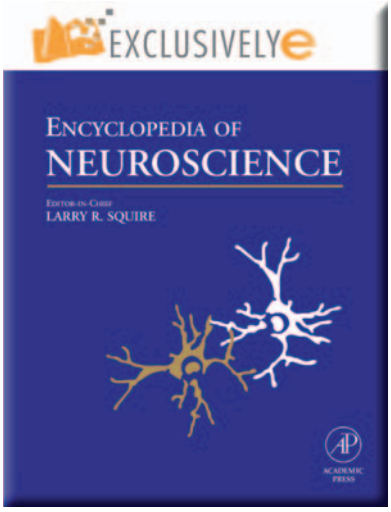

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Olfactory Coding

M Bazhenov, The Salk Institute for Biological Studies, La Jolla, CA, USA
M Stopfer, National Institutes of Health, Bethesda, MD, USA

Introduction

Olfactory circuitry provides unique advantages for the analysis of information processing by neurons. The task of olfaction is challenging; it demands the ability to rapidly detect, identify, categorize, and prepare for memory storage of myriad odorants that vary in molecular structure and concentration. Yet, olfaction is achieved by relatively few layers of neurons, with anatomical structures and physiological mechanisms that appear repeatedly in widely divergent species. Thus, a study of olfaction offers the promise of insight into a successful and perhaps optimal biological algorithm for processing complex information. Theoretical and computational approaches have contributed substantially toward understanding the functions of olfactory circuitry.

Much current thinking about olfactory processing has been shaped by the compelling observation that the projections of olfactory receptor neurons delineate spatial maps within the olfactory bulb: histological and *in situ* hybridization studies demonstrate convincingly that receptor neurons expressing the same receptor gene converge on a small and specific subset of glomeruli. Based on these observations and on electrophysiological evidence, a model of olfactory information processing has emerged that proposes that individual structural features of odorants are recognized by different receptor neurons, each expressing a specific receptor gene, and that each receptor cell responds to many odorants sharing the same structural features. According to one version of this model, each odorant elicits responses from, and is thus represented by, a more or less static map – a unique spatial ensemble of activated glomeruli.

In addition to such results, a variety of experimental approaches have revealed that olfactory neurons (and those of other sensory systems as well) respond to a static stimulus with oscillatory and temporally structured responses. An example of temporal structure in responses of the olfactory system is the relatively slow, complex sequences of excitation and inhibition in olfactory neurons superimposed on stimulus-evoked oscillations. These patterns have been observed in neurons of the olfactory bulb of amphibians and mammals and within the antennal lobe of insects. In the locust olfactory system, these slow temporal firing patterns generally vary with the odor, and they are reproducible over repeated trials. Intracellular recordings made *in vivo* from locust antennal lobe projection neurons (PNs) have also revealed that individual PNs transiently phase-lock with population oscillations at times that vary with the stimulus. Thus, there is a fine temporal structure to the timing of PN action potentials within the population response that is stable over trials and is different for different PNs. This temporal structure appears to arise mainly from circuit interactions within the antennal lobe. Evidence for odor-evoked spatiotemporal patterns of neuronal activity is not unique to the insect; in salamander olfactory bulb complex spatiotemporal patterns of activity were revealed by voltage-sensitive dye imaging. Recordings from the turtle olfactory bulb have revealed that different assemblies of cells are activated during different cycles of field oscillations, supporting the hypothesis that odors are encoded by spatiotemporal patterns. Thus, the antennal lobe and olfactory lobe appear to process, or reformat, the olfactory information from a diverse population of receptors into a spatiotemporal code.

In vertebrates, output fibers from olfactory bulb neurons project onward to another level of processing in the olfactory (piriform) cortex. In insects, odor information processed in the antennal lobe is transferred to the mushroom body, a structure analogous to the olfactory cortex, and one important for memory formation. Normal cyclic AMP signaling specifically in mushroom body neurons is required for olfactory learning. In honeybees, mecamylamine injection into the mushroom body calyces strongly impaired olfactory learning, suggesting that the cholinergic network in the mushroom body is involved in memory formation. Genetic studies indicate that synaptic transmission from mushroom body neurons is required during memory retrieval but not during memory acquisition or storage. This indicates that acquisition and storage of olfactory memory may both occur upstream of synaptic transmission from the mushroom body, and it suggests that processes contributing to associative learning may reside within mushroom body neurons.

Whatever strategies the antennal lobe or olfactory bulb employs for encoding odors, its follower mushroom body, olfactory cortex, or other circuitry should be able to decode and categorize the information it receives. Therefore, it is of great interest to explore how odor decoding strategies at the downstream levels (mushroom body or olfactory cortex) match the encoding achieved at the first olfactory relay

(antennal lobe and olfactory bulb), providing efficient and optimal odor information processing. In this article, we discuss these coding strategies and specifically emphasize the use of computer models to test several interesting hypotheses of odor encoding and processing.

Encoding Olfactory Information at the First Olfactory Relay

The relative simplicity of the invertebrate olfactory system makes it an attractive system for theoretical and computational studies of olfactory coding. In the locust, each antenna contains approximately 50 000 cholinergic olfactory receptor neurons (numbers range from 2000 to 350 000 in different insect species) that send their axons to the ipsilateral antennal lobe. There, each axon terminates in a few glomeruli, where it forms synapses with the dendrites of GABAergic local neurons (LNs; ~300 in locust) and cholinergic projection neurons (PNs; ~830 in locust). PNs provide the only pathway for olfactory information from the antennal lobe. The number of glomeruli varies among insect species (e.g., from ~50 in *Drosophila melanogaster* to ~1000 in locust). Within the antennal lobe, PN projections can be mainly uniglomerular (e.g., *D. melanogaster*, bee, and cockroach) or multiglomerular (e.g., locust and wasp). Each PN makes connections with a large fraction of LNs, and each LN connects with many PNs as well as with other LNs.

PNs of the antennal lobe provide olfactory input to the mushroom body. In the locust, each mushroom body contains approximately 50 000 Kenyon cells (KCs). In addition to the direct excitatory input from PNs, the KCs of the locust mushroom body also receive competitive, inhibitory input, provided by lateral horn interneurons, which are themselves driven by PNs.

To a remarkable extent, the antennal lobe shares many features with the vertebrate olfactory bulb (OB). Similar to LN–PN circuitry of the antennal lobe, the OB includes interacting excitatory mitral cells and inhibitory granular cells. Lateral inhibition has been reported between granule/periglomerular cells of OB. Axons of the mitral cells project to the olfactory cortex, where they make connections with pyramidal cells and inhibitory interneurons that provide feed-forward inhibition to the pyramidal neurons. The anatomy and functions of OB circuitry are under intensive study.

In this article, we focus on computational approaches to olfactory coding in the insect olfactory system, emphasizing, when possible, similarities to the vertebrate system.

Oscillations and Fine Temporal Structure of Spiking in Olfactory Neurons

The presence of odor-elicited oscillations in the olfactory systems of many animals including insects suggests that oscillatory neural synchrony may play a fundamental role in odor encoding. A number of experimental results provide strong support for this idea. In the locust, pharmacologically blocking the inhibitory $GABA_A$ receptors in the antennal lobe by locally injecting picrotoxin eliminates the 20 Hz oscillations and leads to a breakdown in the specificity of odor responses in beta lobe interneurons, which are followers of KCs. Furthermore, behavioral experiments with honeybees demonstrate that oscillatory synchronization of the antennal lobe neurons is needed for fine odor discrimination; picrotoxin-induced antennal lobe desynchronization causes a loss of precise odor discrimination. Similarly, suppressing synchronous oscillations in the procerebral lobe of the terrestrial slug *Limax* by blocking nitric oxide with L-NAME impairs the animal's ability to discriminate between similar odorants.

In insects, physiological studies in which $GABA_A$ receptors were blocked with picrotoxin indicate that fast feedback inhibition within the antennal lobe is essential for the generation of network oscillations during odor stimulation. Also, similar roles for feedback inhibition mediated by local interneurons have been established for many well-investigated brain models, including those for cortical and hippocampal gamma oscillations. In these models of synchronized network oscillations, spikes in excitatory cells trigger spikes in postsynaptic inhibitory neurons, whose spikes in turn produce inhibitory postsynaptic potentials in excitatory cells. This inhibition systematically delays and synchronizes the generation of the next excitatory response, thereby creating widespread network oscillations. The frequency of the oscillations depends on the time constant of inhibition and synaptic conductance strength. **Figure 1** presents an example of periodic oscillations recorded *in vivo* from the locust antennal lobe (**Figure 1(a)**) and comparable oscillations simulated by a computational network model of the antennal lobe (**Figure 1(c)**) that includes populations of randomly connected PNs and LNs stimulated by an external input (**Figure 1(b)**). The oscillations in the model were triggered by a constant (except for low-amplitude additive noise) depolarizing input to an odor-specific subset of antennal lobe neurons (**Figure 1(b)**) and were mediated by excitatory–inhibitory connections between PNs and LNs.

Oscillation-generating networks in a variety of species have been studied with computational models. Typically, the emergence of synchronized oscillations has been shown to depend on fast feedback inhibition

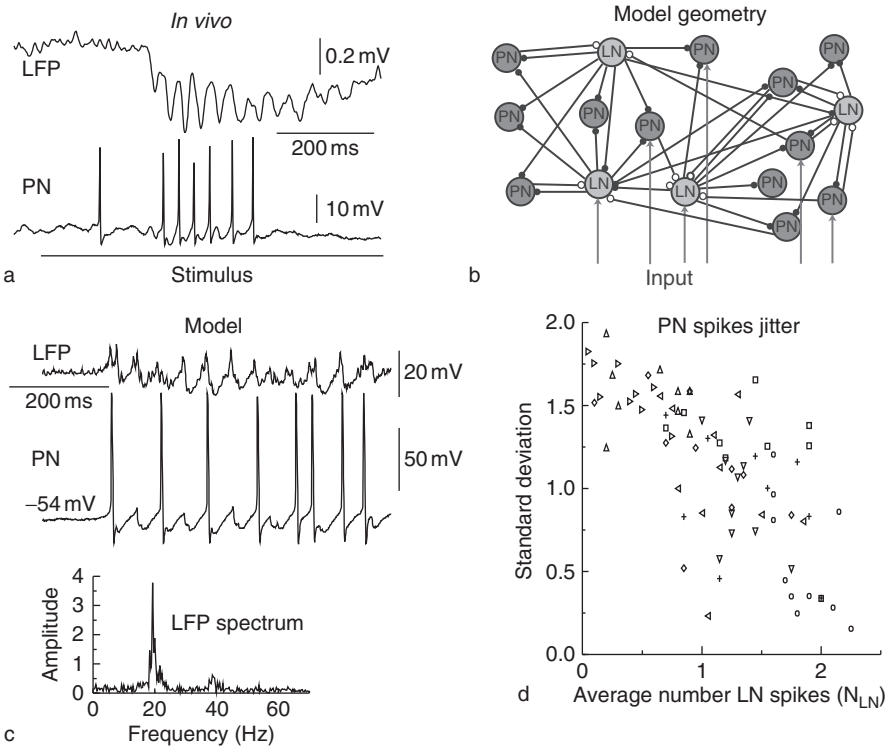

Figure 1 Synchronization of PN responses in the antennal lobe. (a) Typical odor responses recorded *in vivo*. Odor stimulation evoked oscillations in the local field potential (top, recorded in the mushroom bodies) and action potentials in a PN (bottom). (b) Antennal lobe model. (c) Averaged PN activity (LFP) in the model shows periodic oscillations at approximately 20 Hz during stimulation. (d) For each PN, standard deviation of PN spike phases across trials plotted against the total number of LN spikes in all presynaptic LNs. Adapted from Bazhenov M, Stopfer M, Rabinovich M, et al. (2001) Model of transient synchronization in the locust antennal lobe. *Neuron* 30: 553–567, with permission from Elsevier.

within a circuit. Ermentrout and colleagues described stimulus-evoked synchronization of olfactory neurons in a model of the *Limax* olfactory lobe that requires input from inhibitory interneurons. A model of spike synchronization in the honeybee antennal lobe, also dependent on local inhibition, has been proposed by Linster and Cleland to explain the experimentally observed impairment of sensory discrimination when inhibition is blocked. Also, a role for inhibition in memory formation in the *Limax* olfactory lobe has been proposed by Ermentrout and colleagues. In this model, global inhibitory connections between oscillating cells were proposed to suppress activity in all but a small population of neurons, thus forming a single and unique 'memory band.' In this model, odor localization was transient and became possible only after the network activity was synchronized.

Interestingly, antennal lobe oscillations are generally not evoked by the first presentation of an odorant. As shown by Stopfer and Laurent, oscillations emerge gradually during the course of multiple encounters with a given odorant, provided the encounters occur close together in time. Electrophysiological and computational evidence suggests that the gradual increase in oscillatory synchronization results from activity-dependent neural plasticity within the antennal lobe. Models of this mechanism proposed by Bazhenov and colleagues indicate that this plasticity, when engaged by repeating odor stimuli (as often occurs in nature), achieves robust stability against noise. Such stability is essential in a neural system that works to amplify small differences in input patterns.

Odor-induced oscillatory activity in the gamma (30–60 Hz) frequency range has been described in many mammals, including primates. Despite intensive studies, the primary mechanism for generating these oscillations is unclear. Olfactory bulb circuitry includes feedback inhibition mediated by granule cells. Interactions between granule and mitral cells in the OB appear to resemble those between the PNs and LNs of the insect antennal lobe. A number of computational models support the idea that excitatory–inhibitory interactions between mitral cells and granule cells could underlie gamma oscillations in the OB. This hypothesis is also supported by recordings from OB neurons under conditions that mimic natural odor stimuli. Electrical coupling between mitral cells whose primary dendrites form

synapses within the same glomeruli appears to enhance the synchrony of mitral cell oscillations. However, important questions remain. The relatively slow decay time of inhibition from granule cells may not be consistent with the synchronization underlying fast oscillations observed in mitral cells. A different type of model suggests that aperiodic but correlated input from widely branching granule cells could provide for the synchronization of mitral cells. Galan and colleagues showed that the slow inhibition from granule cells can lead to the synchronization of mitral cells in the gamma frequency range when partially correlated aperiodic fluctuations are fast and mitral cells fire at a rate that is roughly constant.

Computational modeling work has led to several alternative proposals for mechanisms for the synchronization of olfactory neurons in the OB. One mechanism that does not rely on synaptic interactions among neurons within the bulb but, rather, on common oscillatory drive from receptor cells has been suggested by Hopfield and Brody. According to this model, mitral cells synchronize when they receive similar inputs during odor stimulation. If this input represents the sum of common drive from receptors, and a random bias current which is different for different mitral cells is applied, then only a fraction of the mitral cell population would become synchronized during a given odor stimulation. This and number of other models suggest, therefore, that similar to antennal lobe dynamics, the patterns of synchronization across mitral cells are critical for odor representation in the OB.

A model of the OB based on chaotic attractors has been proposed by Skarda and Freeman. In this model, the resting state of the OB before odor recognition is chaotic; this state keeps the bulb far from equilibrium and allows a more rapid conversion to limit cycles (corresponding to previously reinforced odorants) during odor recognition.

In the locust, $GABA_A$-dependent synchronization of a given pair of PNs is generally transient. Usually after only a few hundred milliseconds of firing spikes that are phase-locked to the oscillations, the synchrony between action potentials in a given PN and the field potential oscillations is lost; then, other subsets of PNs become synchronized. However, the times during repeated trials at which a given PN will phase lock are reliable and odor specific. A number of hypotheses have been proposed to explain mechanisms behind such odor-specific, transient synchronization of the olfactory network. Computer models of the locust antennal lobe have suggested that the transient nature of PN synchronization could be explained by variations in inhibitory drive from inhibitory LNs over the duration of the odor-elicited response. In a model by Bazhenov and colleagues, as *in vivo*, a portion of the PNs become phase locked to the oscillatory local field potential at different times when driven by an odor; the identities of the PNs and the times at which they phase-lock change when a different stimulus is presented. When the activity of sets of LNs that are presynaptic to each PN in the network, and for each cycle of oscillation, was analyzed, it became clear that the total number of Ca^{2+} spikes in presynaptic LNs and the degree of coordinated firing in their PNs were highly correlated (**Figure 1(d)**). As feedback inhibition increased in strength, the timing precision of PN spikes across trials also increased: Jitter in PN spike timing decreased (**Figure 1(d)**). Note that in this model, inhibition only controls the timing of PN spikes when PN firing is induced by excitatory input from receptors. In other studies, disinhibition complimented by intrinsic conductances could trigger firing in PNs. Factors such as lateral LN–LN inhibition, spike adaptation in LNs, and the identities of activated neurons contribute to the variations in LN activity in this model, consistent with other theoretical studies.

A number of computational models have also investigated a potential role for lateral inhibitory projections in contrast enhancement – a process hypothesized to amplify differences between sensory representations, improving the signal-to-noise ratio. In these models, stronger inputs typically suppress nearby, weaker inputs. Some models of the OB implement contrast enhancement either at the level of lateral mitral cells dendrites (by granule cells) or at the glomerular layer (by periglomerular cells). It was shown by Linster and Hasselmo that the latter mechanism could help keep the number of active mitral cells stable, independent of the intensity of the olfactory input. Earlier models explored a potential role for lateral inhibition in promoting competition among olfactory glomeruli, and a model of olfactory memory based on altering lateral inhibition in the honeybee's antennal lobe was proposed by Linster and Masson. Computational studies by Linster and colleagues suggest that the contrast enhancement between odorants in the honeybee antennal lobe is best achieved when inhibition between each pair of glomeruli is organized based on glomerular odor response profiles rather than on anatomical neighborhood relations. Further experimental and modeling work is needed to clarify the possible role of lateral inhibition in contrast enhancement in the olfactory system.

Slow Temporal Patterning of Olfactory Neuron Responses

Experiments performed *in vivo* have established that only the synchronization of PNs in the insects'

antennal lobe is eliminated by picrotoxin; the slower firing pattern structures (alternating periods of depolarization and hyperpolarization) remain intact. Such temporal structure has been described in the projection neurons of locusts and *Drosophila*, as well as in the mitral cells of vertebrates. To explain the origins of slow temporal patterns in the insect antennal lobe, two alternative hypotheses have been proposed and evaluated using computer models. According to a model by Bazhenov and colleagues, the slow inhibitory receptors between LNs and PNs, which are not sensitive to picrotoxin and which operate with a time constant of a few hundred milliseconds, could account for the stimulus-specific slow temporal patterning of PN responses. When slow inhibition was provided in this model, odor stimuli induced characteristic slow temporal patterns in the responses of individual cells. The pattern consisted of alternating depolarizing modes, during which Na^+ spikes were generated, and hyperpolarizing modes, during which only subthreshold oscillations were evident in PNs. Each mode usually lasted a few hundred milliseconds, in agreement with recordings made *in vivo*. The sequences in which these modes appeared differed among PNs and varied reliably with the stimulus. Blocking slow inhibitory receptors in the model, a test not currently possible in the locust, eliminated the slow temporal patterns; groups of PNs then showed similar responses that did not vary when a new stimulus was applied. Also, similar to findings obtained *in vivo*, the slow temporal patterns in individual PN responses remained essentially intact after the model's $GABA_A$ inhibition was blocked.

Work on *Drosophila* by Olsen et al. suggests that excitatory interactions within the antennal lobe, likely mediated by interneurons, also contribute to the spatiotemporal structure of olfactory responses.

In a model proposed by Sivan and Kopell, relatively slow calcium and calcium-dependent potassium channels of PNs, rather than slow inhibitory input from LNs, were used to provide for picrotoxin-resistant slow temporal patterning in projection neurons. This model, as well as the one by Bazhenov et al., displayed little change in the average firing rate of PNs after the blockade of fast inhibition, in agreement with experimental data from locust. Both approaches highlight the power of computational modeling because they lead to predictions that can be tested *in vivo*.

A possible role for inhibitory input from granule cells in controlling mitral cell firing rate has been explored in a simplified model of the OB by Linster and Gervais. This model demonstrated that modulation of granule cell inhibition can alter the firing frequencies of mitral cells and can also decrease overlap between output patterns. Reminiscent of models of the insect antennal lobe, this study suggests that alternations of granule cell activity over the duration of an odor response can mediate odor-specific slow temporal patterning in mitral cell activity.

In *Drosophila*, Wilson et al. have shown that the extent of activity and the complexity of temporal responses in groups of PNs exceed those of the sensory neurons that provide direct input. What is the functional significance of the temporal structure in olfactory neuron responses? As shown by Friedrich and Laurent, in zebra fish, the slow temporal patterning in mitral cells appears to play a major role in the decorrelation of odor representations. The responses of a population of mitral cells to chemically similar odorants were highly correlated immediately after the onset of the odor stimulation, but they became progressively less correlated over the duration of the odor response. This type of gradually evolving decorrelation was also tested by Bazhenov and colleagues with a computational model of the locust antennal lobe. When similar odors were presented, the response patterns of PNs at first greatly overlapped. Over the course of a few hundred milliseconds, overlaps between the distributed firing patterns representing similar odorants decreased, and the initial clusters of activated PNs disappeared; cross-correlations between PN activity patterns (calculated across all PNs) was reduced by 30–50%. These works suggest that the intrinsic dynamics of antennal lobe circuitry depend on interactions between PNs and LNs, and such dynamics can amplify small differences between similar odors, thus improving odor discriminability over time. Therefore, the evolving temporal structures appear to be important for the resolution of odor identity. However, behavioral evidence obtained from rodents suggests that some olfactory tasks can be achieved within the time of a single sniff, less than 150 ms. In another study, it has been proposed that spatial representation of odor in the OB evolves across a sniff; therefore, difficult discriminations of similar odors may require the olfactory system to 'wait' for later activated components.

Decoding Olfactory Information at Downstream Levels of Processing

In insects and vertebrates, output from relatively small populations of olfactory neurons in the antennal lobe or the OB fans out broadly to large interneuronal ensembles in the mushroom body or the olfactory cortex. Work on locust by Jortner et al., for example, demonstrates that half of all PNs synapse directly upon each KC, a connectivity scheme that maximizes the coding space available for odors.

Electrophysiological recordings from insects indicate that KCs of the mushroom body respond with high specificity to odors: A given odor induces a reliable response in only a very small subpopulation of KCs. Several mechanisms operating in parallel appear to contribute to this response specificity, including the intrinsic nonlinear membrane properties of the KCs. Intracellular recordings from KCs suggest that activation of certain intrinsic conductances can amplify and sharpen excitatory postsynaptic potential-in'duced depolarizations, thus generating narrow time windows during which KCs can integrate inputs from multiple PNs. Another mechanism, drawing on inhibitory input from lateral horn interneurons (LHIs), regulates the integration window as well: Feed-forward inhibition from LHIs, which are driven by PNs, faithfully follows, with a delay, the periodic excitation of KCs by PNs, thus creating independent and brief temporal windows over which KCs can summate their input from PNs. The existence of these relatively short integration windows suggests that KCs are extremely sensitive to synchronized inputs from the antennal lobe; KCs may respond only when sufficient numbers of input spikes arrive together.

A realistic computer model by Bazhenov and colleagues of an olfactory network endowed with coincidence detection properties was used to test the extent to which KCs can detect synchrony in the input spike trains from a population of PNs (**Figure 2(a)**). Each stimulus consisted of many spike trains, which were delivered to a single cell through a large set of distributed cholinergic synapses. Individual spike trains had temporal structures designed to match experimentally observed PN firing patterns and included transient synchrony among synaptic inputs. For each stimulus, only a very small fraction of KCs responded reliably with a Na^+ spike on each trial despite small variations in the inputs from one trial to the next (input spike number and timing were slightly varied) (**Figure 2(b)**). As *in vivo*, different KCs spiked at different times, and their spike timing depended on the timing of transient correlations between inputs. In most cases, however, KCs were silent or produced only a few random spikes when input spikes happened to coincide, exceeding the KC's threshold. Results from this computational model suggest that a network of KCs with a sufficiently small integration window can respond with a unique spatiotemporal pattern for different inputs, decoding the correlation structure of the input spike train.

Modeling work by Assisi et al. indicates that the integration window of KCs can vary with odor concentration. Higher concentrations of odors, which elicit greater oscillatory synchrony, also elicit stronger feedback inhibition from LHIs. The resulting shifting balance of coordinated excitation and inhibition maintains the sparseness of spiking in KCs over wide ranges of stimulus intensity.

Physiological and modeling results from Cassenaer and Laurent indicate that the precise timing established by antennal lobe circuitry is maintained not only within KCs but also by their neural followers in the beta lobe. Interestingly, odor-specific timing precision is maintained in the beta lobe neurons, in part, by spike timing-dependent plasticity.

Modeling studies of odor decoding in the mushroom body further suggest that a strategy of coincidence detection offers a number of advantages for encoding sensory information compared to a classical integrator model. The sensitivity of a coincidence detector to timing on a very fine scale provides an additional coding dimension that could allow the olfactory system to discriminate between similar odors, whose neural representations may differ only in the fine temporal structure of the antennal lobe input. In contrast, a decoding system integrating over longer timescales would have no such ability. Furthermore, because the coincidence detector model focuses on specific time windows within an oscillation cycle, in agreement with theoretical studies in other systems, it is thus less sensitive to uncorrelated noise in its input. When the KC model operating as a coincidence detector was explicitly compared to an integrator model possessing a large integrating window, the integrator model showed much greater sensitivity to the presence of random noise in the input (**Figure 2(c)**). In the locust, these coincidence detection mechanisms provide a powerful strategy with which to solve complex problems that every olfactory system encounters.

In the olfactory cortex, local inhibitory interneurons receive afferent input and provide feed-forward inhibition to the pyramidal cells, thus creating a circuit that can operate as a precise coincidence detector. This circuitry is similar to that found in insect mushroom body. It is unknown, however, whether the vertebrate olfactory system utilizes a similar coding strategy. Many types of studies in this rapidly developing field are under way. Studies in mice have shown that afferent inputs from mitral cells connected to specific OB glomeruli terminate in broad patches which overlap with the terminal patches of other glomeruli. As a result, individual odorants are represented by subsets of sparsely distributed cortical neurons. Individual pyramidal cell of the olfactory cortex can make a few thousand connections to other pyramidal cells, further facilitating the redistribution of afferent activity patterns. Furthermore, molecular analysis strategies applied to mouse olfactory cortex have revealed

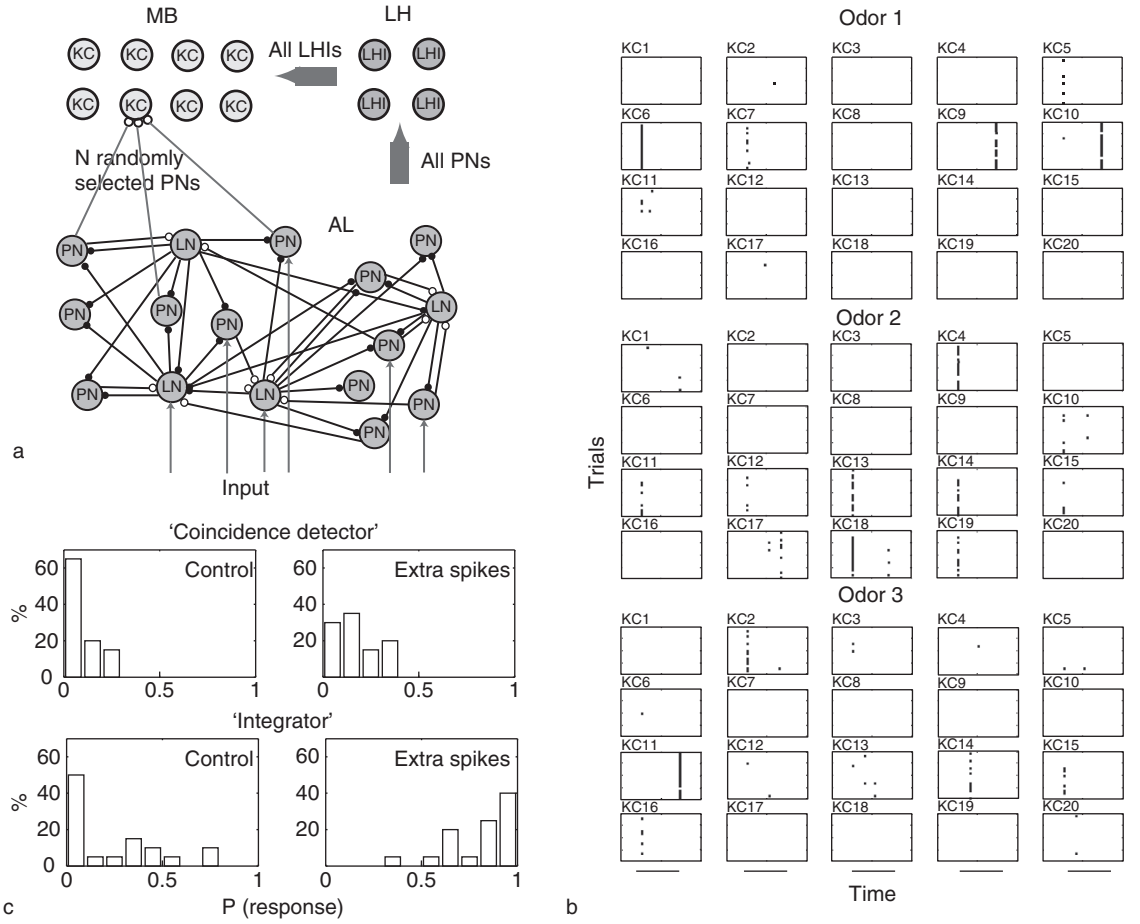

Figure 2 Decoding olfactory information in the mushroom body (MB). (a) Olfactory model. (b) KC responses for odor stimuli. Each box represents one KC operating as a coincidence detector; 20 cells are shown. Each stimulus (1 s duration; bars) was presented 20 times (raster) and included small variations between trials. Two to four KCs fired reliably in response for each stimulus. Identities of these active KCs changed between odors. (c) Frequency distribution of KC response probabilities before and after noise (extra spikes) was added to the input. The coincidence detector model shows only a slight increase in response probability, whereas the integrator model exhibits a drastic reduction in response specificity. Adapted from Perez-Orive J, Bazhenov M, and Laurent G (2004) Intrinsic and circuit properties favor coincidence detection for decoding oscillatory input. *Journal of Neuroscience* 24(26): 6037–6047, with permission from the Society for Neuroscience.

that binary odorant mixtures activate many cortical neurons that do not respond to the individual components of the mixture. This finding supports a coincidence detection function for the olfactory neurons. However, electrophysiological work in slice preparations has revealed that relatively small numbers of mitral cells are sometimes able to activate individual pyramidal cells in rat olfactory cortex. Based on this finding, it has been proposed that complex odors are represented in olfactory cortex in a broadly distributed manner. It is unknown to what extent the temporal structure found in activity patterns of the OB neurons is reflected in olfactory cortex. Multichannel and single-unit electrophysiological recordings made in the rat olfactory cortex suggest that individual odorants evoke activity in a spatially scattered ensemble of olfactory cortex neurons, and the ensemble activity includes a rich temporal structure.

The literature regarding modeling of the information processing in the olfactory cortex is growing but is currently rather limited. Aforementioned work by Hopfield and Brody incorporates models of the cortical cell population with individual units operating as coincidence detectors on the input from the OB. Results from a study by Wilson and Bower, using a large-scale computer model of the olfactory cortex, suggest that during each 40 Hz cycle of EEG activity, there is a convergence of afferent information from the OB and from caudal cortex. This model reproduced patterns of activity recorded physiologically in response to electrical shocks to the afferent input. A series of models simulating cortical EEG dynamics were proposed by Walter Freeman.

Conclusion

Experimental and modeling studies of odor coding have developed, extended, and tested a wide range of ideas about information processing by networks of neurons. Computational models of the insect olfactory system have explored the proposal that antennal lobe circuitry reformats information about odors, distributing it into the identities of PNs responding to the odor and into the relative timing of spikes in those PNs. Although temporal patterning may not be required for relatively easy tasks, such as the discrimination of ensembles of PNs that do not significantly overlap with one another (activated, perhaps, by odorants with chemically distinct structures), temporal features appear to be critical when discrimination tasks are more challenging – when it is necessary to discriminate activated PN ensembles that substantially overlap. Thus, the antennal lobe actively sharpens information about the olfactory stimulus by employing time and transient synchrony as coding dimensions. The massive convergence of afferents from the olfactory epithelium to the antennal lobe contributes to the creation of reliable and reproducible odor-specific patterns of activity in the antennal lobe. The intrinsic dynamic properties of the antennal lobe optimize these spatiotemporal structures, helping to reduce overlap between representations of similar odors. Contained within the spatiotemporal patterns of antennal lobe activation is information not only about odor identity but also about odor concentration. KCs of the mushroom body, postsynaptic targets of the PN ensemble, decode the stimulus-specific spatiotemporal patterns of PN activity. Operating as coincidence detectors, and thus employing the useful coding dimension of precise timing, KCs transform spatiotemporal patterns of antennal lobe activity into new and very sparse distributed firing sequences. The very large number of KCs enables the insect olfactory system to minimize the overlap between response patterns elicited by even very similar odors. Thus, temporal coding implemented by the antennal lobe can magnify differences in odor representations while minimizing the influence of noise, dramatically reducing odor code overlap in the mushroom body compared to the initial coding by olfactory receptor cells. Understanding and testing hypotheses about these complex biological processes has been greatly facilitated by the use of computational models.

See also: Neural Synchrony and Feature Binding; Olfactory Bulb Anatomy; Olfactory Bulb Physiology; Olfactory System: Circuit Dynamics and Neural Coding in the Locust; Population Coding.

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Relevant Website

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