Olfactory computation and object perception

(neural network/learning/sensory systems)

J. J. HOPFIELD

Divisions of Chemistry and Biology, California Institute of Technology, Pasadena, CA 91125

ABSTRACT   Animals that are primarily dependent on olfaction must obtain a description of the spatial location and the individual odor quality of environmental odor sources through olfaction alone. The variable nature of turbulent air flow makes such a remote sensing problem solvable if the animal can make use of the information conveyed by the fluctuation with time of the mixture of odor sources. Behavioral evidence suggests that such analysis takes place. An adaptive network can solve the essential problem, isolating the quality and intensity of the components within a mixture of several individual unknown odor sources. The network structure is an idealization of olfactory bulb circuitry. The dynamics of synapse change is essential to the computation. The synaptic variables themselves contain information needed by higher processing centers. The use of the same axons to convey intensity information and quality information requires time-coding of information. Covariation defines an individual odor source (object), and this may have a parallel in vision.

Humans rely chiefly on vision for their description of the world around them. As a result, most of the olfactory psychophysics and electrophysiology literature is chiefly concerned with the question of identifying or analyzing a single odor presented to the nose. Such studies ignore deeper questions of the function of olfaction in highly olfactory animals, which is to define and locate individual odor sources in a complex environment.

This computational problem is also posed by vision. The visual system must transform detailed retinal images into a much smaller amount of significant information describing physical objects and their locations. In a natural environment, vision allows us to parse our environment into objects even when the objects are unfamiliar and many objects are simultaneously present.

Consider an animal that has only an olfactory sense. To what extent can it solve the remote sensing problem, understanding the nature and location of distant objects, particularly when the objects are not familiar? In the visual system, analysis of the computational problem provided by the data and the task led to an understanding of what the "early" visual system must compute (1). I describe here a similar problem for the early processing in the olfactory system.

A description of a natural olfactory environment illustrates the one important problem the earliest processing of an olfactory system must solve if the system is to be able to define and localize unknown odor sources in a complex odor environment. Behavioral evidence suggests that animals can solve this problem. This problem has a mathematical solution, which can be implemented by an elementary learning network. Dynamic changes of the synaptic strengths are essential to this solution. Part of the information needed by higher processing areas is explicitly contained in the connection strengths themselves. The last two sections present

simulations of these ideas and discuss their relation to olfactory physiology and psychophysics.

The Olfactory Environment and Task

In most olfactory environments, the simple diffusion of odorant molecules is a negligible means of dispersing odorants. Odors of distant objects are brought to the nose by wind. Odorant molecules leaving the object follow the path of the air packet to which they are added. This packet already contains odorant molecules from other objects further upwind. The packet will move with the local wind, mixing slowly with other nearby packets containing odors from other objects, due to microturbulence in the air. Local winds fluctuate markedly in both magnitude and direction. As a result, the odor plume has a complex spatial structure (2) and is increasingly mixed with odors from other parts of the environment as time increases. Thus, the stimulus at the nose due to distant objects contains mixtures of odors from many sources, whose relative contributions are constantly changing. Physical studies with a single odor source and detector in a natural environment verify these ideas (3). (Because velocities and time scales of turbulence are very different for water and air, aquatic environments are not necessarily similar to atmospheric environments.)

Highly olfactory animals need to be able to understand the location and odor properties of the various sources or "odor objects" in their space in order to hunt for food or flee from danger. When a single odor source is present, the problem is simple. The perceived odor quality (i.e., the relative strengths of different components of an odor) is a fixed property of this sole source. The strength of the odor will fluctuate with wind direction. For an object that is near, the odor will be strong only for a narrow range of wind directions, and when the wind shifts from that direction the odor will quickly grow weak. An object that is further away has an odor plume that is more contorted and on average is also broader and weaker. Its odor strength will correlate less well with the local wind direction. The relative time scale of fluctuation also contains information about distance. Thus, when a single odor source is present approximately upwind, information about the direction and even the approximate distance of the object is available to a stationary olfactory animal. The essential computation is an analysis of the fluctuations of the odor intensity with time and the relation of these to fluctuations in the local wind direction.

The problem of one odor object is trivial compared to the real problem of many unknown objects. Except when sniffing an object at the nose, an animal is always in an environment of mixed and changing odor patterns. If each odor object were to stimulate a different set of receptor cells in the sensory epithelium, then the problem of separating objects would be simple. However, physiological studies of the vertebrate olfactory system generally indicate broadly tuned receptor cells and the excitation of a large number of cells by a given odor, so odors of different objects are believed to be discriminated on the basis of the patterns of excitation, as

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recently reviewed by Kauer (4). Similar conclusions are reached through behavioral studies (5, 6). Broad tuning makes the problem of separating unknown objects in natural environments appear very difficult.

Suppose that it is possible to analyze the fluctuations of the instantaneous stimulation pattern in such a way that the contributions of different odor sources to the mixture can be separated. By next analyzing the fluctuations of each odor object intensity in conjunction with fluctuations in the local wind direction, the animal will generate an excellent representation of the location and isolated odor of each odor source in its vicinity. This paper investigates the hypothesis that the function of the earliest part of olfactory processing in highly olfactory animals is to accomplish this first separation task—namely, to analyze the fluctuations of multisource environments into individual odors.

Behavioral Evidence for Fluctuation Analysis

Many animals are able to search for a known odor such as a favorite food. In concept, the animal computes a projection of the ambient odor input against the known template and thus measures the intensity of the target odor present. If the environment has a substantial odor, whose excitation pattern strongly overlaps the pattern of the search template (but with different relative amplitudes), a simple template match to look for a weak target odor becomes impossible. The environment itself will always appear to have an appreciable component of the target odor. A fixed environment could be removed by subtractive adaptation, but realistic environments reflect constantly changing strengths and mixtures of odors from a variety of sources. That an animal with a broadly tuned set of sensory cells can locate a weak known odor source indicates that an analysis of fluctuations is being carried out to provide information not available from elementary processing.

Experiments in *Limax maximus* have demonstrated the importance of fluctuations for odor learning. Hopfield and Gelperin (7) carried out learning experiments on mixtures of two food odors A and B. Slugs were aversively conditioned while on a mesh 1 cm above a piece of filter paper painted with a solution containing a 1:1 mixture of odorants A and B. When later tested, the animals were found to be aversively conditioned to the 1:1 mixture AB, but they had the same nonaversive behavior as control animals to the individual odors A and B. These experiments indicate that the mixed odor object AB is perceived as an odorant distinct from A or B. When different animals were trained with the same protocol, except that the initial conditioning was done with alternating stripes of A and B 0.9 cm apart, the slugs exhibited aversive behavior to A alone, B alone, and the mixture AB.

The distance from the odor source to the slugs was always greater than the separation between the stripes. The diffusional mixing time for stripe sources of this separation is ≈1 sec. Thus, the odor available to the animals must always be somewhat mixed and fluctuating due to thermally induced air flows within the closed chamber. Since conditioning with odor stripes results in aversive response to the individual odors A and B (as well as to the mixture AB), the existence of the individual odors A and B was presumably deduced from odor fluctuations. The crucial difference between the two experiments was the presence of fluctuations in the relative amount of A and B presented by the stripes but not by the 1:1 AB mixture, which allowed the animals to come to different conclusions about the odor objects present.

Do Fluctuations Contain Enough Information?

The following analysis shows that while fluctuations do not contain enough information to solve the source separation

problem in the most general case, in the usual case they do contain enough information. A model of the olfactory world and its processing can be described as follows. There are N different types of olfactory processing cells receiving inputs from sensory cells. Any particular odor k can be described by a vector S_k whose components S_{kn} describe the strength with which that odor excites the olfactory processing cells of type n when odor k is present at a standard concentration. When odor k alone is present, the input to a cell of type n is then given by

$$I_n(t) = a_k(t)S_{kn} \qquad n = 1, 2, \ldots, N \qquad [1]$$

where $a_k(t)$ describes the time-dependent concentration of odor k at the sensory epithelium. The details of olfactory receptors and connections from sensory cells to the processing cells are implicitly contained in the matrix S_{kn}. The function $a_k(t)$ does not depend on n. A single odor source will, by definition, have all sources of odorant molecules colocated in space, so all the components of the odor will have the same time dependence $a_k(t)$ (or if it is extended in space, they will have the same odor quality at each point).

When multiple odor objects are present, the time-dependent input to the sensory cells will be the sum of Eq. 1 over K different odors k, l, m . . . . The nervous system measures the various $I_n(t)$. An ideal olfactory system would be able to determine both the vectors S_k and the intensity time dependences $a_k(t)$ for all the odor objects sampled by the fluctuating wind pattern. To what extent is it possible to determine these quantities from the measurements available?

Consider the case of two odors and two processing cells. The scale of the odor vectors is arbitrary, as is the scale of the functions $a_k(t)$. Each odor vector S_1 and S_2 has two components, one of which can in each case be picked as "1" to define the arbitrary scale. The two odor vectors can therefore be taken to be

$$S_1 = \begin{pmatrix} 1 \\ a \end{pmatrix} \qquad S_2 = \begin{pmatrix} b \\ 1 \end{pmatrix} \qquad [2]$$

Odor 1 thus excites processing cell 2 with strength a relative to its excitation of cell 1. The components a and b will be assumed to be positive, although this is not essential. From Eq. 1

$$I_1(t) = a_1(t) + a_2(t)b \qquad I_2(t) = a_1(t)a + a_2(t). \qquad [3]$$

At any single time t, the measurement of $I(t)$ yields two equations in four unknowns—namely, $a_1(t)$, $a_2(t)$, a, and b. They cannot be determined from two equations. Adding more sampling times does not help, for each new sampling time t' introduces two more equations and two more unknowns, $a_1(t')$ and $a_2(t')$. The problem is unsolvable in the general case.

There are, fortunately, a variety of circumstances under which the functions $a_k(t)$ are less than completely general and which lead to an ability to solve for all the desired information. The simplest of these is the case in which the fluctuations with time of one odor are not correlated with the fluctuations of the other odor. Such a description could be appropriate when the turbulence and wind fluctuations bringing one odor to the nose are independent of those that bring another odor via a rather different path. Under these circumstances, useful expectation values over these fluctuations can be computed by time averaging, denoted by ⟨ ⟩. (Neurobiology can evaluate such expectation values through learning and adaptation procedures.) The first moments obey

$$\langle I_1 \rangle = \langle a_1 \rangle + b\langle a_2 \rangle \qquad \langle I_2 \rangle = a\langle a_1 \rangle + \langle a_2 \rangle. \qquad [4]$$

The quantities on the left are measurable time averages, while the two expectation values and the two parameters on the right are unknown. Similarly, time averages can be taken of higher moments, as

$$\langle I_1^2 \rangle = \langle a_1^2 \rangle + 2b\langle a_1 \rangle \langle a_2 \rangle + b^2 \langle a_2^2 \rangle$$

$$\langle I_2^2 \rangle = a^2 \langle a_1^2 \rangle + 2a\langle a_1 \rangle \langle a_2 \rangle + \langle a_2^2 \rangle$$

$$\langle I_1 \times I_2 \rangle = a\langle a_1^2 \rangle + (1 + ab)\langle a_1 \rangle \langle a_2 \rangle + b\langle a_2^2 \rangle. \quad [5]$$

These three equations contain two new parameters, $\langle a_1^2 \rangle$ and $\langle a_2^2 \rangle$. Third moments yield

$$\langle I_1^3 \rangle = \langle a_1^3 \rangle + 3b\langle a_1^2 \rangle \langle a_2 \rangle + 3b^2 \langle a_1 \rangle \langle a_2^2 \rangle + b^3 \langle a_2^3 \rangle$$

$$\langle I_1^2 \times I_2 \rangle = a\langle a_1^3 \rangle + (2ab + 1)\langle a_1^2 \rangle \langle a_2 \rangle$$
$$+ (2b + ab^2)\langle a_1 \rangle \langle a_2^2 \rangle + b^2 \langle a_2^3 \rangle$$

$$\langle I_1 \times I_2^2 \rangle = a^2 \langle a_1^3 \rangle + (2a + a^2 b)\langle a_1^2 \rangle \langle a_2 \rangle$$
$$+ (1 + 2ab)\langle a_1 \rangle \langle a_2^2 \rangle + b\langle a_2^3 \rangle$$

$$\langle I_2^3 \rangle = a^3 \langle a_1^3 \rangle + 3a^2 \langle a_1^2 \rangle \langle a_2 \rangle + 3a\langle a_1 \rangle \langle a_2^2 \rangle + \langle a_2^3 \rangle. \quad [6]$$

These four equations contain two new parameters $\langle a_1^3 \rangle$ and $\langle a_2^3 \rangle$. Eqs. 4–6 overdetermine all unknowns, including parameters a and b. Their knowledge allows the computation of the individual odor fluctuations $a_1(t)$ and $a_2(t)$ from $\mathbf{I}(t)$. The analysis works in the same fashion for a larger number of neurons and odors as long as $N \geq K$.

The odor fluctuations have been assumed to be asymmetric about the mean because of the large physical difference between the causes of maximal upward and downward odor fluctuations. A steady wind in the wrong direction produces essentially no odor from some particular source, while the largest odors from that source occur when the wind is roughly in the correct direction and there is a chance favorable fluctuation of the microturbulence. A positive third moment about the mean is therefore to be expected, as the distribution has longer tails in the positive direction.

With one reasonable supposition—namely, the statistical independence of the fluctuating contributions of two separate objects to the composite odor—the hopeless problem of identifying the contributions of unknown fluctuating odors becomes solvable. Alternative suppositions, such as an assumed parametrized functional form for the fluctuations or differences in the time structure of the fluctuations from the two sources, could also serve as the basis for separating the two odors. Approximate algorithms involving usual-case suppositions are common in vision where, for example, the perception of a three-dimensional surface from monocular intensity information (shape-from-shading) is based on the assumption of a single localized illumination source (8).

Solving the Problem by Adaptation in a Simple Network

A set of interacting processing neurons is described, with individual neurons denoted by a subscript. The dendrites of each neuron n receive direct or indirect time-varying input $I_n(t)$ from sensory cells. The processing cells will be assumed to be compact (small compared with the electrotonic length), so a cell potential $u_n(t)$ is the same throughout its dendritic arborization. The processing cells make inhibitory dendro–dendritic synapses with each other. T_{nk} denotes the strength of the inhibitory synapse from neuron k to neuron n. This circuit description can be viewed as an idealization of the structure of the olfactory bulb (see *Discussion*). It is also an instantiation of the kind of network equations described by

Herault and Jutten (21) for decorrelating signals in an engineering context. The equations of motion of the cell potentials u_n are

$$du_n/dt = -u_n/\tau - \Sigma T_{nk} u_k + I_n(t). \quad [7]$$

The resting potential of the cell in the absence of external or synaptic input has for convenience been chosen as zero. With the sign convention of Eq. 7, all T_{nk} will be positive. Eq. 7 describes the evolution of the cell potentials due to the sensory input and the present values of the synaptic connection strengths. However, the synapses also change with time.

Eq. 8 describes the learning rule for the inhibitory synapses, where δ, γ, and ε are constants determining the learning speed

$$dT_{nk}/dt = +fu_n \times fu_k[\delta + \varepsilon(fu_k - \gamma fu_n)]. \quad [8]$$

The fu_n are a high-pass filtered version of the potentials u_n. [It is assumed that the synapse change mechanism can filter out the average potential by simple chemical means, just as the chemosensory system of *Escherichia coli* is sensitive to concentration changes, not absolute concentration (9, 10). Alternatively, the average of the input variables could be removed by the sensory cells themselves.] The synapse change rule is of the Hebbian type, involving only variables of the pre- and postsynaptic neurons.

The idea behind this structure of network and learning rule can be seen from examining the case of two odors and two neurons, and the simplification τ is small. Suppose the synaptic matrix is such that the first column of $(\mathbf{E}/\tau + \mathbf{T})$ is the vector $\mathbf{S}_1$, and the second column is the vector $\mathbf{S}_2$. ($\mathbf{E}$ is the identity matrix.) It directly follows from Eq. 7 that $u_1(t) = a_1(t)$ and $u_2(t) = a_2(t)$, and all other $u_k(t)$ will vanish. If a learning rule could be made to converge to this $\mathbf{T}$, the information about the relative components of a particular odor will occur as a column in the $\mathbf{T}$ matrix, while the information about the fluctuations in the intensity of the individual odor objects will be faithfully conveyed by the $u_k(t)$. (The choice of which neuron will represent the strength of which odor is made by the operation of the learning rule; in simple cases, it selects the neuron most strongly driven by a particular odor.) Thus, the network has a structure that allows it to solve the problem if the learning rule can cause the $\mathbf{T}$ matrix to take on the desired form.

The learning rule of Eq. 8 has been chosen, consistent with a linear analysis of the stability of the desired solution for $\mathbf{T}$ for the positive asymmetry expected for the fluctuations. This linear analysis guarantees that if $\mathbf{T}$ is initially roughly correct, the learning rule will lead to the correct matrix for $\mathbf{T}$. Many other forms of modification rules have this property, including the simpler case $\gamma = 0$. Without the term in ε, the learning rule is the same as that used by Barlow and Foldiak (11) and Foldiak (12) to decouple two mixed Gaussian communication channels by minimizing their covariance. (In the present case, merely minimizing covariance cannot generate the desired solution, since minimizing the covariance results in a symmetric matrix for $\mathbf{T}$, while the desired result is not symmetric.) A non-Gaussian mixed channel problem has been examined by Herault and Jutten (21). The olfactory problem is simpler than their case in that the third moment of the distribution will be nonzero. Olfaction is made complicated by the fact that the synapse strengths have important meaning, which needs to be available to higher processing centers. The approach is related in spirit to the work of von der Malsburg and Bienenstock (13), who have emphasized the role of fast synaptic modification as a computational element in biology, and to novelty filters (14). Further mathematical analysis suggested that the learning rule should be adequate to generate the desired $\mathbf{T}$ even without initial

information concerning the desired solution, so a simulation was carried out to examine this question.

Simulations

A computer simulation of the model (Eqs. 7 and 8) has been carried out for a network of six processing neurons. Two odors were used, each having fluctuations of random duration and random amplitude above a base line, with an asymmetry between upward and downward fluctuations. The model intensities $a_A(t)$ and $a_B(t)$ are shown at the top left of Fig. 1. The net odor was composed according to Eq. 1, with odor A components chosen as (4, 7, 5, 2, 8, and 10) and odor B components were (7, 3, 10, 8, 4, and 1). The connection matrix was initially set to zero. The bottom six traces on the left in Fig. 1 show the potentials $u_n(t)$ of the six processing neurons in the presence of the odor mixture. Initially, the fluctuations of both odors appear in each channel. After synaptic learning is turned on (for clarity, the time before $t = 20$ was run without synaptic modification) the output pattern in the network changes. T changes so that eventually only channels 3 and 6 remain with any output at long times. As shown, the output of channel 3 then follows the strength of odor B, while the output of channel 6 follows A. At $t = 200$ the synaptic matrix T_{nk} (with diagonal entries zero) has become

—	0.00	0.69	0.03	0.01	0.33
0.02	—	0.30	0.01	0.01	0.66
0.04	0.01	—	0.04	0.01	0.53
0.02	0.00	0.79	—	0.00	0.13
0.02	0.00	0.40	0.02	—	0.76
0.03	0.01	0.11	0.02	0.01	—

The entries in column 3 above closely approximate the 0.7, 0.3, —, 0.8, 0.4, 0.1 pattern of the strengths of components 1, 2, 4, 5, and 6 of odor B relative to the strength of component 3 of odor B. Column 6 is similarly close to 0.4, 0.7, 0.5, 0.2, 0.8, —, the relative strengths of components 1, 2, 3, 4, and 5 of odor A relative to 6. The network has developed a connection matrix that solves the problem and that makes two of the neurons into cells, each of which responds only to the fluctuations of a corresponding single odor intensity. At the same time, the relative components of the individual odors (the odor quality) have been imprinted in the matrix T.

Discussion

I have shown that an adaptive neural network with changing synaptic connections can solve the essential problem in olfactory object perception—namely, using an analysis of fluctuations to deduce the individual odors in a mixed odor environment. An olfactory system that can solve this problem is capable of discerning the nature and location of odor objects in a complicated and ever changing environment, which is essential for the olfactory abilities displayed by highly olfactory land animals. This change in the pattern of synapses due to the fluctuations can be thought of as a process of network adaptation to the present environment.

The conventional connectionist viewpoint considers the synaptic connections as an algorithm that processes information. Although the connections may be formed through learning-induced adaptation, their usual importance is the transformation performed by the connections on the signals flowing through them. The actual connections or architecture that performs the computation are not viewed as being of primary interest.

The way in which this network uses changing connections leads to an entirely different way of thinking about the connections (see also ref. 13). There are two separate parts of the desired information, one having to do with discerning the varying strength of an individual odor object, and the other having to do with discerning the odor quality. The adaptive network produces an activity signal representing the separate strengths of the multiple odors. The knowledge of the components of these odors becomes embedded (after learning) in the strengths of the connections. Thus, the connection strengths are not merely algorithm, they are also essential data for understanding the environment. A complete system must have an ability to query the connection strengths in order to perceive (after adaptation) the odor quality of a particular source. This can be done by a procedure that queries a particular cell about the strengths of its synapses.
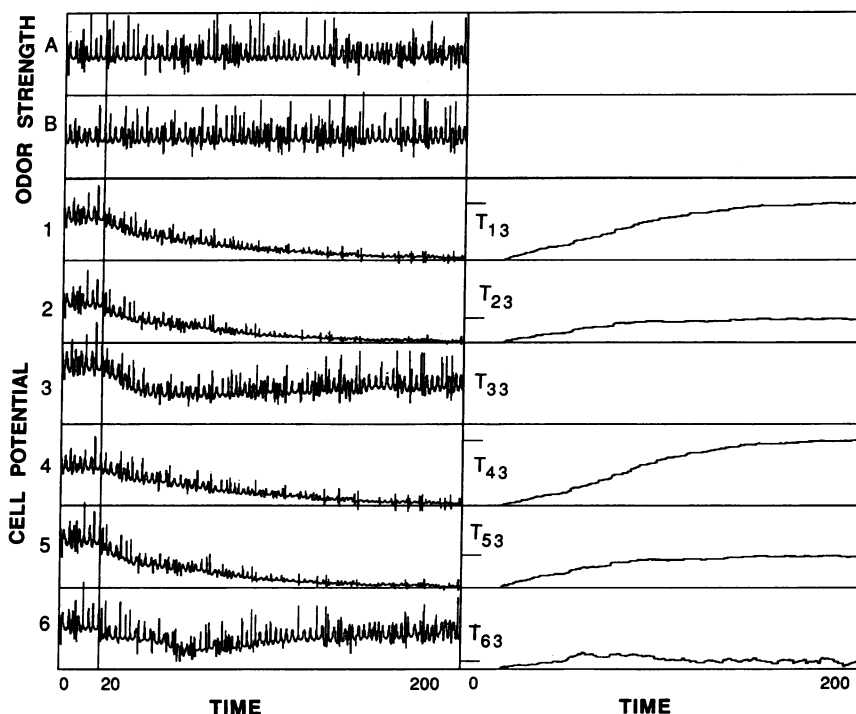

FIG. 1. A simulation for six dimensions of odor and two independent sources. The intensities of the two sources are given in the top two traces on the left. Synapse change begins at $t = 20$ sec. The time scale of the average odor fluctuation is 3 sec; $\tau = 0.01$ sec. The bottom six traces on the left are the dendritic potentials u_k of the processing neurons. After ≈ 100 sec of learning-induced network adaptation, the two that still have sizable output reflect the network view of the fluctuating intensities of the two odor objects present. During this time period, the synapses also change into a pattern that reflects the components of the individual odors. The strengths of the synapses of neuron 3, which has captured the response to odor B, are displayed on the right. The relative strengths of the actual odor components of this odor object are shown by the horizontal bars. The implicit strength of component 3 is unity. The synapse learning algorithm had $\gamma = 1$ for mathematical simplicity and was augmented by an exponential forgetting, which occurs when the presynaptic neuron is silent.

After network adaptation, a particular set of $N-1$ synapses take on values that describe the relative strength of the components of a particular odor. These synapses are all associated with the particular cell that now responds to the strength of that particular odor. (While the simple network generates a temporary "grandmother cell" representation of odor intensity, the concept described can be embedded in a distributed representation more appropriate to neurobiology.) Thus, to find out the odor quality of a particular odor, the system needs to send a signal to the dendrite of the principal neuron that is reporting out the strength of that odor. The signals back from other processing cells will then correspond to the relative strengths of that odor. Only one odor quality can be queried at once, for the same set of axons is being used to report the quality for each particular odor. This querying process must be made in a way that distinguishes activity generated by the query from the ongoing processing of odors. One possible answer is to multiplex a second signal on the same set of output axons. Since the intensities only vary slowly, information about them can be carried on the axons as a low frequency or "DC" response, while a high-frequency signal can be used to query the synaptic strengths and to carry that information on the same axons. It should be noted that the DC information carried by the outgoing axons changes greatly during adaptation. Before adaptation, it represents the total odor quality, while after adaptation it represents the information about the time fluctuation of the intensity of various odor objects.

If a computation of the sort described is to be carried out by a nervous system, it must be performed before there are major nonlinear transformations of input signals. In the mammalian olfactory system, the glomeruli [each of which is innervated by 1000 sensory cells (15)] may provide reliable pooled information from sensory cells. Eq. 1 potentially describes the response of a glomerulus to odors. The next stage of processing would then be used for a decomposition computation, while signals are still reasonably linear. In the mammalian system, the secondary mitral cells of the olfactory bulb are each innervated by a single glomerulus and could correspond to the processing cells of the model. (It is not clear whether mitral and tufted secondary neurons should have fundamentally different computational roles; for example, one could be involved in adaptive processing, while the other could be used to convey odor quality or the sensory stimulus itself.) The model makes use of inhibitory interactions between the mitral cells. Real mitral cells are excitatory, but the dominant synapse type in the olfactory bulb is a reciprocal dendro–dendritic connection between a mitral cell and an inhibitory axonless granular cell (15). This local circuit produces an effectively inhibitory dendro–dendritic connection between mitral cells. Dendro–dendritic computation is preferable to using action potentials, since linear processing is desired. The anatomical elements essential for the bulb to carry out the anticipated computation exist. (The inhibitory periglomerular cells could play a similar role in dendro–dendritic processing.) These general features seen in the vertebrate olfactory system (15) are also present in highly olfactory terrestrial mollusks (16–18). The one essential additional property is that the efficacy of the dendro–dendritic connections be appropriately modified during behavior, either by direct change (e.g., Hebbian learning) or indirectly via descending pathways. Synaptic modifications in the olfactory bulb would be the basis of the short-term memory of the present environment of several odor objects. Long-term memory of odors, and the facility for the comparison of present and distant past odors, would lie in higher areas.

Within the present model, the adaptation of the network is to odor quality and is not dependent (presuming linearity) on the strength of the odors. When only one odor is present, most of the neurons become silent and are capable of

responding to new odors but not to the fluctuations in intensity of the adapted odor. Recent experiments (22) suggest the modifiability of synapses in the accessory olfactory bulb, closely related in both anatomy and function, on a time scale of several minutes.

The separation of the individual odors by such a network is based on the assumption of independent fluctuations of the contributions of different odor objects. This will not be universally correct, and when this supposition is violated, an "olfactory illusion" should occur. In the case of the *Limax* A–B stripe experiment, fluctuations can take place involving diluting A with pure air, or diluting B, or exchanging A for B, or mixed AB for A, etc. With two such nearby sources, some correlation of fluctuations will be inevitable. A variety of effects can be seen in simulations involving partial correlation, depending on the similarity of the two objects and the model of the correlation. These have ranged from a failure to construct objects at all to the perception of a phantom odor object lying between A and B. The A–B stripe experiment suggests the presence of an olfactory illusion in *Limax*.

In the presence of fluctuating olfactory signals, correlations define what is a single odor object, and the dynamically changing synapses manage to capture information about individual objects. Visual processing could have a similar way of using correlation for understanding moving objects, and the oscillatory behavior due to signals from different parts of a moving stimulus (19) might reflect a mechanism to probe synaptic strengths set up by correlated motions. Such processing would require very rapid synapse changes (20) in the visual system.

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