Biol. Cybern. 62, 349–361 (1990)

Biological Cybernetics

A Model of Olfactory Adaptation and Sensitivity Enhancement in the Olfactory Bulb

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Abstract. It has been suggested that the olfactory bulb, the first processing center after the sensory cells in the olfactory pathway, plays a role in olfactory adaptation, odor sensitivity enhancement by motivation and other olfactory psychophysical phenomena. In a mathematical model based on the bulbar anatomy and physiology, the inputs from the higher olfactory centers to the inhibitory cells in the bulb are shown to be able to modulate the response, and thus the sensitivity of the bulb to specific odor inputs. It follows that the bulb can decrease its sensitivity to a pre-existing and detected odor (adaptation) while remaining sensitive to new odors, or increase its sensitivity to interested searching odors. Other olfactory psychophysical phenomena such as cross-adaptation etc. are discussed as well.

1 Introduction

The odor inputs are sensed by the olfactory receptor cells (Lancet 1986) which send signals to the olfactory bulb. The bulb after some processing sends outputs to the olfactory cortex which, together with a part of brain called diagonal band, send the feedback signals to the bulb (Shepherd 1979). Many anatomical and physiological experiments have revealed the structure and the properties of the bulb (Scott 1986; Shepherd 1979). It is ciefly composed of excitatory mitral cells and the inhibitory granule cells, each sending inputs to, and receiving inputs from, the neighboring cells of the other type. The mitral (Shepherd 1979) cells effectively receive the input from the olfactory receptors. The activity pattern of the mitral cells is modulated by the granule cells. Axons from the mitral cells carry bulbar output to the olfactory cortex. The cortex and other higher olfactory centers send feedback inputs chiefly to the granule cells (Shepherd 1979) in the bulb. When the animal is motivated, the bulb responds to odor inputs with a 35–90 Hz coherent oscillatory activity pattern in the cell population (Freeman 1978; Freeman and Schneider 1982). This oscillatory output goes to olfactory cortex which has oscillation responses with similar frequencies to that in the bulb (Freeman 1978).

Many attempts have been made to model the computational functions of the olfactory bulb (Freeman 1979b, c; Baird 1986; Freeman and Skarda 1985; Skarda and Freeman 1987). In a previous paper (Li and Hopfield 1989), a mathematical model based on the bulbar anatomy and physiology was developed. Its simulations successfully produce the odor-specific rhythmic activity mimicing the oscillations observed physiologically. These patterns are the decision states of the odor information made by the bulb. In this paper, it will be shown how the central inputs can modulate the response of the bulb to the odor inputs, enhancing or suppressing the sensitivity to particular odors. Psychophysical phenomena such as olfactory adaptation (Pryor et al. 1970; Steinmetz et al. 1970) and sensitivity enhancement in odor searching can be understood in this model.

2 The Olfactory Problem

The olfactory system needs to solve two problems: *1)* what is the identity of the input odor? *2)* what is the intensity of the input odor object? If there is only one odor type ("odor object") in the actual sensory input, the computation will be straight forward. But when there are odor mixtures in the input, the problem becomes complex, and the olfactory system often cannot tell the individual odor sub-components (Moncrieff 1967). Since most receptor cells respond to more than one odor type (Lancet 1986; Sicard and Holley 1984), and a given odor may contain a mixture of molecules which bind predominantly to different receptors, the information about any one odor object may be distributed across the whole receptor population. It will generally be inappropriate to focus

attention on a small subset of receptors to search for a particular odor object. The integrative processing done by olfactory centers must be responsible for identifying individual odor objects, separating multiple objects if possible, or sensing an odor mixture as a whole new odor type. [Odor mixtures have a complex psychophysics. For example, two substances odorous singly may be inodorous together – counteraction; or only one odor type is sensed when two are mixed – masking (Moncrieff 1967).]

Since the major olfactory problem of an animal in a rich olfactory environment is to identify odor objects, it would be desirable if the olfactory system could detect individual odors in a mixture. Olfactory adaptation may be a strategy used to detect individual odor components. It should not be understood as an olfactory fatigue (Moncrieff 1967), but as an active mechanism used by the olfactory system to screen out a pre-existing odor object, which has already been detected, and stay sensitive to new odors mixed with the pre-existing odors. For example, after a human adapts to vanillin, a mixture of vanillin and coumarin smells only of coumarin (Moncrieff 1967). Without adaptation, the new odors may be masked or counteracted by the pre-existing odors and not detected as the appropriate odor object.

If the olfactory system can reduce its sensitivity to particular odors in adaptation, it is reasonable to expect that it may also be able to increase the sensitivity to certain odors when odor searching. Psychophysical experiments are not generally done on the olfactory sensitivity enhancement by motivation since the subject is not as easy to handle as olfactory adaptation. Enhanced sensitivity to a particular stimulus is evident in other sensory system such as vision and audition – attention can be focused on a particular object in a large input image to eyes, or a particular speaker in a noisy cocktail party. It would not be surprising that the olfactory system can also focus its attention to a particular odor stimulus. Dogs searching for a particular odor after the searching object is known can be a behavior evidence for this.

What can be the mechanism for olfactory adaptation or enhancement? It is known that the olfactory adaptation is not due simply to the exhaustion of receptor cells (Moncrieff 1967). The receptor cells keep firing, but within a second, change from phasic to tonic response during continuous stimulus (Getchell and Shepherd 1978; Lancet 1986), while the olfactory adaptation occur in the time order of minutes (Pryor et al. 1970; Steinmetz et al. 1970). So the olfactory structure responsible must then be at the bulb or higher in the olfactory pathway. Physiological experiments (Chaput and Panhuber 1982) shows that the bulbar mitral cells' firing decreases with long exposure to (a single) odor, suggesting the bulb's involvement in olfactory adaptation.

There are several (not strong) theoretical reasons suggesting that the feedback signal from higher olfactory centers to the olfactory bulb is the source for bulbar adaptation. First, bulbar cell exhaustion should not be the source for adaptation since the sensitivity to new odor inputs remain intact after adaptation to the pre-existing odor. [Active mitral cell populations for different odors should overlap since the responsive receptor cell populations for different odors overlap (Lancet 1986; Sicard and Holley 1984).] Second, with the same odor input and no bulbar cell exhaustion, the bulbar response should not change from one sniff to another unless the other bulbar input, namely the central input, changes in time. Third, the selectivity of the sensitivity reduction to only the pre-existing odors suggests that the bulb is instructed by a well computed information signal which could only be available from higher centers. Fourth, the signals from the higher centers should serve some information processing purpose by their existence. Olfactory adaptation as one of the processing used to detect new odors, may very likely have the central signal involved in it.

Here a possible mechanism is suggested for a central signal to participate in the adaptation. After the pre-existing odor object is detected, the higher olfactory centers have knowledge about this odor. They can then send a computed signal to the bulb to cancel the effect of this particular odor object input on the bulb output. If the cancellation is complete and exact, the bulb output would ideally be as if no such odor exists. Due to the selectivity of the cancelling, a new input odor object mixed with the pre-existing and cancelled odor object would be detected by the bulb as if it is the only component in the odor input mixture.

Extention can be made to olfactory enhancement. If a signal S from higher centers can cancel the effect of a particular input odor on the bulb output, an opposite of this signal (i.e., $-S$, the enhancing signal), may increase the effect of this particular odor. In this case, a sensitivity enhancement to this odor object results. However, it is essential that S and $-S$ are not merely additive to the odor input signals, for otherwise $-S$ would be mistaken for the sought-after odor. The higher centers should have a knowledge of the odor in order to send a right enhancing signal. This requires that the odor information is known either through genetics and development or by experience.

If this suggested mechanism for olfactory adaptation and enhancement is correct, there will be the following consequences. Suppose we have a situation in which an odor object is detected, and adaptation is set up such that a cancelling signal is sent for this pre-existing odor object in every sniff. If in the next sniff, a

new odor object is introduced and at the same time the pre-existing odor object is withdrawn, the cancelling signal will not be compensated by an expected odor, and will instead affect and impair the bulbar sensitivity and detectability to the new odor object. This cross-adaptation effect is psychophysically observed (Cain and Engen 1969). Experiments show that after sniffing one odor, another odor at next sniff smells less strong as it would be and may even smell different (Moncrieff 1967). [The recovery from olfactory adaptation after the pre-existing odor is removed takes a few minutes (Pryor et al. 1970; Steinmetz et al. 1970). In the present description it implies that the cancelling signal does not disappear immediately when the pre-existing odor is removed.] Cross-adaptation is observed to depend on both the pre-existing and new odor types, and it is non-symmetric on the odor types (Cain and Engen 1969), i.e., the extent to which odor A cross-adapted by B is different from that of B by A. An analogous cross-enhancement should occur. Suppose an animal is motivated to search for an odor object, instanciated by an enhancing signal sent from the higher centers to the bulb for that particular odor. If a different odor object is inhaled instead of the expected one, the enhancing signal will distort the bulbar response to this odor object. There are no experimental data on the this hypothesized cross-enhancement.

This paper is to show how the olfactory adaptation and enhancement mechanism suggested above can be realized in a mathematical model, and confirmed by simulation.

3 A Mathematical Model of the Olfactory Bulb

A model of the olfactory bulb's computational function is described in detail in a previous paper (Li and Hopfield 1989). N mitral cells and M granule cells are included in the model, with their internal states described by $X=\{x_1, x_2, \ldots, x_N\}$ and $Y=\{y_1, y_2, \ldots, y_M\}$ respectively. These cell outputs are $G_x(X)=\{g_x(x_1), g_x(x_2), \ldots, g_x(x_N)\}$ and $G_y(Y)=\{g_y(y_1), g_y(y_2), \ldots, g_y(y_M)\}$ for the mitral and granule cells respectively, where g_x and g_y are the non-linear sigmoid input-output functions (Fig. 1). The mitral cells receive the receptor inputs described by an N-d vector $I=\{i_1, i_2, \ldots, i_N\}=I_{\text{background}}+I_{\text{odor}}$ which is the sum of the background input $I_{\text{background}}$ and the input induced by the inhaled odors I_{odor}. In one sniff lasting 200–500 ms with inhaling and exhaling taking about half of the time, I_{odor} is (Fig. 2)

$$I_{\text{odor}}=\begin{cases} P_{\text{odor}}(t-t^{\text{inhale}})+I_{\text{odor}}(t^{\text{inhale}}), \\ \quad \text{if} \quad t^{\text{inhale}}\leqq t\leqq t^{\text{exhale}}, \\ I_{\text{odor}}(t^{\text{exhale}})e^{-(t-t^{\text{exhale}})/\tau_{\text{exhale}}}, \\ \quad \text{if} \quad t\geqq t^{\text{exhale}}, \end{cases} \tag{3.1}$$

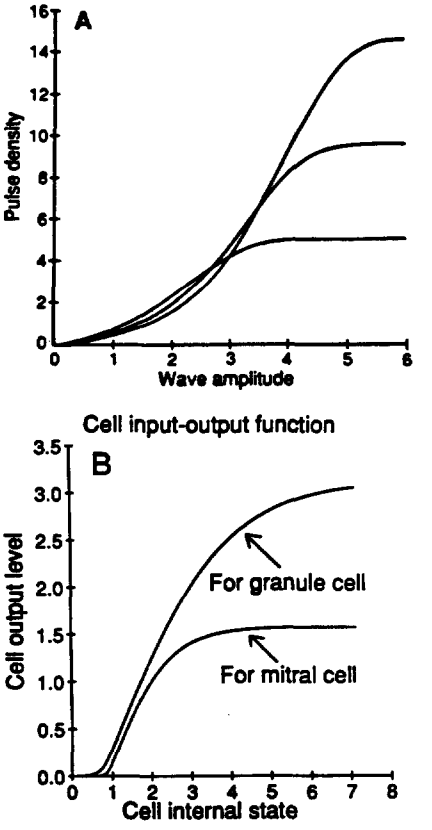

Fig. 1A and B. Cell non-linear input-output functions. **A** three examples of experimentally measured functions in a mass of mitral and granule cells, relating the pulse probability of single or small groups of mitral cells to EEG wave amplitude originated from the granule cells. Taken from Freeman and Skarda (1985). **B** the model functions for mitral and granule cells

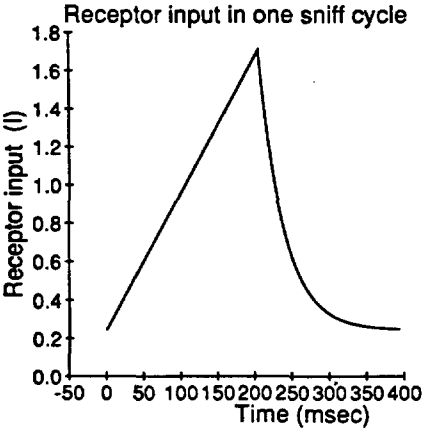

Fig. 2. Receptor input in one sniff cycle

where P_{odor} characterizes the receptor activity pattern which depends on odor type and concentration, t^{inhale} and t^{exhale} are the inhale and exhale onset times respectively, τ_{exhale} is the I_{odor} decay time constant at exhale, $I_{\text{odor}}(t^{\text{inhale}})$ is zero if no odor exists before

inhaling. The central inputs to the granule cells are described by a M-d vector $I_c = \{i_{c,1}, i_{c,2}, \ldots, i_{c,M}\}$. The mitral-to-granule and granule-to-mitral synaptic connections are described by a $M \times N$ matrix W_0 and $N \times M$ matrix H_0 respectively. The system of differential Eqs. is

$$\begin{aligned} \dot{X} &= -H_0 G_y(Y) - \alpha_x X + I, \\ \dot{Y} &= W_0 G_x(X) - \alpha_y Y + I_c, \end{aligned} \tag{3.2}$$

where α_x and α_y are the cell dissipation constants for mitral and granule cells respectively. The minus sign in front of H_0 indicates the inhibitory nature of the granule cell outputs, and thus both H_0 and W_0 are matrices of non-negative elements as synaptic strengths.

For analysis (but not for computer simulation) the adiabatic approximation and linear analysis technique can be used. The system is shown to be a group of coupled non-linear oscillators whose linear approximation is described by equation

$$\ddot{X} + 2\alpha\dot{X} + (A + \alpha^2)X = 0, \tag{3.3}$$

where $\alpha \equiv \alpha_x = 1/7\ \mathrm{ms}^{-1}$ which is taken to be equal to α_y for simplicity, and in matrix $A \equiv H_0 G'_y(Y_0) W_0 G'_x(X_0)$, G'_x and G'_y are diagonal matrices which are the derivatives of G_x and G_y respectively, (X_0, Y_0) is the equilibrium point of the system which depends on the input (I, I_c), X is the mitral cell oscillatory deviation from its equilibrium point X_0. The second term of the equation is the oscillator system dissipation originated in the dissipation of the cells which make up the oscillator system. The third term of the equation is the oscillators' strengths and couplings between them. Such an oscillator system has N oscillation solution modes, and the k^{th} mode is

$$X \approx X_k e^{-\alpha t \pm i\sqrt{\lambda_k}t}, \tag{3.4}$$

where X_k is an eigenvector of A with eigenvalue λ_k for $k = 1, 2, \ldots, N$. The k^{th} mode has oscillation frequency $\mathrm{Re}\sqrt{\lambda_k}$, and the oscillation amplitudes and phases of individual mitral cells are described by the components of X_k. If

$$\mathrm{Re}(-\alpha \pm i\sqrt{\lambda_k}) > 0. \tag{3.5}$$

The k^{th} mode becomes non-damping and the oscillation amplitudes grow in time. The observable oscillation output of the system would be the dominant non-damping mode. The non-linear effect will make the oscillation waveform non-sinusoidal.

In order that the criteria Eq. (3.5) be satisfied for some k, $|\lambda_k| > \alpha^2$ should be satisfied, suggesting that matrix A has large enough elements. Since $A = H_0 G'_y(Y_0) W_0 G'_x(X_0)$, both the gain $G'_x(X_0)$ and

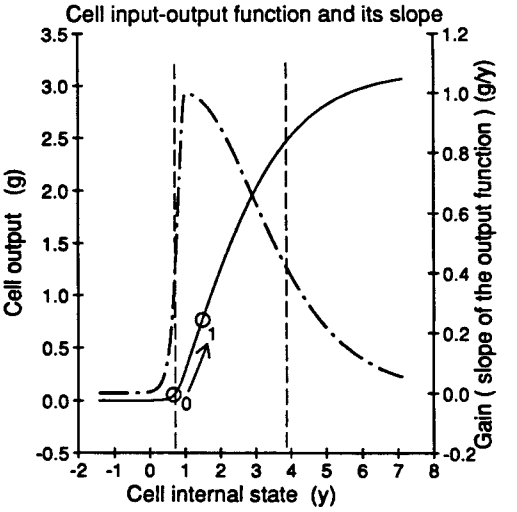

Fig. 3. This figure illustrates the cell input-output function G (G_x or G_y) with the solid curve and its slope G' with the dotted curve. For the X_0 or Y_0 value on or outside dashed lines, the cell internal states can be considered either before firing threshold or at saturation regions, the gain G' is too small for the possibility of non-damping oscillation modes. While for the X_0 and Y_0 values inside the dashed lines, the gain is larger and non-damping oscillation modes are possible in some circumstances. The circle indicated with "0" is the possible X_0 and Y_0 locations with no odor input $I_{\text{odor}} = 0$, and the circle "1" for possible X_0 and Y_0 locations during the inhale with odor inputs. The arrow indicates the direction in which the X_0 and Y_0 are raised by input odors

$G'_y(Y_0)$ of the input-output curves should be high enough for the existence of the non-damping oscillations. For sigmoid function (G_x, G_y), it follows that both X_0 and Y_0 should be high enough to have the high gain $(G'_x(X_0), G'_y(Y_0))$ (Fig. 3). When the central input I_c is fixed, (X_0, Y_0) is determined by receptor inputs I as

$$\begin{aligned} \mathrm{d}X_0 &\approx (\alpha^2 + HW)^{-1}(\alpha\,\mathrm{d}I + \mathrm{d}\dot{I}) \\ &\approx (\alpha^2 + HW)^{-1}\alpha\,\mathrm{d}I, \\ \mathrm{d}Y_0 &\approx (\alpha^2 + WH)^{-1}(W\,\mathrm{d}I - \alpha H^{-1}\mathrm{d}\dot{I}) \\ &\approx (\alpha^2 + WH)^{-1} W\,\mathrm{d}I, \end{aligned} \tag{3.6}$$

where $H \equiv H_0 G'_y(Y_0)$ and $W \equiv W_0 G'_x(X_0)$. When no odor input exists in the inhaled air, $I_{\text{odor}} = 0$, (X_0, Y_0) is too low for substantial non-damped oscillations (Fig. 3). Inputs $I_{\text{odor}} \neq 0$ during inhalation can raise the (X_0, Y_0) to higher gain $(G'_x(X_0), G'_y(Y_0))$. When the gain is high enough that the inequality (3.5) is satisfied for some k, the k^{th} oscillation mode becomes the bulbar output. This dependency of the bulbar output on the odor input ensures that the bulbar output carries the odor information and fulfills the pattern classification task. The particular mode which emerges during inhalation can be thought of as the decision state made for the input odor information. It corresponds to the

particular odor identity in a particular concentration range. The input will be ruled as irrelevant if no observable bulbar oscillation exists during a sniff (Freeman and Skarda 1985; Li and Hopfield 1989).

4 A Model of Central Control on Bulbar Response

In this model of the olfactory bulb, the mitral cell output has an oscillatory part determined by X in (3.3), and a baseline shift part determined by X_0 which is the oscillation center or the equilibrium point. The granule cell response also has a baseline shift state level Y_0 and an oscillatory part Y determined by (3.2), although this activity is invisible outside bulb. (The mitral cells are the only output neurons of the bulb.)

The oscillatory response X is determined by (X_0, Y_0) via matrix A, thus (X_0, Y_0) completely determines the bulbar output. By (3.6), the receptor input I determines the bulbar output provided that the central input I_c stay fixed. When the central input I_c is not fixed, it can control the bulbar output by shifting (X_0, Y_0). Calculations show that:

$$\begin{aligned} dX_0 &\approx (\alpha^2 + HW)^{-1}(\alpha dI + d\dot{I} - H d\dot{I}_c + \alpha W^{-1} d\dot{I}_c) \\ dY_0 &\approx (\alpha^2 + WH)^{-1}(W dI - \alpha H^{-1} d\dot{I} + \alpha dI_c + d\dot{I}_c). \end{aligned} \tag{4.1}$$

Let

$$I_c \equiv I_{c,\,\text{background}} + I_{c,\,\text{control}}, \tag{4.2}$$

where $I_{c,\,\text{background}}$ is the central background input which does not change during a sniff and controls the motivation level such as sleeping, resting, hunger states, while $I_{c,\,\text{control}}$ is the control signal which changes during a sniff. I_{odor} and $I_{c,\,\text{control}}$ determine the bulbar output activities during a sniff.

Suppose for a particular odor input I_{odor}, there is a central control signal $I_{c,\,\text{control}}$ which cancels the effect of I_{odor} on (X_0, Y_0), such that (X_0, Y_0) stays the same as if neither I_{odor} nor $I_{c,\,\text{control}}$ exist – cancelling, i.e.,

$$\begin{aligned} dX_0 &\approx (\alpha^2 + HW)^{-1}(\alpha dI_{\text{odor}} + d\dot{I}_{\text{odor}} \\ &\quad - H dI_{c,\,\text{control}} + \alpha W^{-1} d\dot{I}_{c,\,\text{control}}) = 0 \\ dY_0 &\approx (\alpha^2 + WH)^{-1}(W dI_{\text{odor}} \\ &\quad - \alpha H^{-1} d\dot{I}_{\text{odor}} + \alpha dI_{c,\,\text{control}} + d\dot{I}_{c,\,\text{control}}) = 0. \end{aligned} \tag{4.3}$$

Then not only the baseline bulbar response X_0, but also the oscillatory X by its dependency on (X_0, Y_0) in (3.3) stay the same as if no odor input exists. In this case, a complete self-adaptation to that odor input is achieved, and the control signal will be denoted as I_c^{cancel}.

When $(\Delta X_0, \Delta Y_0)$ depends linearly on $(I_{\text{odor}}, I_{c,\,\text{control}})$, a central control signal $I_c^{\text{enhance}} \equiv -\gamma I_c^{\text{cancel}}$ for $\gamma > 0$ will enhance rather than cancel the effect of I_{odor}, and thus enhance the bulbar output level or the sensitivity to that particular input odor. Since $H = H_0 G_y(Y_0)$ and $W = W_0 G_x(X_0)$, (4.1) is a non-linear equation. Such an enhancing signal is certain to work when (X_0, Y_0) is in a near linear range of the gain curves G_x and G_y with I_{odor}. Physiological experiments shows that when the oscillation signals are small, the bulbar system operates in a near linear range (Freeman 1979a) with odor input. When the near linear approximation is not valid, the enhancing signal can not simply be a negative constant times the cancelling signal.

An absolute self-adaptation signal I_c^{cancel} satisfying (4.3) for odor input I_{odor} can not be achieved generally. Since X_0 and Y_0 are N and M dimensional vectors respectively, (4.3) is a system of $N + M$ equations. This number of equations is too many for solving M unknown components of an M dimensional vector I_c^{cancel}. Therefore no cancelling signal I_c^{cancel} will satisfy (4.3) for a given odor I_{odor} generally.

Compromises are possible by modifying I_c^{cancel} (and thus I_c^{enhance}) such that less strong requirements for cancelling is satisfied. Since the mitral cells are the only output cells of the bulb, we only need to demand that the mitral cell activity induced by I_{odor} be cancelled, while the granule cell activity can be different from the no-odor input case. To have the baseline response X_0 raised by I_{odor} be cancelled (suppressed) by I_c^{cancel}, we need

$$\begin{aligned} dX_0 &\approx (\alpha^2 + HW)^{-1}(\alpha dI_{\text{odor}} + d\dot{I}_{\text{odor}} - H dI_c^{\text{cancel}} \\ &\quad + \alpha W^{-1} d\dot{I}_c^{\text{cancel}}) = 0. \end{aligned} \tag{4.4}$$

It is known from Sect. 3 that the necessary condition for oscillatory response is to have both X_0 and Y_0 be high enough. Therefore the above suppressed baseline response X_0 also makes non-damped oscillatory mode impossible, as if no odor input exists. An effectively complete self-adaptation is therefore fulfilled. Such an I_c^{cancel} however, cannot cancel the effect of I_{odor} on the baseline shift of the granule cells Y_0. A solution of (4.4) for I_c^{cancel} with M unknown variables will generally exist, since the number of equations N, which is number of the mitral cells, is much smaller than M, which is the number of the granule cells (Shephers 1979).

It is not easy to calculate the I_c^{cancel}, since (4.1) is non-linear [H and W depend on (X_0, Y_0)]. In our simulation, a simplification is used. If the inputs (I, I_c) change in a time scale much longer than $1/\alpha \approx 7$ ms, then (4.1) becomes (Li and Hopfield 1989)

$$\begin{aligned} dX_0 &\approx (\alpha^2 + HW)^{-1}(\alpha dI - H dI_c) \\ dY_0 &\approx (\alpha^2 + WH)^{-1}(W dI + \alpha dI_c). \end{aligned} \tag{4.5}$$

And (4.4) becomes

$$dX_0 \approx (\alpha^2 + HW)^{-1}(\alpha dI_{\text{odor}} - H dI_c^{\text{cancel}}) = 0. \tag{4.6}$$

This is true for I since a sniff cycle is about a few hundred milliseconds, and it is reasonable to assume that the central control I_c is also modulated in a time scale of a sniff cycle. By (4.6), $dI_c^{\text{cancel}} = H^{-1}\alpha dI_{\text{odor}}$, suggesting that I_c^{cancel} will change in about the same time scale as I_{odor}. Therefore the approximation is self-consistent. (Note that if mitral and granule cells are switched, and at the same time switch $-H$ and W, I and I_c, an equivalent system results. So I and I_c are analogous.)

Now if

$$I_c^{\text{enhance}} = -\gamma I_c^{\text{cancel}}, \tag{4.7}$$

instead of suppressing X_0 which is being raised by I_{odor}, I_c^{enhance} helps I_{odor} to raise X_0 in the same direction. To the mitral cells, it is almost as if the odor input is stronger in concentration than it actually is. If Y_0 is also raised to the extent as if a stronger input odor is inhaled, then the oscillatory bulbar output determined by (X_0, Y_0) will be enhanced as if a stronger input odor in inhaled. But on the contrary, Y_0 is being suppressed by the I_c^{enhance} while being raised by I_{odor}. By (4.5)–(4.7),

$$dY_0 \approx (\alpha^2 + WH)^{-1}(W dI_{\text{odor}} - \gamma\alpha^2 H^{-1} dI_{\text{odor}}). \tag{4.8}$$

The larger the I_c^{enhance} (or γ), the more is Y_0 suppressed.

Let us examine closely the role of Y_0 and how odor enhancement works. The (weak) odor input I_{odor} raises (X_0, Y_0) to higher gain $(G_x'(X_0), G_y'(Y_0))$ point. Let us denote this Y_0 as $Y_0^{\text{weaker-odor}}$ (which can be raised further to $Y_0^{\text{stronger-odor}} > Y_0^{\text{weaker-odor}}$ if a stronger odor is inhaled). The negative central control signal I_c^{enhance} lowers the central input $I_c = I_{c,\text{background}} + I_c^{\text{enhance}}$ to the granule cells, and thus lowers Y_0 to $Y_0^{\text{enhance}} < Y_0^{\text{weaker-odor}}$ (Fig. 4). This effectively reduces the granule inhibitory drive to the mitral cells and raises X_0, as if a stronger odor is inhaled for the mitral cells. But for granule cells, $Y_0^{\text{enhance}} < Y_0^{\text{stronger-odor}}$, so enhancing is *not* exactly equivalent to inhaling a stronger odor. Since granule cells affect bulbar oscillatory response by the gain $G_y'(Y_0)$, thus as long as Y_0^{enhance} and $Y_0^{\text{stronger-odor}}$ are in about the same linear range on the gain curve $G_y(Y_0)$, the mitral cell output will be insensitive to the exact Y_0. In such cases, X_0 will be the only important factor to determine bulbar output, and it will appear as if a stronger odor is inhaled because of the raised X_0. Y_0 without odor input is in a very non-linear range of $G_y(Y_0)$, and has a gain $G_y'(Y_0)$ too low for oscillatory bulbar response. Therefore two necessary conditions for olfactory enhancement are: *a)*: I_c^{enhance} to lower Y_0 and thus raise X_0 to higher level; *b)*: I_c^{enhance} should not be so strong as to make Y_0^{enhance} lower than Y_0 without odor inputs such that $G_y'(Y_0^{\text{enhance}})$ is too small. By (4.5) and (4.8), condition *b* means

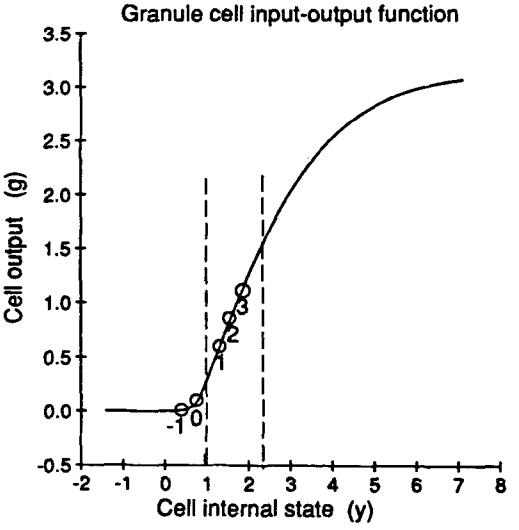

Fig. 4. This figure illustrates the possible positions of Y_0 indicated by circles on the input-output curve G_y under different circumstances. The circle numbered "0" is the Y_0 with no odor input $I_{\text{odor}} = 0$, "2" with inhaled odor without enhancing, "1" with the same odor input with enhancing, "3" with a stronger odor input, "-1" without odor input while with enhancing. The region inside the dashed lines is the linear region of G_y where the oscillation output is insensitive to the exact position of Y_0

$$\alpha|dI_c^{\text{enhance}}| < W dI_{\text{odor}} \quad \text{or} \quad \gamma\alpha^2 H^{-1} < W. \tag{4.9}$$

Since the scales of α, H, and W satisfy the relation (Li and Hopfield 1989) $\alpha^2 \ll HW = A$, Y_0 will be raised as the combined effect of I_{odor} and I_c^{enhance} as long as γ is not too much larger than unity. In a previous paper (Li and Hopfield 1989), it was argued that G_y (for the granule cells) has a relatively long linear range. Thus, with a not too strong enhancing signal, an enhanced baseline shift bulbar output $G_x(X_0)$ will enhance the oscillatory part of the output as well.

An important consequence of this argument is that no odor will be detected (no oscillation) if no odor exists *even if sensitivity enhancement* is going on for a particular odor. When $I_{\text{odor}} = 0$, the condition *b* mentioned above or inequality (4.9) is violated (Fig. 4), and non-damping oscillation bulbar output becomes impossible, although the baseline shift output determined by X_0 is raised by the enhancing signal (Fig. 7). Since it appears that the oscillation pattern output carries the essential part of the odor information (Freeman and Skarda 1985; Li and Hopfield 1989), a higher baseline output without oscillation means no odor information inputs to the olfactory cortex.

The central input to the bulb during enhancement is $I_c \equiv I_{c,\text{background}} + I_c^{\text{enhance}}$, since I_c^{enhance} is negative, enhancing corresponds to lowering the central input from the background level. For biological synapses of a definite sign (excitatory), $I_c \geqq 0$ or $|I_c^{\text{enhance}}|$

$\leqq I_{c,\text{background}}$ should always be satisfied. This implies that I_c^{enhance} amplitude is restricted below a maximum value. For a not too weak odor input, a small I_c^{enhance} is enough to enhance the output to be observable. While for a too weak an odor input, inequality (4.9) implies that too strong an I_c^{enhance} would not help the enhancement. Thus in most cases for the purpose of enhancement, only $|I_c^{\text{enhance}}| \leqq I_{c,\text{background}}$ is needed.

Cross-adaptation and cross-enhancement automatically follows by the argument above. For odor a, denote $I_c^{\text{cancel}-a}$ and $I_c^{\text{enhance}-a}$ as the cancelling and enhancing central signal respectively for its receptor input $I_{\text{odor}-a}$. The cancelling signal $I_c^{\text{cancel}-a}$ for odor a can not cancel quite completely odor input $I_{\text{odor}-b}$ for odor $b \neq a$. However, $I_c^{\text{cancel}-a}$ will impair the bulbar response for $I_{\text{odor}-b}$ since $I_c^{\text{cancel}-a}$ does actually suppress the mitral baseline X_0 (4.5), although not quite as if a weaker odor b is inhaled. Similarly, an enhancing signal $I_c^{\text{enhance}-a}$ for odor a can only distort the bulbar response to odor input $I_{\text{odor}-b}$. Even though $I_c^{\text{enhance}-a}$ raises X_0, it does not raise it in the same direction as if a stronger input of odor b is inhaled. The bulbar output will be a information mixing or distortion of odor a and b.

5 Simulations

Computer simulation is done to verify the olfactory adaptation and enhancement in the olfactory bulb. The simulated model with all its parameters is the same as the one in the previous paper (Li and Hopfield 1989) where it is described in detail. 10 mitral and 10 granule cells are used in the model. The equation

$$dX_0 \approx (\alpha^2 + HW)^{-1}(\alpha dI_{\text{odor}} - H dI_c^{\text{cancel}}) = 0$$

solves for the cancelling signal I_c^{cancel} for odor input I_{odor}. It follows that:

$$dI_c^{\text{cancel}} \approx H^{-1}\alpha dI_{\text{odor}} = (H_0 G_y'(Y_0))^{-1}\alpha dI_{\text{odor}}. \tag{5.1}$$

This is very difficult to solve since H depends on Y_0 which changes with time as

$$dY_0 \approx (\alpha^2 + WH)^{-1}(W dI_{\text{odor}} + \alpha dI_c^{\text{cancel}}). \tag{5.2}$$

Further approximations are used in the simulation to calculate I_c^{cancel}. First neglect the change of Y_0 (or H) with time and take

$$\begin{aligned} H(t) &= H_0 G_y'(Y_0(t)) \approx H(t=0) \\ &= H_0 G_y'(Y_0(t=0)) = \text{const}, \end{aligned} \tag{5.3}$$

where $Y_0(t=0)$ and $H(t=0)$ are respectively Y_0 and H at the beginning of the inhale $t=0$ when $I_{\text{odor}} = I_c^{\text{cancel}} = 0$. Thus

$$I_c^{\text{cancel}}(t) \approx H(t=0)^{-1}\alpha I_{\text{odor}}(t) \tag{5.4}$$

But such an approximation only works well when I_{odor} is small. A second stage of approximation is to take

$$I_c^{\text{cancel}} \approx \beta H(t=0)^{-1}\alpha I_{\text{odor}} \tag{5.5}$$

where β is a constant which is tuned in the simulation until a best cancellation is achieved. Here the better cancellation means that not only the bulbar output $G_x(X)$, but also the oscillation equation operation point (Li and Hopfield 1989) X_0 is closer to $G_x(X)^{\text{null}}$ and X_0^{null} respectively of the no odor input case. Consequently, not only the bulbar output after cancellation resembles that of the no-odor case, but also an inhalation of a new odor input mixed with the pre-existing odor induces a response closer to the response to the new odor alone. Quantitatively, the quantity $c(G_x(X) - G_x(X)^{\text{null}})^2 + (1-c)(X_0 - X_0^{\text{null}})^2$ (c is a constant satisfying $0 < c < 1$) integrated over the sniff cycle should be minimized for better cancellation. $\beta = 0.452$ is used for a sniff cycle of 370 ms in which the first 180 ms is inhalation.

With such an approximated cancelling signal, the enhancing signal is

$$I_c^{\text{enhance}} \approx -\gamma I_c^{\text{cancel}} \qquad \gamma > 0. \tag{5.6}$$

The value of γ used in most of the simulation is 0.5. Other values can be used to make the olfactory enhancing signal stronger or weaker. This ad hoc procedure generates an adequate cancellation and enhancement, but not as good a signal as could in principle be done. In order to see the effect of cancelling and enhancing, some measure is needed to see the difference between the two bulbar response patterns in a sniff cycle. Define (Li and Hopfield 1989).

O_{mean}: a real vector describing the mean baseline shift bulbar output of each mitral cell averaged over the sniff cycle.

O_{osci}: a complex vector describing the oscillation amplitudes and phases of mitral cell outputs averaged over the sniff cycle.

$\bar{O}_{\text{mean}}$ and $\bar{O}_{\text{osci}}$ are positive numbers describing the root-mean-square of the O_{mean} and O_{osci} respectively averaged over all the mitral cells (or the components of O_{mean} and O_{osci} respectively). Both of them reflect the bulbar response levels. Then for two bulbar output patterns a and b indicated by super-indices, define:

$$\begin{aligned} d_1(a,b) &= 1 - \frac{\langle O^a_{\text{mean}} O^b_{\text{mean}} \rangle}{|O^a_{\text{mean}}|\,|O^b_{\text{mean}}|} \\ d_2(a,b) &= 1 - \frac{|\langle O^a_{\text{osci}} O^b_{\text{osci}} \rangle|}{|O^a_{\text{osci}}|\,|O^b_{\text{osci}}|} \\ d_3(a,b) &= \frac{\bar{O}^a_{\text{mean}} - \bar{O}^b_{\text{mean}}}{\bar{O}^a_{\text{mean}} + \bar{O}^b_{\text{mean}}} \\ d_4(a,b) &= \frac{\bar{O}^a_{\text{osci}} - \bar{O}^b_{\text{osci}}}{\bar{O}^a_{\text{osci}} + \bar{O}^b_{\text{osci}}}, \end{aligned} \tag{5.7}$$

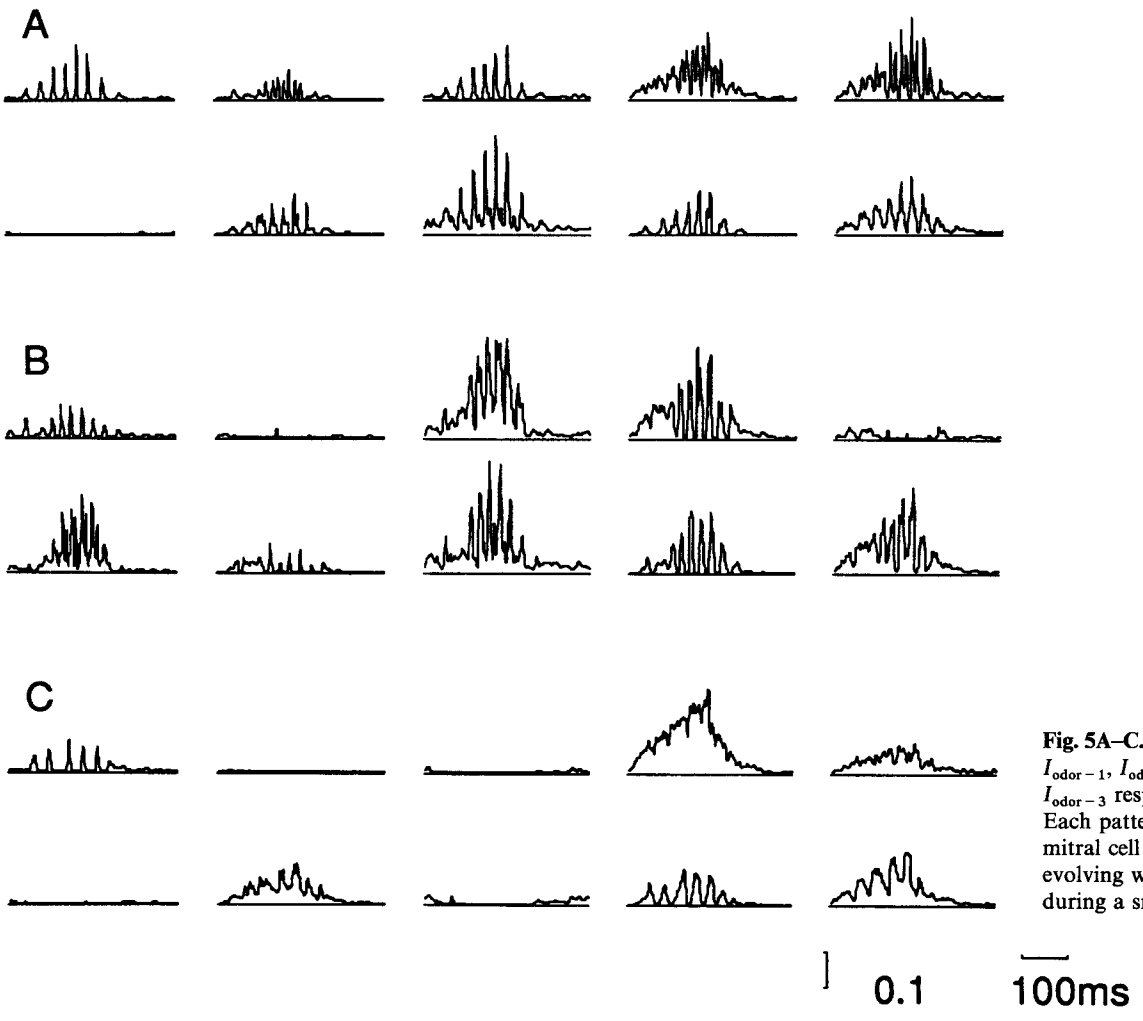

Fig. 5A–C. Responses to I_{odor-1}, I_{odor-2}, and I_{odor-3} respectively. Each pattern shows 10 mitral cell outputs evolving with time during a sniff cycle

Table 1. Differences between responses to different odor inputs and between responses to same odor inputs with different system noises

	$i=$	$j=$	$d_1(a,b)$	$d_2(a,b)$	$d_3(a,b)$	$d_4(a,b)$
a, b: responses to same odor inputs but different system noises	1	1	0.001	0.068	0.002	−0.016
	2	2	0.001	0.008	−0.001	0.010
	3	3	0.000	0.092	−0.012	0.098
a: response to I_{odor-i}	1	2	0.253	0.243	−0.210	−0.112
b: response to I_{odor-j}	1	3	0.226	0.556	−0.180	0.321
	2	3	0.486	0.474	0.031	0.419

where $\langle UV \rangle$ means the dot product of vectors U and V, while $|U|$ is the length or absolute value of U. d_1 and d_2 give the response pattern waveform differences, while d_3 and d_4 give the response level differences. $d_1, d_2, |d_3|, |d_4| \ll 1$ implies the similarity between two response patterns. $d_3(a,b)$, $d_4(a,b) > 0$ implies response level in a is higher than that in b. With three different odor inputs I_{odor-1}, I_{odor-2}, and I_{odor-3} of three presumably different odor types, Table 1 gives the differences measured between them, compared with differences measured between two patterns with the same I_{odor} input but different system noises. These examples show that these three odor inputs are easily distinguishable (Fig. 5) while same odor inputs with different system noises are classified as same odor outputs. The three odor vectors which are used in

Table 2. Difference between adapted and nonadapted response

	Odor	$d_1(a,b)$	$d_2(a,b)$	$d_3(a,b)$	$d_4(a,b)$
a: Non-adapted response	1	0.003	0.039	0.271	0.399
b: Half-adapted response	2	0.014	0.041	0.274	0.471
	3	0.012	0.078	0.309	0.313
a: Non-adapted response	1	0.144	0.803	0.690	0.728
b: Fully-adapted response	2	0.166	0.736	0.743	0.770
	3	0.642	0.788	0.774	0.589

simulations have P_{odor} (3.1) respectively

$$P_{\text{odor}-1}=1/70\{0.3,0.3,0.3,0.3,0.3,0.3,0.3,0.3,0.3,0.3\}$$

$$P_{\text{odor}-2}=1/70\{0.6,0.5,0.5,0.5,0.3,0.6,0.4,0.5,0.5,0.5\}$$

$$P_{\text{odor}-3}=4/700\{0.7,0.8,0.5,1.2,0.7,1.2,0.8,0.7,0.8,0.8\}. \tag{5.8}$$

These three odor input types will be used in the simulations for olfactory adaptation and enhancement.

Simulations of self-adaptation (self-cancelling) show that (referred to as fully adapted response in Table 2) $I_c^{\text{cancel}-i}\equiv\beta H(t=0)^{-1}\alpha I_{\text{odor}-i}$ diminishes quite well the bulbar response to the odor $I_{\text{odor}-i}$ for $i=1,2,3$. Simulations also show that after the adaptation to an odor input ($I_{\text{odor}}=0.5I_{\text{odor}-i}$), doubling the strength of the original odor input (i.e., I_{odor} becomes $I_{\text{odor}-i}$) while keeping the cancelling signal the same induces the bulbar response which, although not as strong as it would be without adaptation, is similar to the original response without adaptation. (These simulation are referred to as half-adapted response in Table 2.) This implies that a stronger input of the pre-existing and adapted odor type will still be detected by the bulb although it would smell less strong. Figure 6 shows an example of self-adaptation, and Table 2 gives the measured differences between the adapted and non-adapted responses to odors. Notice that $d_3, d_4\approx 1$ between the original response and self-adapted response means a complete self-adaptation is achieved. d_3 and d_4 between the simulated original and fully adapted responses are $\approx 0.6-0.8$, this is partly because the granule cells are raised to highly responsive internal state Y_0 which enhances the system noise and raises up the $\bar{O}_{\text{osci}}$ and $\bar{O}_{\text{mean}}$ levels. Another reason is possibly because the cancelling signal used is an approximation. The fully adapted response waveform, which is mostly amplified system noise, is very different from that of the original response.

Simulations also show that the model bulb can remain sensitive to new odor inputs $I_{\text{odor}-j}$ after being completely self-adapted to the pre-existing odor $I_{\text{odor}-i}$ for $i\neq j$. Assume the total receptor input to the bulb is a linear sum of the odor components in a mixture:

$$I_{\text{odor}}=I_{\text{odor}-i}+I_{\text{odor}-j}. \tag{5.9}$$

Since the bulb is adapted to $I_{\text{odor}-i}$, the cancelling signal $I_c^{\text{cancel}-i}$ is sent to the bulb from the higher centers. Simulations show that both the response waveform and the response level in this situation are quite similar to the response to only $I_{\text{odor}-j}$ without adaptation (Fig. 6, Table 3).

In the simulation for olfactory enhancement, $I_c^{\text{enhance}-i}=-\gamma I_c^{\text{cancel}-i}$ is taken with $\gamma=0.5$ for $i=1,2,3$. Figure 7 compares the bulbar response to an odor example of half the input strength, i.e., $I_{\text{odor}}=0.5I_{\text{odor}-i}$, with and without enhancing. Enhancing raises the response to half-strength-input to about the level of original response, while the response waveform stay similar to the original response (Table 4). Similar simulations can be done with a even weaker odor input or with different strength enhancing signals (different γ values). Since the quality of the enhancing relies on the linearity of the granule cells, the weaker the enhancing signal, the more likely the Y_0 value stays in the same linear region, and less distortion in the enhanced response, although a weaker

Table 3. Differences between the original response to an odor and the response to this odor after fully adapted to another odor
Response *a*: the original response to $I_{\text{odor}-i}$ for all i.
Response *b*: the response to $I_{\text{odor}}=I_{\text{odor}-i}+I_{\text{odor}-j}$ with cancelling signal $I_c^{\text{cancel}-j}$ for $j\neq i$

i=	j=	$d_1(a,b)$	$d_2(a,b)$	$d_3(a,b)$	$d_4(a,b)$
1	2	0.025	0.039	0.010	0.070
	3	0.016	0.013	0.008	0.065
2	1	0.030	0.038	−0.029	0.087
	3	0.022	0.009	−0.023	0.027
3	1	0.006	0.029	0.005	0.151
	2	0.009	0.037	0.021	−0.002

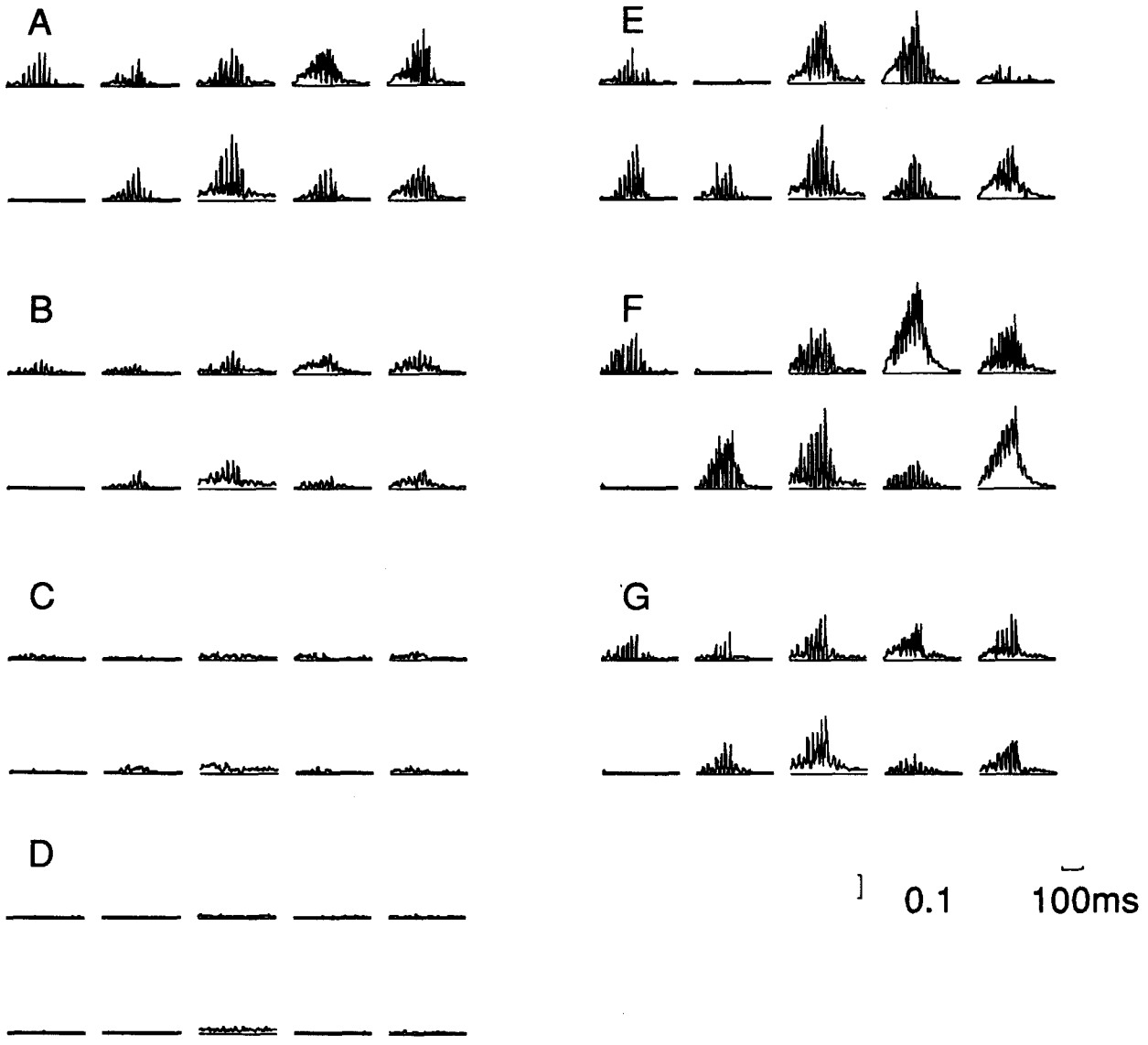

Fig. 6A–G. Demonstration of olfactory adaptation. **A, E** Original responses to I_{odor-1} and I_{odor-2} respectively. **B, C** Half-adapted and fully-adapted response to I_{odor-1}. **D** Response to no odor input without adaptation. **F** Response to $I_{odor-1}+I_{odor-2}$ without adaptation. **G** Response to $I_{odor-1}+I_{odor-2}$ with full-adaptation to I_{odor-2}

Table 4. Differences between the enhanced and non-enhanced responses

	Odor number	$d_1(a,b)$	$d_2(a,b)$	$d_3(a,b)$	$d_4(a,b)$
a: Non-enhanced original response	1	0.001	0.083	0.272	0.423
	2	0.013	0.048	0.286	0.420
b: Non-enhanced response to half-strength input	3	0.001	0.045	0.272	0.399
a: Non-enhanced original response	1	0.003	0.014	0.010	0.081
	2	0.002	0.007	−0.001	−0.009
b: Enhanced response to half-strength input	3	0.005	0.023	0.006	0.165

Table 5. Differences between the original responses and the cross-adapted responses
Cross-adapted response is response to odor input I_{odor-i} with cancelling signal $0.5I_c^{cancel-j}$

	$i=$	$j=$	$d_1(a,b)$	$d_2(a,b)$	$d_3(a,b)$	$d_4(a,b)$
a: Original response to I_{odor-i}	1	2	0.246	0.595	0.320	0.646
		3	0.272	0.266	0.118	0.421
b: Cross-adapted response to I_{odor-i}	2	1	0.072	0.131	0.095	0.188
		3	0.106	0.115	0.040	0.575
	3	1	0.015	0.755	0.189	0.362
		2	0.038	0.266	0.296	0.490

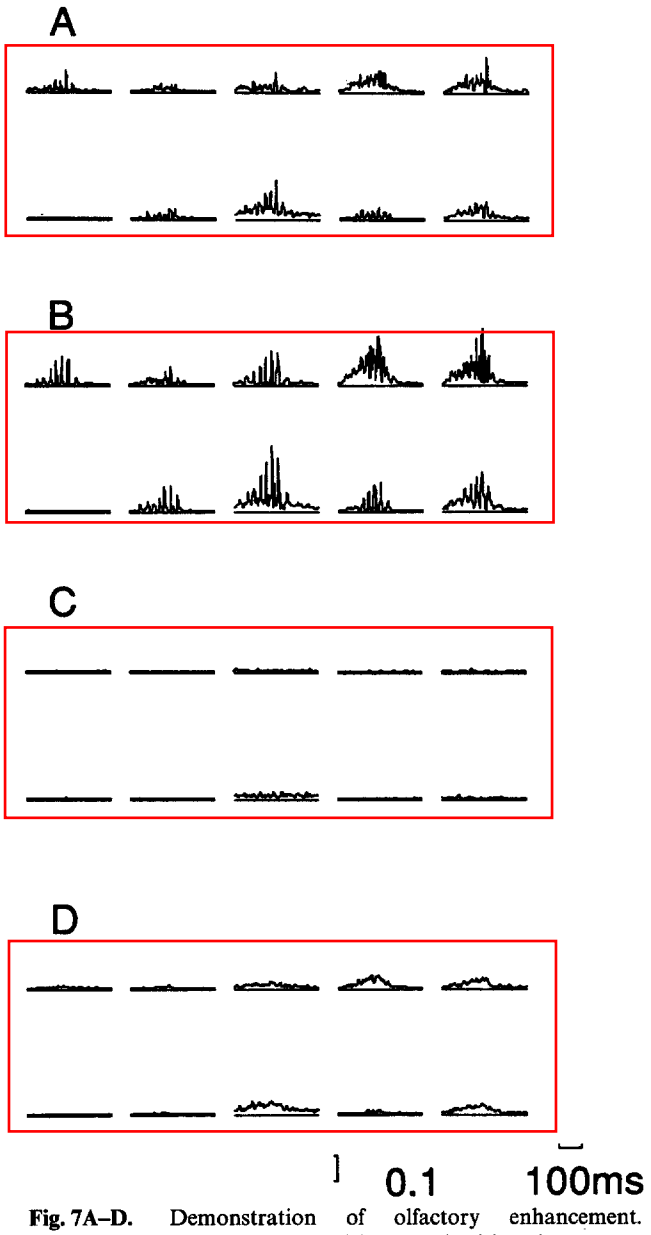

Fig. 7A–D. Demonstration of olfactory enhancement. **A, B** Responses to $0.5I_{odor-1}$ without and with enhancement respectively. **C, D** Responses to no odor input without and with enhancement for I_{odor-1} respectively

enhancing signal results in less response level enhancement. Caution should be taken to always have $I_c \geqq 0$. Violating the inequality (4.9) or having too strong an enhancing signal implies no oscillatory response.

Cross-adaptation or cross-enhancement can be simulated as well. One of these types of simulated examples are those with odor input I_{odor-i} and the cancelling $\delta I_c^{cancel-j}$ for cross-adaptation, and those with odor input $0.5I_{odor-i}$ and enhancing signal $-\delta I_c^{cancel-j}$ for cross-enhancement for $i \neq j$. δ is a positive number whose value is taken as 0.5. Other strengths of the input odors and the cancelling or enhancing signals can be used for simulations as well. Different degrees of information mixing and distortion are seen in both the cross-adaptation and cross-enhancement, and they depend on the odor pair, i.e., odor i can be cross-adapted or cross-enhanced by odor j to a different extent as that of vice versa. For instance, response to $0.5I_{odor-1}$ with enhancing for I_{odor-2} is quite simular to the original response to I_{odor-1}, while the response to $0.5I_{odor-2}$ is more distorted by enhancing for I_{odor-1} resembles the original response to I_{odor-1}, even though the strength of I_{odor-1} is weaker than that of I_{odor-2}. Table 5, 6 and Fig. 8 show the differences between the cross-adapted or cross-enhanced responses and the original responses.

6 Conclusion and Discussion

Sensitivity enhancement or suppression by central control is postulated for olfactory bulb. For olfactory adaptation, the model explains the observed psychophysical phenomena of both the self-adaptation and cross-adaptation. The model bulb can remain sensitive to new odor inputs, including a stronger input of the pre-existing odor type, after being adapted to the pre-existing odor inputs. Distorted and reduced responses are seen for odor inputs replacing the pre-existing and adapted odor inputs before recovery (cross-adaptation). For olfactory enhancement, the model bulb produces response level enhancement when sniffing a

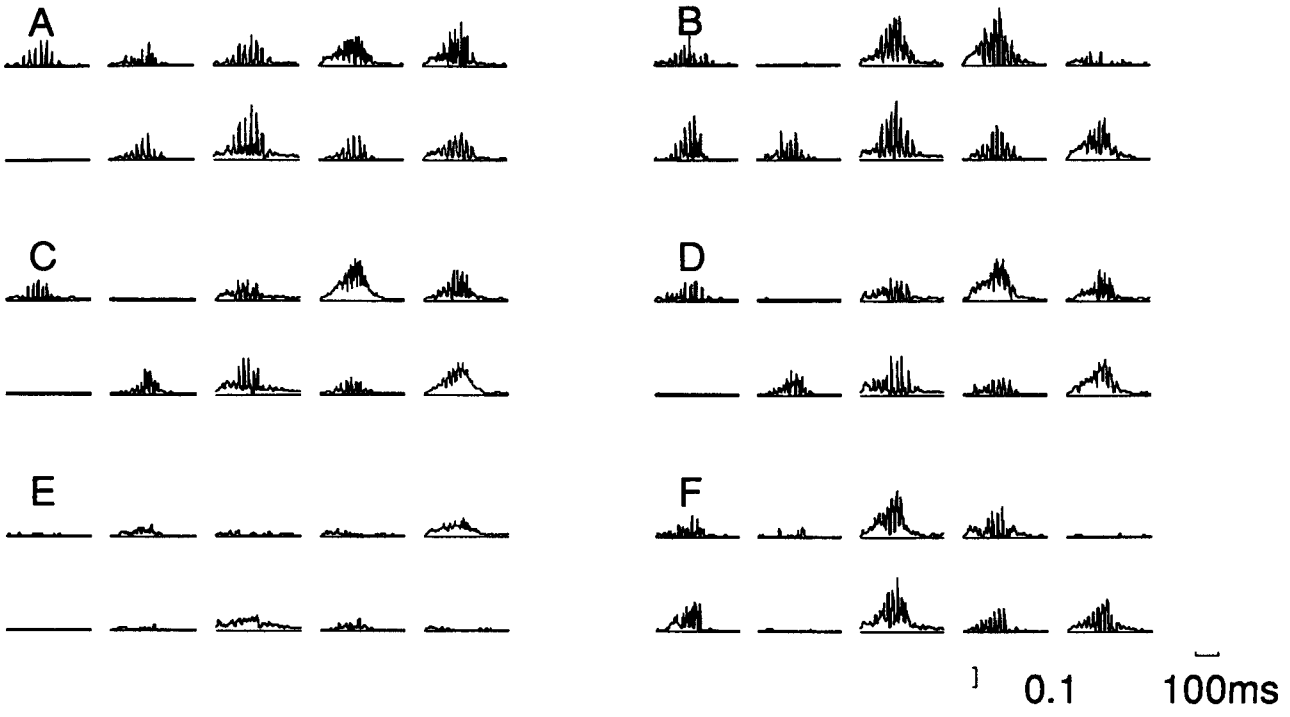

Fig. 8A–F. Demonstration of cross-adaptation and cross-enhancement. **A, B** Original responses to I_{odor-1} and I_{odor-2} respectively. **C** Response to $0.5I_{odor-1}$ with enhancement for I_{odor-2}. **D** Response to $0.5I_{odor-2}$ with enhancement for I_{odor-1}. **E** Response to I_{odor-1} with half-adaptation to I_{odor-2}. **F** Response to I_{odor-2} with half-adaptation to I_{odor-1}

Table 6. Differences between the original and cross-enhanced responses
Cross-enhanced response is response to $0.5I_{odor-i}$ with enhancing signal $0.5I_c^{enhance-j}$ for $i \neq j$

	i=	j=	$d_1(a,b)$	$d_2(a,b)$	$d_3(a,b)$	$d_4(a,b)$
a: Original response to I_{odor-i}	1	2	0.050	0.046	−0.102	0.184
		3	0.177	0.316	−0.091	0.560
b: Cross-enhanced response to $0.5I_{odor-i}$	2	1	0.121	0.126	0.079	0.239
		3	0.291	0.356	−0.005	0.330
	3	1	0.008	0.036	0.076	0.107
		2	0.012	0.042	−0.019	0.100
a: Original response to I_{odor-j}	1	2	0.134	0.175	−0.089	−0.290
		3	0.017	0.250	−0.088	−0.321
b: Cross-enhanced response to $0.5I_{odor-i}$	2	1	0.065	0.095	0.112	−0.131
		3	0.019	0.061	0.018	0.070
	3	1	0.193	0.559	0.103	−0.386
		2	0.310	0.403	0.006	−0.473

weaker odor (self-enhancement). It does not respond oscillatorily (or sensibly) to no odor inputs even when an olfactory enhancement signal is present. Different degrees of odor information mixing and distortion can be seen if the bulb has its sensitivity enhanced for one odor while another odor in inhaled (cross-enhancement). These will be analogous to the psychophysically observed cross-adaptation. Physiological experiments demonstrate that when the central inputs to the bulb is blocked, the neural oscillatory activity induced by breathing is increased substantially (Gray and Skinner 1988). Our model of olfactory enhancement agrees with this experimental result by showing that reducing the excitation central inputs to the granule cells

enhances the bulbar (oscillatory) response to the odor inputs. To verify the model experimentally, the first stage is to check whether the central inputs to the granule cells are increased (decreased) in a distributed fashion during adaptation (enhancement).

The cancelling and enhancing signals in our computer simulation is calculated with several stages of approximations: the slow input approximation described in Sect. 4, and the linear approximation in Sect. 5. The simulated results are quite satisfactory with these approximated signals. The linear approximation works better with smaller signals. It is believed that if the cancelling and enhancing signal are calculated with less approximations, the simulated results would be better.

A necessary condition for the higher olfactory centers to send adapting (cancelling) or enhancing signal for a particular odor is that they have enough information about that odor to send the appropriate signal. This condition is easily fulfilled in the adaptation process since the adaptation is triggered after the odor is detected, and the higher centers will then have a memory of the recent input odor. To enhance the sensitivity to a particular odor, (which may or may not be present), the higher centers must already know the odor either from long term memory of experience or genetically inherited information.

Acknowledgement. This research was supported by ONR contract N00014-87-K-0377. The author gratefully acknowledges the assistance of Prof. J. J. Hopfield with helpful suggestions and discussions and careful review of the manuscript.

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Received: August 1, 1989
Accepted in revised form: October 2, 1989

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