We can clearly see this if we compare the time evolution of \(Q_i(t)\) for \(\mu \in \{1, \ldots, p\}\) in Fig 4c with that in Fig 4d for \(\mu = p + 1\) (the continuous curves). Thus the stimulus-

induced activity can remain synchronous only when the information on the activity pattern is embedded in the horizontal connections.

As mentioned previously, the olfactory systems of lower animals have been shown to exhibit stimulus-

induced state changes from a propagating wave (i.e., oscillations with phase lags between neighboring oscillators) to a synchronous oscillation. Although such a transition has so far not been found in mammalian olfactory systems, it is worth remarking that a similar transition can occur in the present model if the basal activity for no odorant stimulus is given by an oscillation. In fact, setting \(\theta(M)\) at a smaller value suffices for this purpose. Figure 5 shows an example of the stimulus-

induced state transition where the afferent input was delivered for \(30 \leq t \leq 80\). Unlike the previous case, the basal activity is now a propagating wave, in which the phase lags are generated by the effects of the dendro-
dendritic synaptic connections, and the presentation of stimulus immediately causes the collapse of the phase lags.

I examine the effects of nearest-neighbor connections on the network dynamics when the basal activities are oscillations. Note that the system of the oscillators given by (1), (2) and (3) can be rewritten as

\[
\begin{align*}
\dot{X}_i &= -X_i + af(X_i - \theta(M)) - bf(Y_i - \theta(G)) \\
& \quad - Kf(Y_{i-1} - \theta(G)) - Kf(Y_{i+1} - \theta(G)) \\
& \quad - Kf(Y_{i-1} - \theta(G)) - Kf(Y_{i+1} - \theta(G)) \\
& \quad - af(X_i - \theta(M)) - df(Y_i - \theta(G)) \\
& \quad + af(Z_i - \theta(p)) + Kf(X_{i-1} - \theta(M)) \\
& \quad + Kf(X_{i+1} - \theta(M)) \\
& \quad + Kf(X_{i-1} - \theta(M)) \\
& \quad + Kf(X_{i+1} - \theta(M)) \\
& \quad + \sum_{j} J_{ij} f(Z_j - \theta(p)) \\
& \quad \text{for } i = 1, \ldots, N
\end{align*}
\]

The terms involving \(X_0, X_{N+1}, Y_0, Y_{N+1}, Z_0\) and \(Z_{N+1}\) are understood to be absent from the above

expressions) in terms of a new set of variables

\[
\begin{align*}
X_i &= aM_i - bG_i - KG_{i-1} - KG_{i+1} \\
Y_i &= cM_i - dG_i + wP_i + KM_{i-1} + KM_{i+1} \\
Z_i &= M_i + \sum_{j} J_{ij} P_j
\end{align*}
\]

Since we are interested in the effects of the nearest-

neighbor connections, we neglect the presence of the horizontal connections and regard the model as a chain of oscillators. It is known that a chain of oscillators coupled to their nearest neighbors exhibits a phase-

locked oscillation with certain phase lags as a steady state (Kopell and Ermentrout 1986). This property is independent of the particular structure of oscillators and couplings, so long as the strength of the couplings is not very strong. In fact, by neglecting \(J_{ij}\), we can derive the following equations representing a one-dimensional
chain of phases \( \{ \phi_i \} \) defined appropriately for oscillators at \( K = 0 \) (Kuramoto 1984):

\[
\dot{\phi}_1 = \omega + K \Gamma_E(\phi_1) f(Y^{(0)}(\phi_2) - \theta^{(M)}) - K \Gamma_I(\phi_1) f(Y^{(0)}(\phi_2) - \theta^{(G)})
\]

\[
\vdots
\]

\[
\dot{\phi}_i = \omega + K \Gamma_E(\phi_i) [f(Y^{(0)}(\phi_{i-1}) - \theta^{(M)})] + f(Y^{(0)}(\phi_{i-1}) - \theta^{(M)}) - K \Gamma_I(\phi_i) [f(Y^{(0)}(\phi_{i-1}) - \theta^{(G)})] + f(Y^{(0)}(\phi_{i-1}) - \theta^{(G)})]
\]

(17)

\[
\dot{\phi}_N = \omega + K \Gamma_E(\phi_N) f(Y^{(0)}(\phi_{N-1}) - \theta^{(M)}) - K \Gamma_I(\phi_N) f(Y^{(0)}(\phi_{N-1}) - \theta^{(G)})
\]

In (17), \( \omega \) is the natural frequency of each oscillator, \( \Gamma_E(\phi) \) and \( \Gamma_I(\phi) \) measure the sensitivity of the phases to the perturbations through the local excitatory and inhibitory couplings, respectively, and \( \{X^{(0)}(\phi(t)), Y^{(0)}(\phi(t)), Z^{(0)}(\phi(t))\} \) is a periodic solution to (14), (15) and (16) for \( K = 0 \). Note that \( Z^{(0)}(t) \) does not appear manifestly in (17).

It is in general difficult to solve (17) for given functions \( \Gamma_E(\phi) \) and \( \Gamma_I(\phi) \). If, however, \( \{X^{(0)}(t), Y^{(0)}(t), Z^{(0)}(t)\} \) represents a sufficiently smooth orbit, the following approximate treatment of the interaction terms is suitable for studying the qualitative features of the dynamics:

\[
K \Gamma_E(\phi) f(X^{(0)}(\phi') - \theta^{(M)}) - K \Gamma_I(\phi) f(Y^{(0)}(\phi') - \theta^{(G)})
\approx \mu \sin(\phi' - \phi - \epsilon) + \mu' \sin(\phi' + \phi - \epsilon')
\]

(18)

where \( \mu, \mu', \epsilon \) and \( \epsilon' \) are given in a model-specific manner.

Further, the averaging theorem allows us to neglect the second term in (18) provided the coupled system continues to oscillate (cf. Fukai and Shino 1995). The phase model described by (17) and (18) with \( \mu' = 0 \) has a steady state representing a synchronous oscillation if \( \epsilon = 0 \). Otherwise nonvanishing phase lags exist between neighboring oscillators and their values gradually change along the chain (see Appendix). Because \( \epsilon = 0 \) can occur only accidentally, the effect of the dendrodendritic connections on the model dynamics is to produce a certain degree of phase lag between neighboring oscillators. Therefore, in achieving synchrony, the intrabulbar connections have negative effects which must be overwhelmed by positive effects of the horizontal connections. It is, however, the bulbar connections that desynchronize the phases of oscillations rapidly after the removal of the odorant stimuli. As mentioned later, such rapid desynchronization in the absence of stimulus can be as significant as rapid synchronization in the presence of stimulus for olfactory information processing based on oscillations.

5 Discussion

Using simple neural network models of the mammalian olfactory system, I have pointed out that the presence of backprojection from the olfactory cortex to the olfactory bulb can significantly facilitate the retention of synchrony among a large population of synaptically coupled cells in both bulb and cortex. On receiving sufficiently strong afferent inputs, the bulbar oscillators generate attracting fixed points in the neighborhood of their periodic orbits. The attractors thus generated force the leading oscillators to slow down until the centrifugal inputs eliminate those fixed points. This dynamic process is repeated and consequently the phase lags between oscillators are rapidly reduced.

Information concerning the discrimination of an odor is likely to be encoded in a spatial pattern of firing rates which occurs with widespread synchronous oscillations over the population of the bulbar mitral/tufted cells and cortical pyramidal cells (Freeman 1975). The oscillations seem to provide a mechanism for binding widely distributed populations of cells into functionally meaningful synchronous activity patterns. We have seen that the models exhibit sustained synchrony when they are exposed to afferent stimuli related to the learned memory patterns. This implies that the olfactory pathway at the level modeled in this paper may function as a filter tuned to particular activity patterns of glomeruli related to well-learned odorant stimuli, and that only such activities as are transmitted synchronously from the primary olfactory cortex to higher centres of odor perception may facilitate the perception of an odor. Furthermore, learning of a new odor seems to proceed very quickly in the olfactory systems of mammals and lower animals. For instance, the Kenyon cells in an insect's mushroom body quickly built up new synchronous oscillations during the repeated presentation of new odor (Laurent and Naraghi 1994). Hence, in reality, the rapid learning process may tune the olfactory system optimally to new odorant stimuli.

Another possible functional role of synchronous oscillations, especially in lower animals, is to provide a way of linking the behavioral response of an animal with the sensory signal causing the response. In the mollusk, for instance, anatomical and functional studies suggest that the odor-mediated activity of the procerebral lobe regulates the motor responses. Thus there is very probably synchronization between the activities of the lobe and motor control areas. If this is really the case, such an automatic link between the stimulus and response through synchronous oscillations may provide the animals with an effective way of retaining the causal relation between motor behavior and trigger stimulus.

Some researchers have suggested that a possible functional role of backprojection is backward masking of strong odorant stimuli when more than one stimulus is presented (Granger et al. 1990). A similar masking effect can be obtained also in the present oscillator neural networks provided that a suitable learning rule is assumed for the weight of the centrifugal input. Suppose that the repeated presentation of a strong odorant stimulus strengthens coefficient \( w \) in the type I model or \( b' \) in the type II model for the oscillators receiving this stimulus. Because leading oscillators cannot stay near the fixed points for a sufficiently long time when these coefficients
are large, the retention of synchronization becomes difficult with this afferent stimulus at some values of the coefficients. This desynchronization can be interpreted as the masking of strong odorant stimuli in the oscillator neural networks. From this point of view, the synchronization and desynchronization of oscillations are said to be related to changes of attentiveness of the animal to its olfactory environment.

It was shown that the local dendrodendritic synaptic connections are responsible for generating finite phase lags between oscillators. What is the purpose of these phase lags in olfactory information processing? A possible answer is that it improves the signal-to-noise ratio when a noisy stimulus is presented to the olfactory system. Oscillators which are engaged in coding the odorant information will be synchronized due to the effect of the horizontal connections, while those receiving the noise component remain asynchronous due to the inhibitory effects of the dendrodendritic connections. Thus a higher contrast between a synchronous signal component and an asynchronous noise component is obtained with the presence of the dendrodendritic connections. When the basal activities are oscillations or propagating waves, the connections can play another important functional role by rapidly desynchronizing the phases after removal of an odorant stimulus. Such a desynchronization mechanism is likely to be necessary for the analysis of an olfactory environment that is changing from moment to moment: without it, the olfactory system would not be able to tune its activity quickly to a new odorant stimulus.

So far, the phenomenon of dynamic state transitions between propagating waves and coherent oscillations has been found in the mollusk 

\[ \text{Limax} \]

rather than in mammals. The present model, however, has suggested that it can occur also in the mammalian olfactory system. It is intriguing question whether the phenomenon occurs and plays some functional role only in lower animals or exists also in higher animals such as mammals. The anatomical organization of the olfactory system remains largely unknown and further studies are needed to reveal what type of biological mechanism in the procerebral lobe of 

\[ \text{Limax} \]

achieves the state transitions.

Appendix

Here the steady state of the phase model described by (17) is analyzed. The equation to be studied is
\[
\begin{align*}
\dot{\phi}_1 &= \omega + \mu \sin(\phi_2 - \phi_1 - \epsilon) \\
\vdots \\
\dot{\phi}_N &= \omega + \mu \sin(\phi_{N-1} - \phi_N - \epsilon)
\end{align*}
\]
(A.1)

Only the restricted case of \(|\epsilon| \ll 1\) is explicitly studied. Introducing phase differences \(\psi_i = \phi_{i+1} - \phi_i\) (\(i = 1, \ldots, N - 1\)), we obtain
\[
\begin{align*}
\dot{\psi}_1 &= \mu \sin(\psi_2 - \epsilon) + \mu \sin(-\psi_1 - \epsilon) - \mu \sin(\psi_1 - \epsilon) \\
\vdots \\
\dot{\psi}_N &= \mu \sin(\psi_{N-1} - \epsilon) + \mu \sin(-\psi_N - \epsilon) \\
&- \mu \sin(\psi_N - \epsilon) - \mu \sin(-\psi_{N-1} - \epsilon)
\end{align*}
\]
(A.2)

from (A.1). We are interested in the steady-state solution of (A.2) given by \(\psi_k = 0\) for any \(k\). It is easy to see that \(\psi_1 = \psi_2 = \cdots = \psi_N = 0\) does not solve the first or last equation of (A.2) unless \(\epsilon = 0\) and hence the solution representing perfect synchrony cannot exist for \(\epsilon \neq 0\). Below we show how the presence of small nonvanishing \(\epsilon\) alters the dynamical behavior of the steady state.

To this end, we expand \(\psi_i\) in terms of a small parameter \(\varepsilon\) as
\[
\psi_i = \varepsilon (\psi^{(0)}_i + \psi^{(1)}_i + \cdots)
\]
(A.3)

Substituting (A.3) into (A.2) and retaining only the leading order of \(\varepsilon\) yields
\[
\mu \frac{\partial \tilde{\psi}^{(0)}}{\partial t} = \tilde{x} + \tilde{Q} \tilde{\psi}^{(0)}
\]
(A.4)

where \((N - 1)\)-dimensional vectors and \((N - 1) \times (N - 1)\) matrix are given by
\[
\tilde{\psi}^{(0)}T = (\psi^{(0)}_1, \psi^{(0)}_2, \ldots, \psi^{(0)}_{N-1})
\]
\[
\tilde{x}T = (-1, 0, \ldots, 0, 1)
\]
\[
\tilde{Q} = \begin{pmatrix}
-2 & 1 & & \\
1 & -2 & 1 & 0 \\
& 1 & -2 & 1 \\
& & & \ddots \\
& & & & 0 & 1 & -2 & 1 \\
& & & & & & & 1 & -2
\end{pmatrix}
\]
(A.5)

\((N - 1)\) eigenvalues \(\lambda^{(k)}\) and eigenvectors \(\bar{u}^{(k)}\) of \(\tilde{Q}\) are easily obtained as
\[
\lambda^{(k)} = -2 + 2 \cos \sigma^{(k)} \quad k = 1, \ldots, N - 1
\]
\[
\bar{u}^{(k)} = \sqrt{ \frac{4}{2N - 1 - \sin((2N - 1)\sigma^{(k)}/\sin \sigma^{(k)})}} \sin(\sigma^{(k)}/2)
\]
(A.6)

where \(\sigma^{(k)} = k\pi/N\). Because all the eigenvalues are negative, (A.4) has a stable fixed point. Noting that the inverse of \(\tilde{Q}\) is given by \(\tilde{Q}^{-1} = \sum_{k=1}^{N-1} \bar{u}^{(k)} \bar{u}^{(k)\dagger}/\lambda^{(k)}\), we can obtain the fixed point solution as
\[
\bar{\psi}^{(0)}(t \to \infty) = \sum_{k=1}^{N-1} \bar{u}^{(k)} (\bar{u}^{(k)\dagger} - \bar{u}^{(N-k-1)\dagger})/\lambda^{(k)} \quad l = 1, \ldots, N - 1
\]
(A.7)
This implies that the steady state of the chain of oscillators is in general a propagating wave rather than a synchronous oscillation and the constant phase lag between two neighboring oscillators gradually varies along the chain.

References

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