# Olfactory cortex: model circuit for study of associative memory?

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*The piriform (olfactory) cortex is a phylogenetically old type of cerebral cortex with parallels in its organization to the architecture of certain 'neural network' models for distributed pattern recognition and association. These features, in combination with unique structural characteristics that facilitate experimental study, make the piriform cortex a potentially good model for analysis of associative (content-addressable) memory processes.*

One of the fundamental questions in neurobiology is how the CNS is able to store, retrieve and associate complex patterns of neuronal activity. Over the past several years significant progress in addressing this question has been made on two fronts. First, with the aid of increasingly powerful experimental tools, neurobiologists have derived considerable structural, physiological and biochemical information that may assist in understanding higher order functions. Of particular significance are new insights concerning long-lasting, activity-dependent changes in synaptic efficacies[1]. Second, the question of how brain-like networks behave dynamically and, in particular, how they might store and retrieve information has become a focus of many mathematicians and physical scientists interested in building devices with pattern recognition abilities. The ideas being generated by these theoretical efforts are having a significant influence on the work of an increasing number of neurobiologists.

In this article we attempt to relate the parallel endeavors of biologists and theorists in the context of the mammalian olfactory cortex, which we believe to be a particularly good model system for study of the neural substrate for learned pattern recognition and association. First, however, we will provide an overview of models with brain-like abilities that have been developed by mathematicians and physical scientists. We will then introduce the circuitry of the olfactory cortex and point out parallels in architecture with the theoretical constructs. Finally, we will describe the initial attempts to model the olfactory cortex within the framework of these constructs.

## Neural networks and associative memory

In recent years there has been a rediscovery and rapid development of models and artificial devices for recognition and association of complex patterns that rely on large numbers of relatively simple processing elements that are highly interconnected and operate in parallel. Because of certain similarities between these models and general features of the CNS, they have come to be known as 'neural networks'. The basic design of such neural network models contrasts sharply with conventional digital computers where a highly complex 'central processing unit' carries out computations in a step-by-step serial fashion. For both non-technical and rigorous descriptions of the many forms of artificial neural networks, as well as accounts of the history of their development, the reader is referred to the recent volumes by Anderson and Rosenfeld[2] and Rumelhart and McClelland[3].

One of the principal reasons for interest in neural network models is the fact that many perform associative functions as a direct consequence of their architecture (and are therefore sometimes termed 'associative memory' models). These associative functions include the ability to reconstruct original learned patterns from inputs that are fragmented or distorted versions of these patterns, the related ability for novel input patterns to elicit outputs of related patterns that were previously stored in memory, and the ability to link two or more unrelated patterns, especially when they occur at the same time, so that subsequent input of one elicits the others from memory.

Key features of artificial neural networks that are related to their ability to perform such associative functions are the direct distribution of inputs across the processing array and memory storage via alterations in the strengths of connections between the processing elements (hence the term 'connectionist' models). Memories are coded in a 'distributed' fashion with individual connections participating in the storage of many different patterns. Another key feature of some neural networks is the ability to self-organize by altering strengths of connections based exclusively on local conditions such as the degree of synchrony of inputs converging on to individual processing elements. This allows these networks to develop their own internal representations for stored data. Neural network models of this form can be said to be 'content-addressable' since retrieval occurs when inputs directly elicit output from the array of interconnected processing elements. This form of retrieval contrasts with that of digital computers where information is accessed by a code that is unrelated to content (termed 'location-addressable' memory).

There are intriguing similarities in architecture, operation and other features of certain artificial neural networks and the cerebral cortex. In addition to the brain-like self-organizing associative abilities described above, these models display a relative immunity to the effects of damage to individual processing elements that is characteristic of association areas of the cerebral cortex. Requirements for processing elements are also within the capabilities of cortical



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neurons: because processing occurs in parallel, complex pattern analysis can be carried out rapidly with elements that operate on the time scale of neurons (orders of magnitude slower than logical 'gate' operations in digital computers). Whereas many early associative memory models employed linear summation rules, increasingly, more complex neuron-like input–output operations are being incorporated*. Furthermore, algorithms for modification of the strengths of connections between processing elements in many associative memory models are reminiscent of the properties of cortical synapses where efficacies can be altered by coincident activation of inputs as described below.

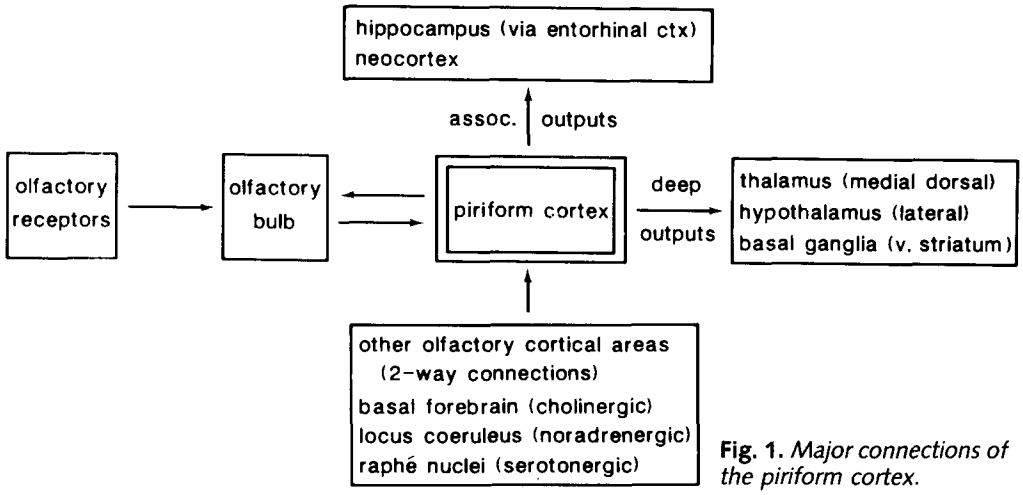


**Fig. 1.** *Major connections of the piriform cortex.*

## Why olfactory cortex?

While computer simulations have established the feasibility of many associative, content-addressable memory models for complex pattern recognition and other tasks, it has not been determined whether any real neuronal circuit functions in a similar fashion. For several reasons the olfactory cortex would appear to be an ideal system for addressing this question[4]. First, as described below, the circuitry in the olfactory cortex matches characteristics of recent associative memory models in important respects. Second, as also described below, there is a convergence of information from different sensory modalities and other brain systems on to different parts of the olfactory cortex. This convergence imparts the potential for complex associative functions. Third, its circuitry is amenable to experimental analysis: the olfactory cortex is only one synapse removed from the peripheral receptors and has a laminar segregation of different neuronal elements including fiber systems, cells of different types and different dendritic segments of pyramidal cells. Fourth, the olfactory cortex has close connections with monoaminergic, cholinergic and hippocampal systems that are believed to play important roles in learning and memory (Fig. 1). Finally, olfactory information at the level of the cortex appears to be in the form of a highly distributed ensemble code (Ref. 53 and Fig. 2C).

## Neuronal circuitry in piriform cortex

Several morphologically distinct parts of the cerebral cortex receive a direct input from the olfactory bulb [the receiving structure for axons from olfactory receptor cells (Fig. 1)] and are therefore termed olfactory cortex. While the present account will be confined to the piriform cortex, which is the largest of the olfactory cortical areas, it should be noted that there are similarities between the piriform cortex and the other types of olfactory cortex so that conclusions for the piriform cortex may apply to other areas[4]. The olfactory bulb is also outside the scope of the present article, but it must be recognized that models for the olfactory cortex will ultimately have to incorporate this structure, especially in view of the presence of two-way connections between the bulb and cortex[5,6]. Several mathematical models for the olfactory bulb have been developed[7–10].

The structure and physiology of the piriform cortex and other olfactory cortical areas have been described in some detail in recent reviews[4,11,12]. Features of the neuronal circuitry in the piriform cortex with relevance to the development of associative memory models are described below.

*Lamination.* The piriform cortex is usually described in terms of three layers (Fig. 3): layer I is a so-called plexiform layer that contains few neuronal cell bodies and is dominated by ascending dendrites from deeper layers and fiber systems. Layer I has been subdivided into a superficial sublamina, layer Ia, where afferent fibers from the olfactory bulb terminate and a deep sublamina, layer Ib, where association fibers terminate[13]. Layer II is a compact zone of neuronal cell bodies. Layer III contains neuronal cell bodies at a lower density than layer II and a large number of dendritic and axonal elements.

*Cells.* Pyramidal cells, which are the principal integrative elements in the piriform cortex, have much in common with their counterparts in the neocortex and hippocampal cortex[14–16] (Fig. 4). As in these other types of cerebral cortex, dendrites consist of an apical tree directed toward the brain surface and a basal tree that radiates from cell bodies. Pyramidal cells are found in both layers II and III (SP and DP, respectively, in Fig. 3). Primary axons give rise to a profusion of fine unmyelinated collaterals that synapse near parent cell bodies as well as at long distances. Afferent fibers from the olfactory bulb and association fibers from other pyramidal cells make excitatory synapses primarily on spines that isolate them from dendritic shafts[17]. Synapses from these two fiber systems are completely excluded from cell bodies. Indirect evidence indicates that inhibitory synapses are distributed over cell bodies, axon initial segments, and the entire extents of apical and basal dendritic trees[12].

* Complex input–output relationships in neurons are a result of many factors. These include non-linearities at three processing levels: in the D/A (digital to analog) conversion from all-or-none action potentials in input axons to graded postsynaptic potentials, in the integration of these graded potentials, and in the A/D conversion for output. Sources of non-linearity include an effect of postsynaptic voltage on D/A conversion when NMDA receptors are activated, the participation of current shunting and voltage-dependent membrane channels in the integration of postsynaptic potentials, and the presence of a threshold for action potential generation.

As in other types of cerebral cortex, a large number of classes of non-pyramidal cell can be distinguished on the basis of location, morphology, connections and neurotransmitters. However, in contrast to the neocortex, these different types tend to be lamina- and position-specific – a feature that greatly facilitates experimental analysis and modeling[14,18]. As in other types of cerebral cortex, a large percentage of non-pyramidal cells in the piriform cortex appear to use GABA as their neurotransmitter and therefore probably mediate an inhibitory effect[18,19].

*Afferent fiber systems.* Afferent fibers from the olfactory bulb, which carry incoming olfactory information, terminate in the sharply delimited layer Ia (Ref. 13). It is of special significance, as discussed below, that this fiber system is highly distributed in the horizontal dimension (parallel to the cortical surface): small areas in the olfactory bulb project to the entire extent of the piriform cortex and, conversely, small areas in the piriform cortex receive inputs from cells in all parts of the olfactory bulb[20] (Fig. 5). There is a non-uniformity in this projection but any patterns present are broad and overlapping with no indication of a topographically organized, point-to-point mapping.

In addition to the afferent input from the olfactory bulb, the piriform cortex and other olfactory cortical areas that include the entorhinal cortex, receive inputs from the amygdala, hippocampal formation and neocortical areas[4,12]. These inputs could allow a convergence of olfactory information with that derived from other sensory systems as well as limbic (emotional, visceral) and motor systems.

*Association fiber systems.* Within the piriform cortex there are intrinsic association fiber systems that, in common with the afferent input, are precisely ordered in the vertical dimension but highly distributed in the horizontal dimension[5,21] (Fig. 3). These association fibers both originate from, and terminate on pyramidal cells[17,21]. As illustrated in Fig. 3, at least three different intrinsic fiber systems can be distinguished that synapse on different dendritic segments of pyramidal cells[12,22]. Physiological data from intracellular recording[15,16,23–25] and current source-density experiments[26–28] (Fig. 6) suggest that following activation of afferent fibers, four different EPSPs occur in different dendritic segments of pyramidal cells consistent with expectations from the morphological data: a monosynaptic EPSP mediated by afferent fibers in distal apical segments is followed successively by disynaptic EPSPs at the level of basal dendrites in layer III, middle apical segments in superficial layer Ib, and proximal apical segments in deep layer Ib. Recent studies[27] suggest that this sequence may recur during each cycle of the 40–60 Hz oscillation that accompanies odor responses (see below).

*Inhibitory systems.* A variety of inhibitory systems have been demonstrated in the piriform cortex as in other types of cerebral cortex. Afferent fibers directly synapse on inhibitory interneurons which project to pyramidal cells, thereby producing a feedforward inhibition[15]. Outputs of pyramidal cells contact inhibitory interneurons which project back to pyramidal cells producing feedback inhibition[29]. Physiological study has revealed fast and slow synaptically mediated inhibitory processes mediated

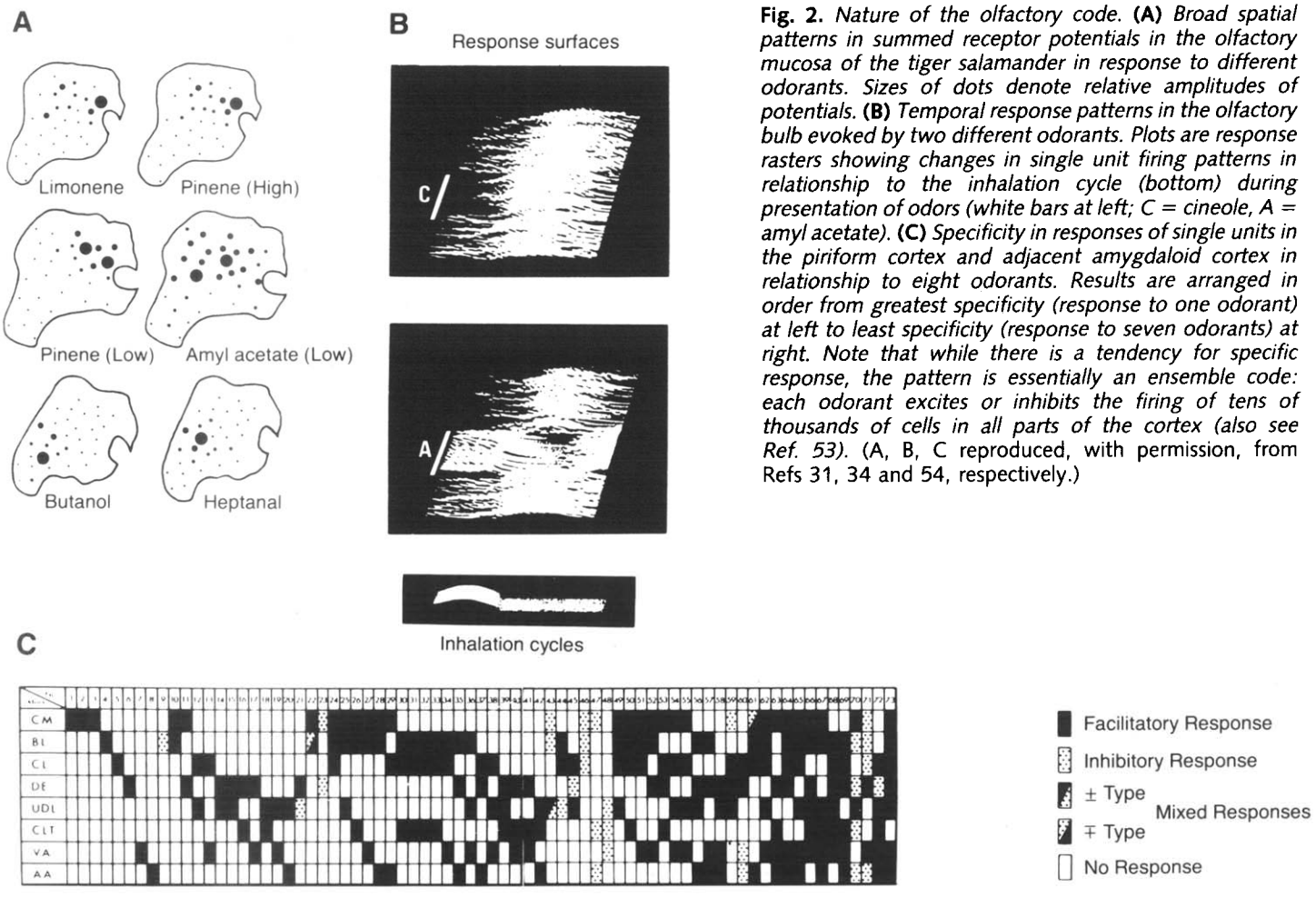


**Fig. 2.** *Nature of the olfactory code.* **(A)** *Broad spatial patterns in summed receptor potentials in the olfactory mucosa of the tiger salamander in response to different odorants. Sizes of dots denote relative amplitudes of potentials.* **(B)** *Temporal response patterns in the olfactory bulb evoked by two different odorants. Plots are response rasters showing changes in single unit firing patterns in relationship to the inhalation cycle (bottom) during presentation of odors (white bars at left; C = cineole, A = amyl acetate).* **(C)** *Specificity in responses of single units in the piriform cortex and adjacent amygdaloid cortex in relationship to eight odorants. Results are arranged in order from greatest specificity (response to one odorant) at left to least specificity (response to seven odorants) at right. Note that while there is a tendency for specific response, the pattern is essentially an ensemble code: each odorant excites or inhibits the firing of tens of thousands of cells in all parts of the cortex (also see Ref. 53).* (A, B, C reproduced, with permission, from Refs 31, 34 and 54, respectively.)

by chloride and potassium[15].

*Efferent systems.* There are direct outputs from the piriform cortex and other olfactory cortical areas to the neocortex, thalamus, hypothalamus, basal ganglia and hippocampal formation[11,12,30] (Fig. 1).

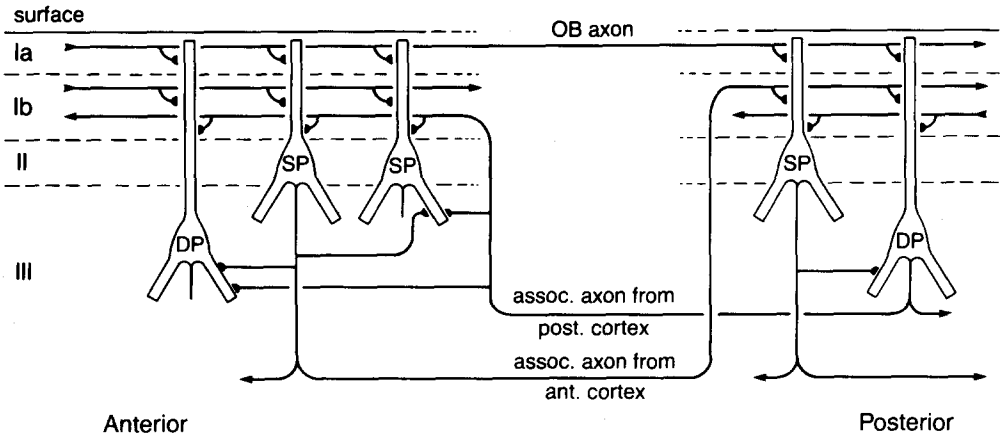


**Fig. 3.** *Summary of excitatory connections of pyramidal cells in the piriform cortex. See Fig. 4 for pyramidal cell morphology. As described in the text, afferent and different intrinsic associational fiber systems synapse in a lamina-specific fashion on different dendritic segments of pyramidal cells. Abbreviations: OB, olfactory bulb (afferent) fibers; SP, superficial pyramidal cells; DP, deep pyramidal cells. Roman numerals denote cortical layers.*

## Olfactory coding and perception

Results from several experimental approaches indicate that the olfactory code includes a highly distributed spatial component[31,32] (Fig. 2A). Studies of summed receptor potentials suggest that this spatial component originates as a consequence of a tendency for receptor cells with similar specificities to be broadly segregated on the receptive surface[31,33]. In addition to the spatial coding, studies at the receptor level and in the olfactory bulb have revealed consistent temporal patterns of activity that could contribute to the olfactory discrimination process[31,34,35] (Fig. 2B). During odor responses high amplitude 40–60 Hz oscillations occur in both the olfactory bulb and cortex[7]. In rodents, rhythmic sniffing that is tied to the θ-frequency[36] evokes envelopes of this oscillatory activity at approximately 200 ms intervals.

An intriguing aspect of the olfactory sense with potential relevance to memory modeling is the strong tendency in man[37] and lower animals[38] for mixtures of odorants to be perceived as single-odor sensations with a poorly developed capacity for dissection into individual components – a feature reminiscent of certain associative memory models where input-triggered activity settles into unitary output patterns (e.g. Ref. 39). It thus resembles the discrimination of colors in the visual system, but stands in marked contrast to visual pattern discrimination where the ability to examine individual stimulus components is well developed.

## Memory modeling

There are several striking parallels between the structure of the piriform cortex and the architecture of certain associative, content-addressable memory models[4]. First, to a large extent the function of artificial associative networks depends upon a spatially distributed input system like that seen in the olfactory bulb projection to the piriform cortex. Second, the discriminative power of many associative networks is greatly enhanced by positive feedback via interconnections between the processing units that receive the distributed input. In the piriform cortex the interconnections between pyramidal cells (associational fiber systems) mediate a distributed positive feedback to dendritic segments that are immediately adjacent to the segments that receive the distributed afferent input[28]. Third, in associative memory models individual inputs are typically weak relative to output threshold, which is also likely to be the case in the olfactory cortex[15]. Finally, many of these artificial networks require activity-dependent changes in excitatory synaptic strengths. While different algor-

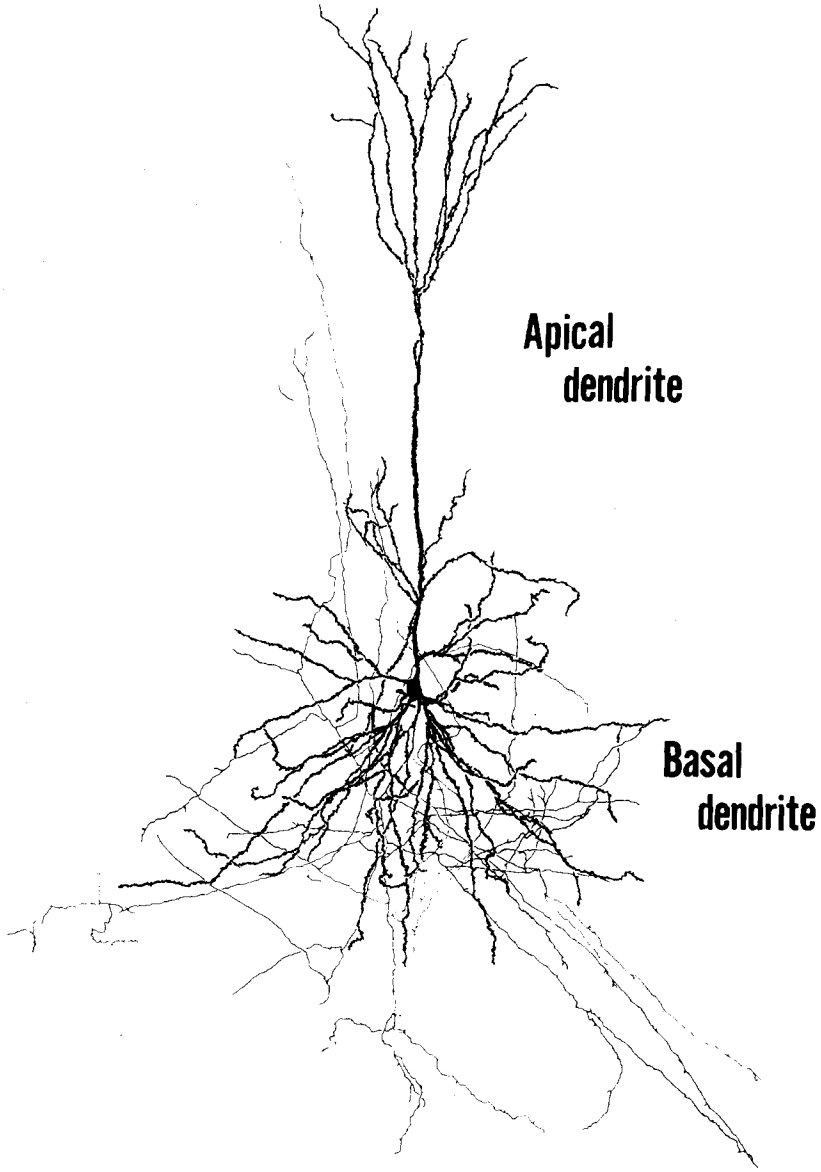


**Fig. 4.** *Pyramidal cell in piriform cortex stained by intracellular dye injection. As in other types of cerebral cortex these cells give rise to an apical dendritic tree that extends toward the cortical surface and a basal dendritic tree that radiates from the cell body. The axon gives rise to many fine collaterals (thin processes interspersed among thicker dendritic processes).* (Figure provided by Guo-Fang Tseng.)

ithms for implementing such changes are employed in different models, many can be thought of as variations of the 'Hebb rule'[40]. These algorithms allow simultaneous activation of multiple inputs, or inputs and outputs, to trigger alterations in the strengths of input connections. While there has been comparatively little study of synaptic plasticity in the piriform cortex, excitatory synapses on to pyramidal cells in the closely related hippocampus display Hebb-like activity-dependent alterations in strength, termed long term potentiation (LTP)[1]. It has recently been demonstrated that interactions between inputs to different portions of the dendritic tree can trigger such alterations[41,42]. If pyramidal cells in the piriform cortex have similar properties, then activation of either afferent or associational fibers with the proper temporal pattern could trigger changes in synaptic strengths. Such changes could also be triggered by coincidence in activation of different dendritic segments by afferent and associational inputs (see Ref. 43 for theoretical implications of this possibility). A recent study[44] has revealed substantial increases in the strengths of excitatory synapses in the piriform cortex when animals are trained to respond to synchronous shock stimuli as if they were odors, but further study will be required to determine whether properties of this process are similar to LTP in hippocampal pyramidal cells.

An important question is whether highly distributed intrinsic connections like those in associative memory models are unique to the olfactory cortex or if they are also present in other types of cerebral cortex – i.e. is there potential for the olfactory cortex to serve as a general model for analysis of associative memory processes? While studies of the intrinsic circuitry in the neocortex have concentrated on the vertical, columnar organization of the receiving areas, recent studies have demonstrated the presence of horizontal intrinsic connections[45] that may be especially well-developed in higher order 'association' areas. Even in area 7 of the cat, however, which appears to have the most extensive intrinsic associational connections yet demonstrated in the neocortex, the horizontal organization is not of a continuous nature as in the olfactory cortex, but is 'fractured' into irregular interconnected patches[46]. Nevertheless, the high degree of convergence and divergence of connections between pyramidal cells that is required for most associative, content-addressable memory schemes does appear to be present.

## Computer simulation models for piriform cortex

Wilson and Bower[47–50] have developed a network simulation for the piriform cortex that replicates basic features of responses to natural and artificial stimuli.

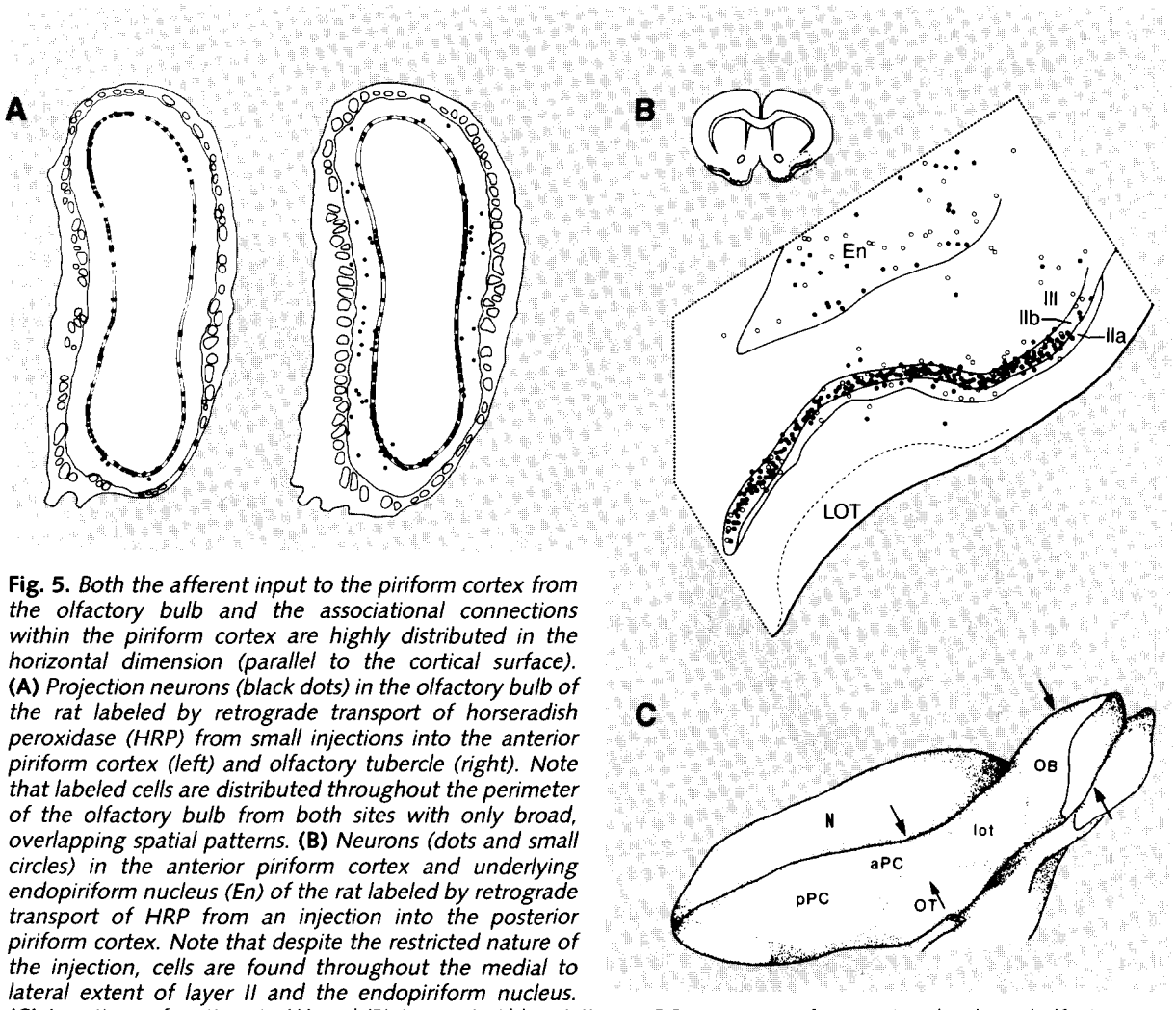


**Fig. 5.** *Both the afferent input to the piriform cortex from the olfactory bulb and the associational connections within the piriform cortex are highly distributed in the horizontal dimension (parallel to the cortical surface).* **(A)** *Projection neurons (black dots) in the olfactory bulb of the rat labeled by retrograde transport of horseradish peroxidase (HRP) from small injections into the anterior piriform cortex (left) and olfactory tubercle (right). Note that labeled cells are distributed throughout the perimeter of the olfactory bulb from both sites with only broad, overlapping spatial patterns.* **(B)** *Neurons (dots and small circles) in the anterior piriform cortex and underlying endopiriform nucleus (En) of the rat labeled by retrograde transport of HRP from an injection into the posterior piriform cortex. Note that despite the restricted nature of the injection, cells are found throughout the medial to lateral extent of layer II and the endopiriform nucleus.* **(C)** *Locations of sections in (A) and (B) (arrows). Abbreviations: aPC, anterior piriform cortex; lot, lateral olfactory tract (afferent fibers to piriform cortex from the olfactory bulb); N, neocortex; OT, olfactory tubercle; pPC, posterior piriform cortex.* (A, B, C reproduced, with permission, from Refs 20, 21 and 55, respectively.)

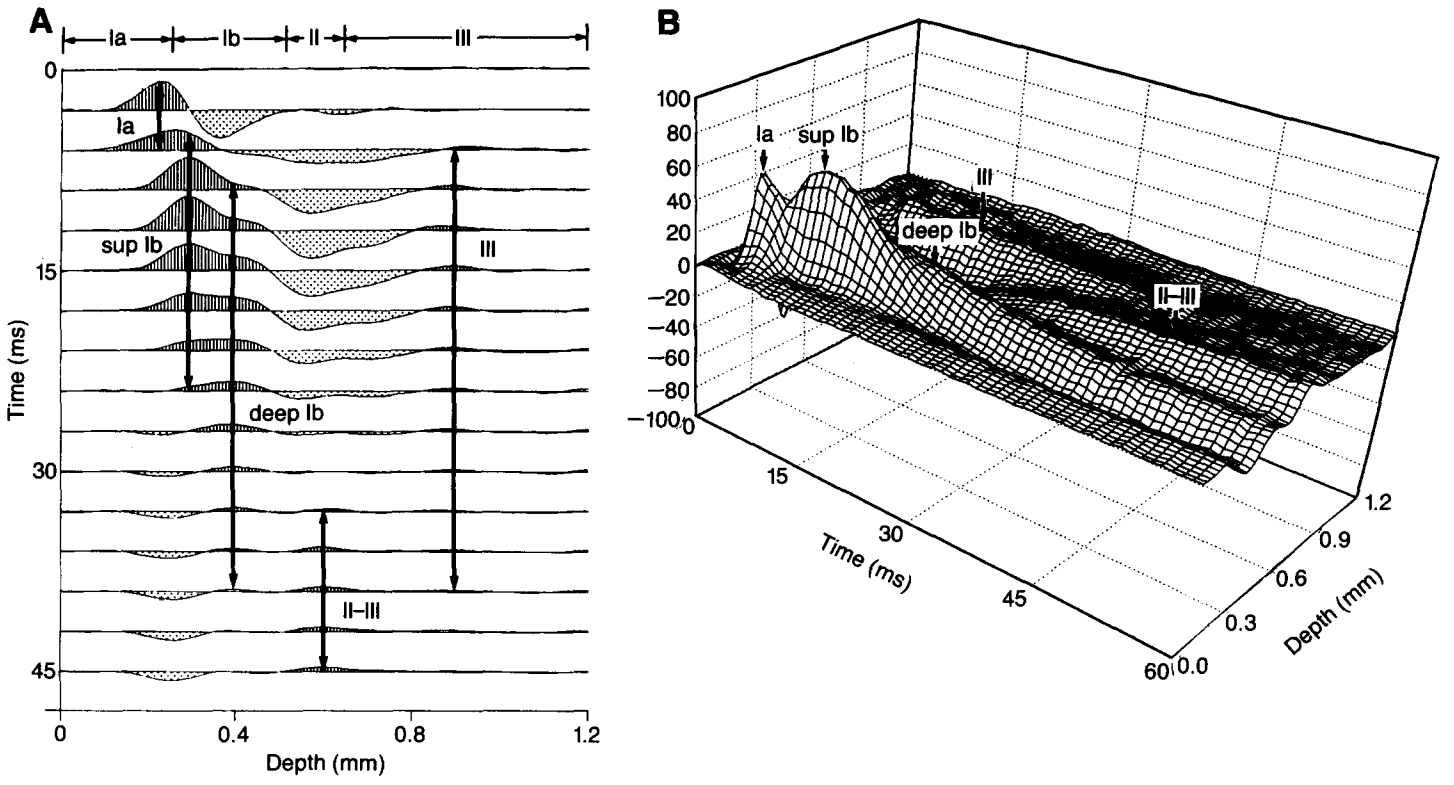


**Fig. 6.** *Synaptic events in the piriform cortex evoked by synchronous activation of afferent fibers as revealed by current source-density analysis.* **(A)** *Raster plot of net membrane currents as a function of depth at a series of times following shock stimulation of afferent fibers from the olfactory bulb. Cortical layers are indicated at the top (compare with the scale on the left in Fig. 3). Net inward currents (sinks) are denoted by vertical hatching; net outward currents (sources) by stippling. Double-headed arrows denote major sinks.* **(B)** *Same data as in (A) represented as a 3-D surface plot. The layer Ia sink [Ia in (A) and (B)] is the inward current that generates the monosynaptic EPSP in distal apical dendritic segments of pyramidal cells. The sinks in the superficial and deep parts of layer Ib [sup Ib and deep Ib in (A) and (B)] and the small sink in layer III [III in (A) and (B)] are believed to be currents that generate the disynaptic EPSPs mediated by different intrinsic associational fiber systems in proximal apical and basal dendritic segments of pyramidal cells (see Fig. 3). The final sink (II–III) is believed to be associated with the fast chloride-mediated IPSP.* (Modified from Ref. 28.)

The ability of a reduced version of this simulated network to carry out pattern recognition and associative functions has been explored[47]. This learning version of the model consists of a 10 × 10 array of simulated input fibers from the olfactory bulb, and 10 × 10 arrays of simulated pyramidal cells and both feedforward and feedback inhibitory neurons. The afferent array projects to the pyramidal cell and feedforward interneuron arrays in a spatially distributed fashion as in the real system. Pyramidal cells project to other pyramidal cells, also in a spatially distributed fashion providing a distributed positive feedback as also demonstrated in the real system. Both the afferent and association systems are randomly distributed with a 0.05 probability of contacting a given neuron in the receiving populations. The simulated synapses of the distributed positive feedback system and both inhibitory systems are modifiable, but synapses of input fibers are not. Synaptic modification is in activity-dependent fashion using a modified Hebb rule. Excitatory and inhibitory inputs to pyramidal cells are integrated in a neuron-like, nonlinear fashion. Outputs from neurons are all-or-none spikes that are triggered at a discrete threshold.

For studies of learning in this model, stimuli consisting of random spatial patterns across ten of the 100 input fibers were presented as 40 Hz bursts to simulate the oscillatory bulb output, and repeated at 200 ms intervals to simulate sniffing at the θ-rhythm. Learning was defined as development of consistent representations in cortical activity for particular input patterns with repeated stimulus presentations. The model has been found to display several types of memory and associative function. First, it has the ability to reconstruct original stimulus patterns from partially degraded inputs. Second, it has the ability to store and retrieve two non-overlapping input patterns without substantial interference, in spite of the fact that interconnections between pyramidal cells result in overlapping response patterns before training. Third, an ability for enhanced differentiation between two partially overlapping stimuli was demonstrated when each was presented during training with non-overlapping 'state' stimuli. This paradigm simulates learning situations where olfactory stimuli are paired with different environmental cues. Because this model was designed to replicate physiological responses, it makes predictions about patterns of activity that should be seen during normal function[49].

A second model for the piriform cortex is being developed by Granger *et al.*[51] to demonstrate the feasibility of a 'sparse combinatorial' approach to classification of olfactory stimuli. This model also consists of a 10 × 10 array of simulated afferent fibers that projects to a 10 × 10 array of simulated layer II pyramidal neurons in a random, distributed fashion. The olfactory code is assumed to be spatial as in the Wilson and Bower model. Alterations in efficacies of the afferent fiber synapses are made according to a modified Hebb rule in local 'unsupervised' fashion,

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although the exact formulation of the algorithm differs from that of Wilson and Bower. Several types of inhibitory process are assumed in the model including a strong local feedback process that imparts a 'winner-takes-all' response mode on sets of 8–12 pyramidal cells. While there are excitatory interconnections between pyramidal cells as in the Wilson and Bower model, in simulations presented thus far, parameters have been adjusted so that these interconnections contribute little to outputs. There is one particularly intriguing feature of this model: its operation requires that each input line contact a relatively small number of simulated pyramidal cells. This is in contrast to most associative networks where performance is enhanced by increasing the degree of connectivity. Another unique feature that underlies operation of this model is a long-lasting 'refractoriness' in inhibitory and excitatory responses of pyramidal cells. The inhibitory refractoriness, which is based on findings for hippocampal pyramidal cells[52], allows responses to inputs that are repeated at the θ-frequency to be strongly facilitated and trigger lasting changes in synaptic efficacy. The excitatory refractoriness suppresses initial strong responses that result from convergence of many input lines so that more selective responses can emerge during continued presentation of input patterns. Test stimuli consist of spatial patterns involving up to 19 of the 100 input lines. Simulations with this model have demonstrated content-addressable memory capabilities that allow categorization of simulated odors (grouping of similar input patterns) as well as increases in the specificity of responses to partially overlapping stimulus patterns with repeated presentations.

## Concluding remarks

While models for the piriform cortex that have been developed thus far consist of relatively small arrays of simulated neurons, and both simplifying assumptions and assumptions concerning unknown parameters are required, they offer encouragement that the theoretical framework provided by associative, content-addressable memory models will be a useful one for study of the nervous system.

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