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CENTRAL PROCESSING OF OLFACTION

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Summary—Studies on the properties of olfactory receptors and of the olfactory glomeruli indicate that there is spatial segregation of response to particular characteristics of odorant molecules at the input level of the olfactory bulb. Existing anatomical information and studies of synaptic mechanisms in the olfactory bulb suggest that the bulb circuitry might act as a contrast detection mechanism analyzing a spatially organized input. Recent electrophysiological studies have supported this idea. Extracellular recordings have shown that the similarity between responses of cell pairs to the same stimulus odor depend upon the distance between those cells. Intracellular recordings from mitral and tufted cells have shown spatially organized excitatory and inhibitory responses to localized electrical stimulation of the input layer of the bulb. Some of the major interneurons of the olfactory bulb have also been identified during odor and localized electrical stimulation. These recordings are also consistent with a spatially based organization.

This meeting has dealt extensively with recent progress in the study of olfactory receptors. The results of studies of the receptor process and the convergence of the sensory information from the receptors onto the glomeruli of the olfactory bulb have important implications for the central nervous system processing of olfaction. I want to address three particular properties of this convergence that were also discussed in the paper by Shepherd and Firestein [1]. It now seems probable that (A) each discriminable odor activates a unique population of receptor cells even though no cell in that population may respond only to that odor; (B) the size of the population of activated cells may change with the odor concentration; and (C) the axons of the receptor cells group their terminations in the olfactory glomeruli in such a way that each glomerulus acts as a "functional unit", responding to an odor ligand determinant.

These considerations point out that the job of the central nervous system is to recognize or discriminate odors on the basis of combinations of these determinates. There are probably neural microcircuits within the glomeruli that help to force these glomeruli to act as units. There are also likely to be excitatory interconnections between neurons with similar function and inhibitory interconnections between neurons with dissimilar functions. These statements make the implicit assumption that the spatial organization of interneuronal connections in the olfactory bulb and olfactory cortices is important in processing. There are long standing anatomical data to support this idea for the olfactory bulb (see reviews [2–4]), while a spatial organization of the olfactory connections to piriform cortex has usually been denied on anatomical grounds (see review [5]). Physiological data to support spatially based processing, even in the bulb, have been lacking until recently. In this discussion, I would like to summarize some of the data about spatial interactions in the bulb and data dealing with the responses of the major interneurons that must be involved in those interactions, the granule cells and the interneurons around the glomeruli.

INDICATIONS OF SPATIAL ORGANIZATION IN MITRAL CELL ODOR RESPONSES

The most direct functional tests of the spatial representation of odorant determinates within the olfactory bulb circuitry were performed by three groups who tested the odor responses of mitral cell groups separated by different distances. Figure 1 illustrates the logic of these experiments and their results. The general reasoning was that if two cells were so close together that they received their olfactory nerve inputs through the same glomerulus, then they should have very similar responses to a series

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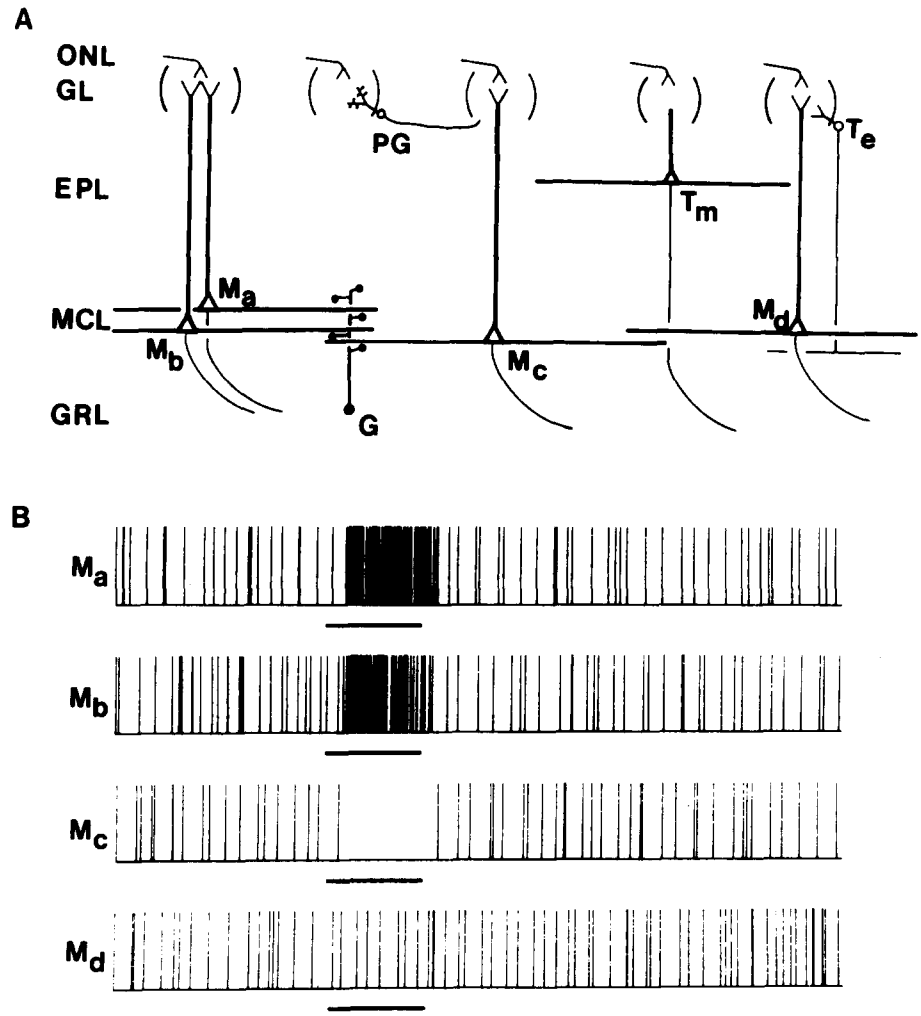

Fig. 1. Schematic of the major cell types of the mammalian olfactory bulb. This figure also illustrates the experiments testing the similarity of mitral cell odor response pairs recorded at various distances. In part A, the curved enclosures represent the glomeruli (GL) which receive olfactory nerve axons via the olfactory nerve layer (ONL). In the walls of the glomeruli are found the cell bodies of periglomerular cells (PG) and of external tufted cells without basal dendrites (T_e). Below is the external plexiform layer (EPL) containing the cell bodies of other tufted cells that do have long basal dendrites, including middle tufted cells (T_m). The mitral cell layer (MCL) contains the cell bodies of mitral cells. In this diagram four individual mitral cells are indicated by the subscripts a–d to indicate their relationship with a population of granule cells (G) whose somata are found in the granule cell layer (GRL). The mitral and tufted cells with basal dendrites are output cells whose axons go to cortical structures. The granule cell and periglomerular cell are inhibitory interneurons entering into dendrodendritic interactions with mitral and tufted cell dendrites. The external tufted cell with no basal dendrites is also an interneuron with an axon confined to the olfactory bulb. The exact terminations and actions of that axon are not known. (Here that axon is shown spreading out collaterals below the mitral cell layer). Panel B shows idealized traces illustrating the extracellular recordings described in the text. The bar under each trace indicates the period of application of an odor to the nose of a rat. The traces are present as though they were all recorded simultaneously. Mitral cells M_a and M_b receive their inputs through the same glomerulus and this communality of input forces them to similar responses. M_c not only receives its olfactory input from a different population of axons entering a different glomerulus, but it receives inhibitory input from the granule cells activated by M_a and M_b. Therefore it has a tendency to be inhibited when those cells are activated. M_d differs in both the glomerular input and in the population of granule cells it contacts. Therefore its odor responses are not closely related to those of M_a and M_b. In this case M_d is represented as having no response.

of odors [6]. A pair of mitral cells separated by a very great distance might have unrelated responses because there is essentially no interaction between them. Mitral cells separated by intermediate distances, that is by distances consistent with sharing the same inhibitory interneurons, might be forced into opposing patterns of response because activation of one of the cells would tend to activate the interneurons and inhibit the other cell [7, 8]. The

effects seen supported these hypotheses. The interpretation depended upon there being an orderly arrangement of the apical dendrites of the mitral cells that carry the inputs from the glomeruli to the somata. This type of arrangement was generally supported by the anatomic study of Buonviso *et al.* [9].

These spatial interactions suggest that inhibitory interactions between cells at different positions in the olfactory bulb are responsible for the fact that mitral cells can show different response patterns when stimulated with different odors. Kauer's [10] classification of odor responses into excitatory and suppressive types reflects this idea because he made it clear that a single mitral cell could display excitatory type responses to one odor and inhibitory responses to another odor. This effect was also demonstrated by Macrides and Chorover [11]. Wellis *et al.* [12] demonstrated that this discriminatory response is independent of odorant concentration by showing cases where the response patterns for two odors differed at all suprathreshold concentrations tested.

It has been suggested that inhibitory interactions in the central nervous system enhance contrasts between activity resulting from activation of different receptor populations [1]. This mechanism is common in sensory systems. For example, retinal ganglion cells have excitatory responses to stimulation in one part of their receptive field and inhibitory responses in another region. Such antagonistic receptive fields were not seen in the two cases where amphibian mitral cell responses were explored by localized stimulation of points on the olfactory epithelium [13, 14]. This failure to see single cells that contained both excitatory and inhibitory regions in their receptive fields could have resulted from the fact that each amphibian mitral cell has inputs through several noncontiguous glomeruli [15, 16], rather than through a single glomerulus as in all mammals studied. In addition, there is evidence that there is some rearrangement of the axons of the olfactory nerve as they enter the bulb in vertebrates [10, 17–19]. This rearrangement may preclude the development of antagonistic receptive fields based simply on position in the epithelium. In the rat, the olfactory nerve layer of the bulb does contain a rather precise parallel arrangement of axons [19]. This raised the possibility of studying the spatial organization of interactions in the bulb by stimulation of the olfactory nerve layer combined with intracellular recording and marking of cells.

INTRACELLULAR RECORDINGS FROM OLFACTORY BULB OUTPUT CELLS AND INTERNEURONS

Recently we have used intracellular recording of identified cells within the olfactory bulb to explore some aspects of spatial coding and of the participation of interneurons in odor responses. Figure 2 shows some typical recordings from mitral/tufted cells, granule cells and cells of the periglomerular regions (tentatively identified as either periglomerular cells or external tufted cells without basal dendrites). These identifications are based on intracellular fills as well as certain functional criteria, including antidromic activation and response to paired electrical stimulus pulses [12, 20, 21]. The preparation we use allows for both odor stimulation and localized electrical stimulation of the olfactory nerve layer. In these experiments, the behavior of tufted cells with basal dendrites (such as T_m in Fig. 1) was generally similar to that of mitral cells. For simplicity, I will refer to these as large tufted cells.

Odor responses of different cell types

There are systematic differences between the types of responses exhibited by the major cell types that may give clues to their function in sensory processing. The mitral cells and large tufted cells with basal dendrites both display complex responses to odors. These responses often have both excitatory and inhibitory components. One such response is illustrated in Fig. 2(A) for a mitral cell. For each odor, the first sniff elicited a large hyperpolarization that prevented spiking for a brief period. This hyperpolarization was followed by a strong depolarization and intense spiking. In many of these cells the size of the initial hyperpolarization declined markedly and reliably for the second and subsequent sniffs. As pointed out above, the form of these responses by mitral cells and large tufted cells often changes with the stimulus odor.

The odor responses of granule cells and cells of the periglomerular regions are also illustrated in Fig. 2. These cells tend to show simpler responses than the mitral and large tufted cells. Granule cells usually respond to odors with a depolarization and often with a few spikes [Fig. 2(B)]. In our population of 15 granule cells

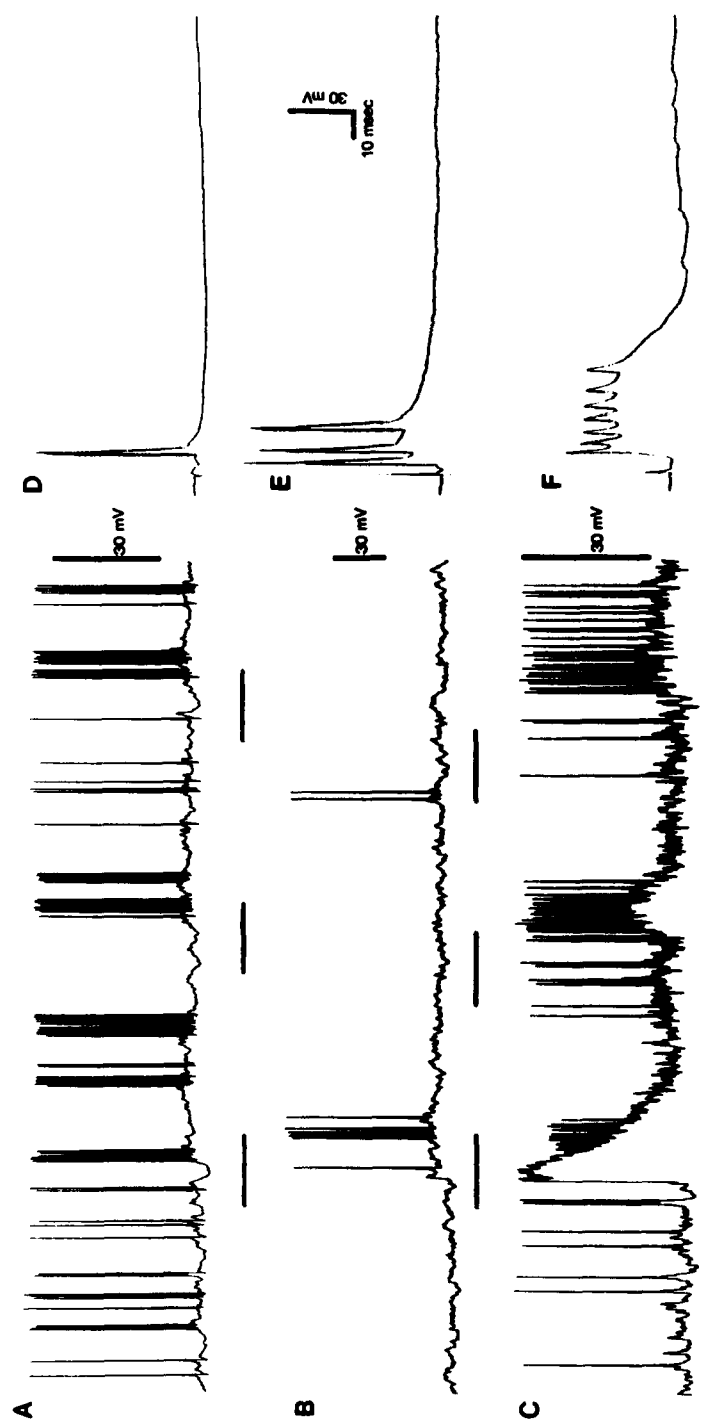

Fig. 2. Examples of responses to odors and electrical stimulation. (A) The response of a mitral cell to the presentation of three inspirations of an odor stimulus (represented by bars under the trace). Note that the odor presentation produces a hyperpolarization that suppresses the spontaneously occurring spikes. That hyperpolarization is often more pronounced during the first inspiration, as represented here. The odor stimulus was amyl acetate. (B) The response of a granule cell to a similar sequence of odor presentations. In this particular cell, there was a pronounced depolarization and spiking during the first inspiration, but the response was diminished to the subsequent stimuli. Membrane potential -72 mV. The odor stimulus was amyl acetate. (C) Odor responses of an interneuron of the periglomerular region. This cell showed a very intense depolarization to some odors. This depolarizing response habituated greatly to successive inspirations for this odor (amyl acetate) but showed sustained responding to a second odor (ethyl butyrate). Membrane potential -60 mV. The odor stimulus was amyl acetate. (D) Mitral cell response to a single pulse stimulation of the olfactory nerve. Note the single spike followed by a hyperpolarization. Tufted cells, such as T_m in Fig. 1, show a qualitatively similar response except for a greater number of spikes. (E) Granule cell response to single pulse stimulation of olfactory nerve. These cells are recorded below the mitral cell layer and usually show multiple spike responses to olfactory nerve stimulation and (F) interneuron of the periglomerular region. These cells show single spike responses to olfactory nerve stimulation at threshold, but at suprathreshold stimulation they show a very long depolarization triggered by the first spike. Note that this depolarization can be even longer when it is driven by odor as in part (C) of this figure.

tested with odors, only 1 showed suppression of ongoing spikes during odor responses. The interneurons of the periglomerular region show marked depolarizations and high rates of spiking elicited by odors [Fig. 2(C)]. One characteristic of these responses is that they often habituate rapidly to some odors. This rapid habituation is complementary to the habituation of the early IPSP seen in many mitral/tufted cells [Fig. 2(A)] and suggests that these superficial interneurons may be involved in driving that early IPSP.

Responses to direct stimulation of the nerve layer

The characteristic responses to nerve stimulation by mitral and large tufted cells, by granule cells, and by the interneurons of the periglomerular regions are illustrated in Fig. 2(D–F). As noted previously mitral and large tufted cells respond to nerve stimulation with a depolarization and long hyperpolarization [2, 3, 22] [Fig. 2(D)]. The most obvious differences between the mitral and large tufted cells are in their probability of spiking during this depolarization (see discussion of spatial aspects of electrical stimulation below). Granule cells respond to nerve stimulation by a large depolarization and multiple spiking followed by an IPSP [3, 21] [Fig. 2(E)].

The interneurons we have observed in the periglomerular region display a characteristic response [21]. At threshold, they respond with one or two short latency action potentials, but at higher stimulus intensities they produce a long-lasting depolarization that may evoke several spikes. This characteristic, which is very different from that of other cells observed in the bulb, along with several fills showing that they have dendrites confined to one glomerulus led us to tentatively identify them as periglomerular cells. It remains to be demonstrated with better fills whether they show the dendritic spines and axon characteristics of the morphologically identified periglomerular cells [23, 24].

The response of these periglomerular region interneurons may have important implications for the postulate of the glomerulus as a functional unit. This idea has achieved wide acceptance because stimulation with single odors evokes extracellularly recorded DC shifts that appear to be localized to single glomeruli [25] and restricted spots of 2-deoxyglucose labeling [26–28]. The mechanism by which many elements in the same glomerulus are simultaneously activated is unknown, although there are suggestions that the glial sheath around the glomerulus may confine extracellular potassium or neurotransmitters [29, 30]. The highest 2-deoxyglucose uptake may actually be in the cell wall of the glomerulus [31], which is made up of somata of periglomerular cells and small tufted cells [23, 24]. The massive depolarization and spiking of the cell population that we have described could well make a substantial contribution to both the 2-deoxyglucose results and to the extracellular fields produced by odors. Whether these cells simply reflect a strong depolarization produced by extracellular mechanisms or they produce the responses by inherent membrane properties, such as voltage sensitive calcium channels, remains a subject for future study.

Spatial aspects of these responses

Using this approach for cell recording and identification along with localized stimulation of the olfactory layer, we have seen that the olfactory bulb has a functional spatial organization. Figure 3 presents a scheme that is generally supported by our results but for which many of the details are missing. It summarizes the orthodromic influences on mitral cells, large tufted cells and interneurons based on our experience with extracellular recordings and intracellular recordings such as those of Fig. 2(D–F). The typical mitral cell has a rather small excitatory zone, perhaps corresponding to the glomerulus through which it receives its olfactory nerve synapses. Even in that zone, a stimulus may not drive it to spike, and we have speculated that firing a mitral cell may require not only excitatory input at its glomerulus, but some diminution of tonic inhibitory drive [12]. A mitral cell has a wide region from which inputs cause inhibition, although it is not yet certain whether this region is exactly coextensive with its basal dendrites. The large tufted cells usually respond with big depolarizations, multiple spikes and smaller hyperpolarizations. In addition, they can be driven to spike by stimuli delivered to more widely spaced sites on the nerve layer [12, 20]. The mechanism for the wider excitatory region is not yet clear, but we suspect that there may be excitatory interneurons involved.

Morphological and modeling studies had suggested that granule cells would mediate spatial interactions like the ones summarized above because of their contacts with the long basal dendrites of mitral and tufted cells

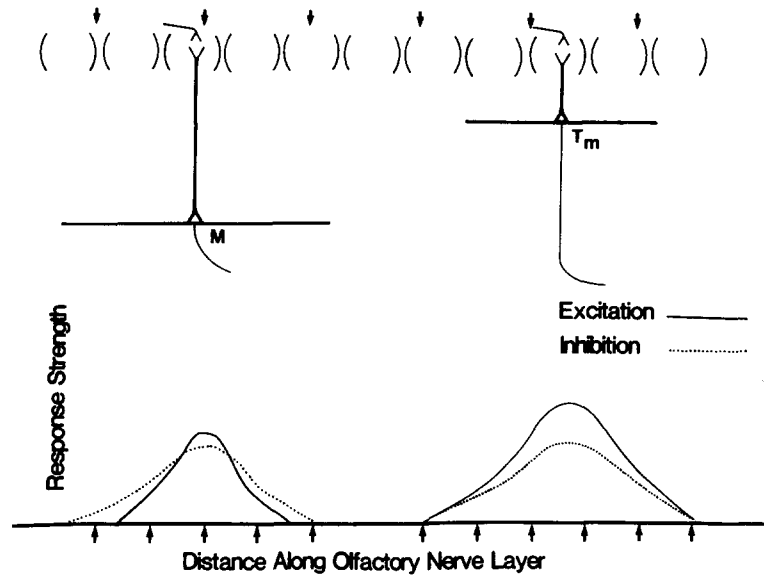

Fig. 3. Schematic of the distributions of excitatory and inhibitory influences on mitral and tufted cells. The mitral and large tufted cell are represented as in Fig. 1. The arrows along the olfactory nerve layer represent the placement of stimulating electrode along that layer for testing the spatial distribution of effective inputs. The distance between the electrodes is actually 400 μm, equal to the width of several glomeruli. Because of this distance, it is not possible to center one electrode directly on the glomerulus containing the apical dendrite of a particular cell. The lower part of the figure illustrates a rough estimate of the effective excitatory and inhibitory influences on mitral cells (left) and large tufted cells (right). The excitatory input distributions are based on probability of spiking responses [20, 33]. The inhibitory input distributions are based on the sizes of IPSPs recorded in mitral and tufted cells [such as those observed in Fig. 2(B) of this paper] (Scott, Wellis and Priddy, unpublished data). The spatial distribution of spiking responses by granule cells is consistent with their driving inhibitory inputs in mitral and tufted cells with these distributions [33].

(cf. [32]). Granule cells can be identified by their physiological properties during intracellular recording [3] and have been shown to be activated during odor stimulation [21]. We applied the technique of local stimulation of olfactory nerve layer to a population of 20 granule cells [33]. These granule cells also show an optimal site for stimulation, in that one site produces the largest EPSPs, lowest spike thresholds, and the greatest probability of spiking. The response of these cells is systematically poorer at sites spatially removed from this best site. The distribution of these granule cell responses is consistent with their driving the inhibitory responses in mitral and large tufted cells illustrated in Fig. 3.

From these recordings we conclude that mammalian mitral cells can have spatially organized input fields with excitatory centers and inhibitory surrounds. The large tufted cells show similar effects, except that the centers are larger and the inhibition is not as strong. This input field organization may not be a perfect reflection of the distribution of activated receptor cells and, therefore, probably should not be spoken of as a receptive field organization. I raise this caution because we know that there is considerable rearrangement of the axons of the olfactory nerve as they enter the olfactory bulb in spite of a generalized topography (see [34]). This rearrangement of axons may well contribute to the organization of unitary function in glomeruli by collecting together axons of similar chemical natures to particular spatial loci. Therefore it is more appropriate to think of these spatial interactions as acting on a transformed representation of the receptive field; it has been suggested that this transformation results in the spatial isolation of odor determinates [1]. It remains to be seen whether the representation of these odor determinates is arrayed in an order that corresponds to functional or behavioral significance and how the spatial interactions that we have observed may participate in the comparison of the odor determinates.

CONCLUDING COMMENTS

While there is evidence that there are some specific pheromone like responses in mammals that are related to specific odorants exciting

particular regions of the olfactory bulb [35, 36], there is also evidence that these responses are modifiable by experience [37] and that they can survive extensive damage to the neural circuitry. Most behavioral responses to odors in mammals are likely to have a learning component. For this reason the general circuitry involved in odor discrimination is of interest when we think of odors of behavioral significance. A number of mathematical and network models have been developed for the study of central olfactory processing [29, 38–40]. In general they have simplified this circuitry, ignoring anatomical differences between cell types and using as outputs the response of bulbar EEG or mitral cell spikes to odors. The difficulties of specifying the odor stimulus exactly and of getting quality information out of the mitral cell spike train have limited the testability of these models. The data reviewed here show that other important data about the spatial distribution of responses and about the responses of interneurons can be obtained. These data should greatly enhance our ability to build and evaluate models of the bulb. Certainly good models are the only way we can digest and interpret the growing amount of information about how the central nervous system analyses odors and learns to respond to their changing significance in the environment. It is my contention that strong spatial interactions exist within the olfactory bulb and these should be an important aspect of successful models.

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