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Seminars in Cell & Developmental Biology xxx (2006) xxx–xxx

seminars in
CELL & DEVELOPMENTAL
BIOLOGY

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Review

Information processing in the olfactory systems of insects and vertebrates

Leslie M. Kay [a], Mark Stopfer [b,*]

[a] *Department of Psychology, The University of Chicago, 940 E 57th St., Chicago, IL 60637, United States*
[b] *National Institutes of Health, NICHD, Building 35, 35 Lincoln Drive, Rm 3A-102, MSC 3715, Bethesda, MD 20892, United States*

Abstract

Insects and vertebrates separately evolved remarkably similar mechanisms to process olfactory information. Odors are sampled by huge numbers of receptor neurons, which converge type-wise upon a much smaller number of principal neurons within glomeruli. There, odor information is transformed by inhibitory interneuron-mediated, cross-glomerular circuit interactions that impose slow temporal structures and fast oscillations onto the firing patterns of principal neurons. The transformations appear to improve signal-to-noise characteristics, define odor categories, achieve precise odor identification, extract invariant features, and begin the process of sparsening the neural representations of odors for efficient discrimination, memorization, and recognition.

Keywords: Odor; Synchrony; Antennal lobe; Olfactory bulb; Coding

Contents

The olfactory systems of insects and vertebrates are a beautiful case of convergent evolution. Their shared olfactory circuit motifs evolved independently [1], suggesting there may be one best way to process information about odorants. The cross-species similarities extend from structural to functional, physiological levels. Focusing on animals where olfactory information processing has been explicitly examined, this review addresses the first order structures and functions that both systems use to process information about general, non-pheromonal odorants. We omit mechanisms of learning and memory, which have recently been reviewed elsewhere [2].

1. Odor receptors

Vertebrate noses and insect antennae have specialized epithelia lined with tens to hundreds of thousands of ciliated olfactory receptor neurons (ORNs). Aside from specialist detectors of pheromones, a given receptor generally responds to a range of odorants, and as the concentration of a given odorant increases, more types of receptors respond [3–5]. Interestingly, the per-

* Corresponding author. Tel: +1 301 451 4534; fax: +1 301 402 4777.
E-mail address: stopferm@mail.nih.gov (M. Stopfer).

1084-9521/$ – see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.semcdb.2006.04.012

formance of insects on odor discrimination tasks improves as the concentration of the odorants increases [6,7]. These results suggest that ORNs represent odorants in a combinatorial fashion.

2. Glomeruli

In insects and vertebrates, ORNs send their excitatory neural processes inward to specialized and analogous brain structures. In insects, this structure is the antennal lobe; in vertebrates, it is the olfactory bulb. Here, cholinergic axons from the antennae and other olfactory structures, or glutamatergic axons from the vertebrate nasal epithelium, sort out to enter spherical glomeruli such that receptor neurons expressing a common olfactory receptor gene converge onto one or a few common glomeruli. Combining the output of many, spatially distributed receptor neurons increases signal strength, provides structural redundancy for the array of exposed and vulnerable receptors, and likely helps minimize noise associated with local fluctuations in odorant concentration [8].

The numbers of glomeruli range from roughly 50–200 (*Drosophila*, honeybees, *Manduca*) to about 1000 (mice, locusts). Within glomeruli, large numbers of ORNs converge upon several types of cells including the principal neurons that convey information to other parts of the brain. In vertebrates, these principal neurons are glutamatergic mitral and tufted cells; in insects, they are cholinergic projection neurons (PNs) (Fig. 1).

Most glomeruli do not function as stand-alone units. In the olfactory bulb, short axon cells, external tufted cells, some types of periglomerular cells, and the distal branches of mitral cells, are all in positions to coordinate cross-glomerular responses in ways that have only partially been elucidated [9–11]. In insects, PNs can be predominantly uniglomerular (i.e. *Drosophila*, *Manduca*, honeybee, cockroach) or multiglomerular (locusts). In mammals, gap junctions and spillover of glutamate between dendrites can link the activities of mitral cells [12–14].

Both the antennal lobe and olfactory bulb are densely woven with GABAergic inhibitory interneurons (local neurons, LNs, and granule cells, respectively) that form reciprocal dendrodendritic synapses with the principal neurons. Many insects have both widely-branching and spatially-restricted LNs [15]. The mammalian olfactory bulb has GABAergic interneurons that branch mainly within the glomerular layer (juxtaglomerular cells) and between mitral cells (granule cells) (Fig. 1).

3. Organizing and reorganizing olfactory information

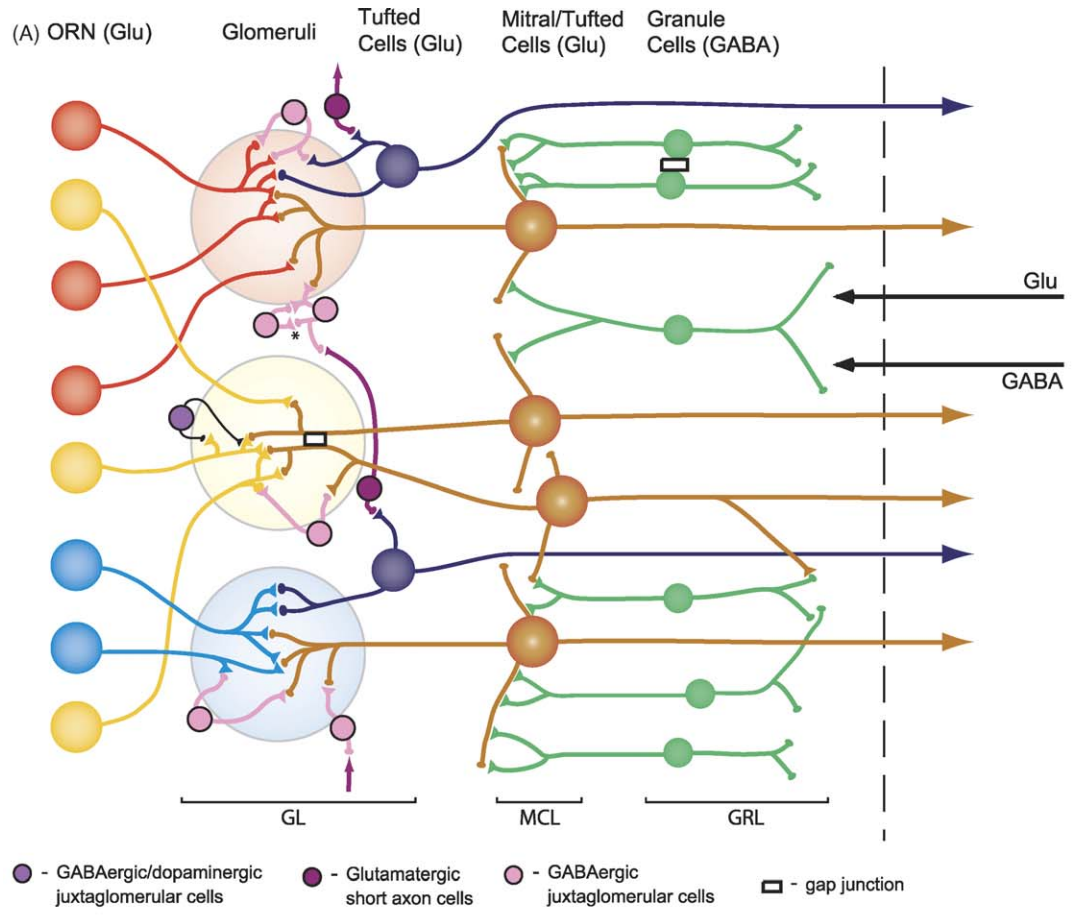
One consequence of glomerular interconnectivity is that olfactory information gets distributed across ensembles of principal neurons. Insect PNs have been shown to respond to a broader range of odorants than do their immediate presynaptic ORNs [16]. Similarly, vertebrate mitral cells can have broader response profiles than their inputs, show response profiles different from their immediate neighbors, and often respond to a range of odorants with different chemical structures [17–20].

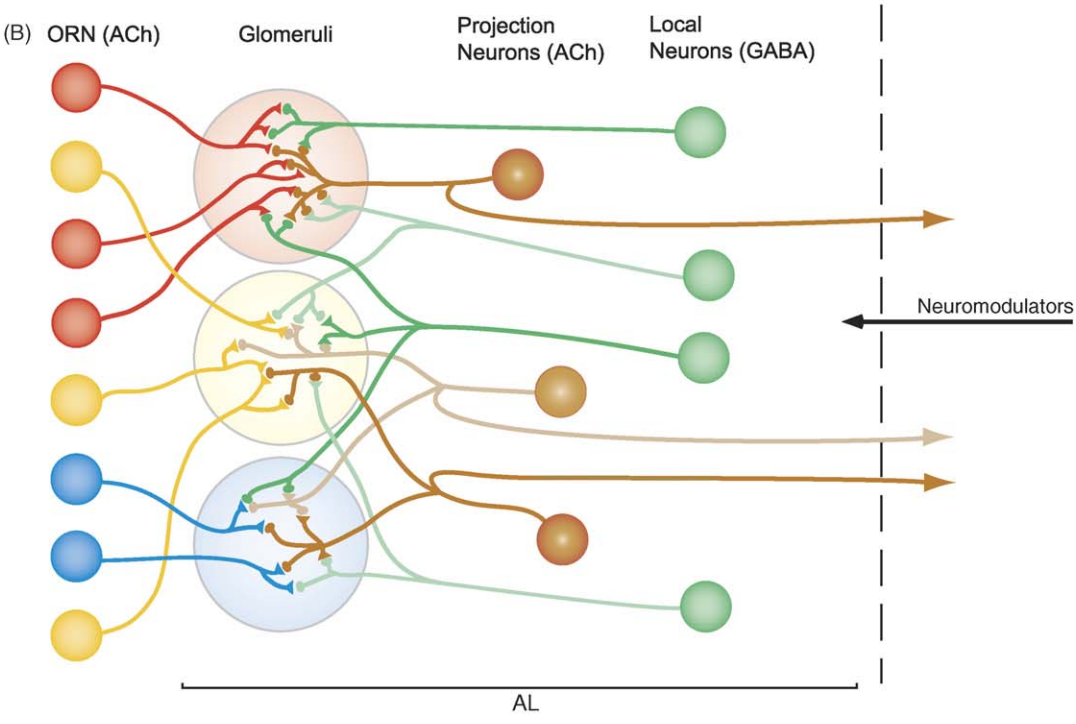
Although broad, the spatial distribution of olfactory information is not uniform. Several imaging techniques that assess afferent or principal neuron responses all indicate that odor stimulation evokes maps of activity that vary with the odorant; not all odorants activate all glomeruli and principal neurons. These activity maps are typically fragmented and overlap with one another, with overlap increasing with odor concentration [21–25].

Direct examinations of olfactory responses by electrophysiological recordings confirm the imaging results, and, with higher temporal resolution, characterize an additional response dimension: temporal patterning in the responses of principal neurons (Fig. 2). When an animal is exposed to an odorant, responsive principal neurons can generate temporally complex patterns of action potentials. An odor response may consist, for example, of a period of rapid spiking, followed by a period of inhibition, followed by another period of spiking [18,26–29]. These response patterns are relatively brief in mammals, where respiration restricts firing patterns to the time of an inhalation cycle [30,31]. Odor-elicited response patterns can change when a different odor, or a different concentration of an odor, is presented [26,29,32,33], and different principal neurons, simultaneously activated by an odor presentation, can respond with different temporal patterns.

Temporal patterns appear to arise mainly from the circuit dynamics of the lobe and the bulb. In insects, for example, GABA released from interacting groups of LNs appears responsible for the sometimes lengthy periods of inhibition [34–36]; in both types of animals, temporally structured responses from ORNs may in some cases contribute to temporal patterning as well [37–39]. The identities of responsive principal neurons that form spatial activity maps, together with their complex temporal responses, comprise the spatiotemporal representations of odors that are conveyed to downstream neurons. Simple classification algorithms applied to these spatiotemporal patterns successfully identify different odors and odor concentrations [32,33,40].

Fig. 1. Vertebrates and insects share remarkably similar olfactory architecture. (A) Olfactory bulb: olfactory receptor neurons (ORNs) expressing the same odorant receptors send their axons to a common glomerulus in the olfactory bulb, where they synapse onto several types of cells. Many of the synapses in the olfactory bulb are reciprocal; for clarity, we illustrate this only for two juxtaglomerular cells (*). Synapses not known to be reciprocal include ORN inputs onto mitral cells and tufted cells and the synapses of short axon cells. Shown are centrifugal GABAergic and glutamatergic projections synapsing onto lateral dendrites of granule cells, as discussed in the text. These centrifugal projections come from many brain areas and project primarily to the granule cell (GRL) and glomerular (GL) layers. MCL: mitral cell layer. Dashed line indicates olfactory bulb boundary. (B) Antennal lobe: insect ORNs are located along the antenna and other olfactory structures. As in the vertebrate, ORNs expressing the same odorant receptor converge upon common glomeruli, as shown in *Drosophila*. In glomeruli these axons synapse upon both local neurons (LNs) and projection neurons (PNs). In many insects, both LNs and PNs come in uni-glomerular and multi-glomerular forms (in locust LNs and PNs are apparently always multi-glomerular). Here, we illustrate multi-glomerular LNs that have only input or output within a single glomerulus; more extensive connectivity may exist. Centrifugal neurons from other areas of the brain deliver to the antennal lobe a variety of neuromodulators; their specific connections in the AL are not known. Dashed line indicates antennal lobe boundary.


(A) ORN (Glu)
Glomeruli
Tufted Cells (Glu)
Mitral/Tufted Cells (Glu)
Granule Cells (GABA)
Glu
GABA
GL
MCL
GRL
- GABAergic/dopaminergic juxtaglomerular cells
- Glutamatergic short axon cells
- GABAergic juxtaglomerular cells
- gap junction


(B) ORN (ACh)
Glomeruli
Projection Neurons (ACh)
Local Neurons (GABA)
Neuromodulators
AL

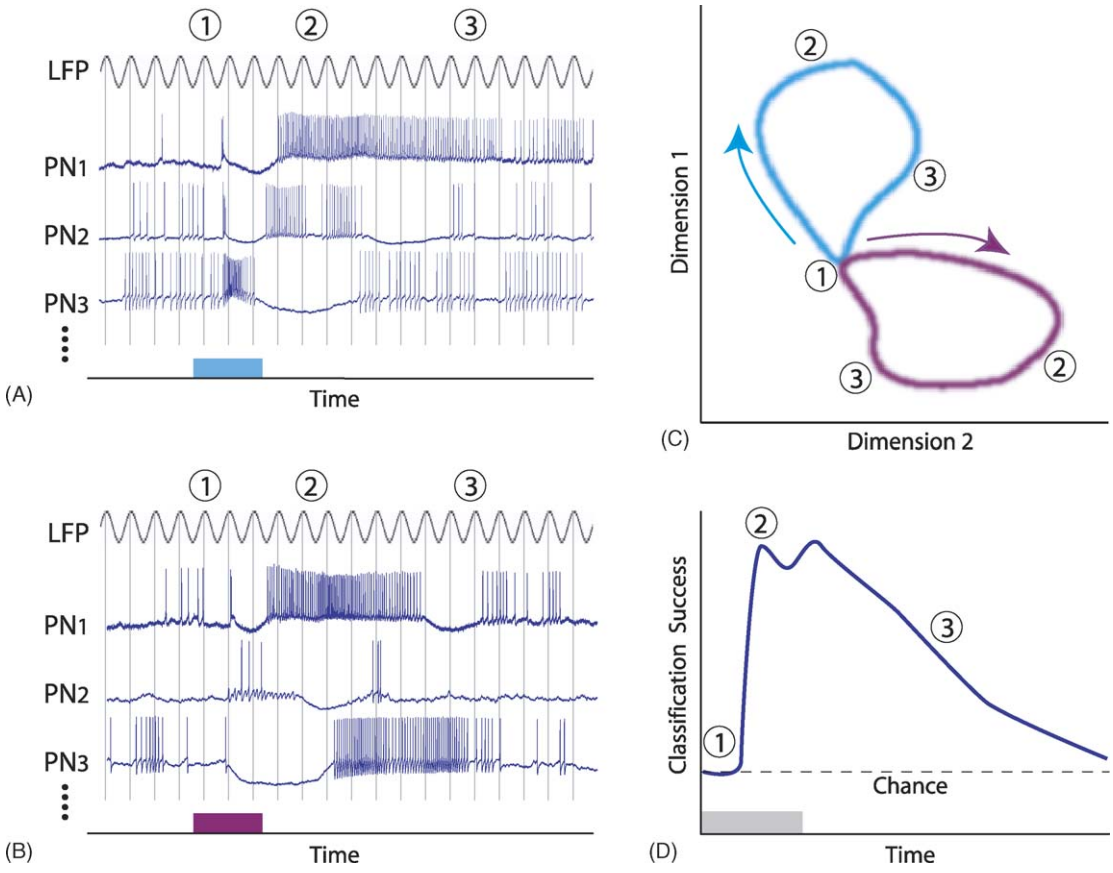


Fig. 2. Odor-elicited spatiotemporal firing patterns in principal neurons. Odors elicit distributed and temporally-complex firing patterns in the principal neurons of both vertebrates and insects. These spatiotemporal patterns are informative about the odors, as illustrated in this cartoon, which is based upon recordings from the locust antennal lobe [33,40]. (A) Presentation of an odor (blue bar) evokes elaborate firing patterns in many PNs (three are shown). These cross-PN firing patterns are analyzed as a series of time bins, defined by the odor-elicited oscillations generated by olfactory circuitry, evident in local field potential (LFP) recordings (represented by a sine wave; the LFP oscillations are faster than illustrated here). These time bins are physiologically meaningful; see text. Each time bin can be graphed as a point in response space, as in C. (B) A different odor (purple bar) elicits different spatiotemporal patterns in the PN ensemble. (C) To visualize the ensemble response, time-varying PN firing patterns can be graphed as a series of points, each of which indicates the PN ensemble firing within a time bin. Trajectories formed by joining these points in sequence move away from the start position ((1), spontaneous activity before the odor presentation), through the response space (2) and then back, along a different route (3), as the response ends. Different odors elicit different spatiotemporal response patterns, shown as different trajectories (blue and purple, corresponding to odors in A and B). When odor stimuli are lengthy (>1 or 2 s), responses settle into stable points before returning to the start position ([44], not shown). (D) The differences between the PN ensemble spatiotemporal response patterns can be used by simple algorithms to classify odors. Classification is most successful following the stimulus onset and offset (gray bar), when spatiotemporal responses elicited by different odors are most different from one another.

First-order interneurons begin the job of extracting several properties of odor stimuli. When ensembles of principal neurons respond to an odor, the spatiotemporal pattern is rather generic at first; it resembles those elicited by many other odors. But, within a few hundreds of milliseconds, the ensemble response to one odor begins to diverge, or decorrelate [26], from those of other odors, and so becomes more readily distinguishable (Fig. 2). Thus, more precise information becomes available to the animal as time passes, consistent with behavioral results showing that animals appear to make context-appropriate trade-offs between response time and accuracy [41–43]. Interestingly, antennal lobe circuitry maximally decorrelates its output during an odor pulse's on and off transients (Fig. 2D) [44,45].

The antennal lobe and olfactory bulb both impose forms of gain control. In locusts, where ORNs synapse directly onto both PNs and LNs, a given concentration of odorant elicits co-varying amounts of excitation and inhibition; as the odor concentration changes, the relatively stable mix of excitation and inhibition gives rise to new spatiotemporal patterns of activity, but generates similar ensemble-wide numbers of action potentials. Thus, the antennal lobe regulates numbers of output spikes while transmitting information about both odor identity and concentration [33]. In mammals, mitral and tufted cells also change their firing rates and temporal patterns with changing odorant concentrations [31,32]. Presynaptic inhibition mediated by $GABA_B$ receptors on ORN terminals decreases the release of glutamate onto postsynaptic mitral cells, in a form of negative feedback [46,47]. Similarly, dopamine released from periglomerular cells that receive ORN input activates D2 receptors presynaptically, also decreasing glutamate output [48]. Conversely, ACh released from basal forebrain input to olfactory bulb juxtaglomerular cells may serve to amplify the input from ORNs onto mitral cells. The result is likely a compression of dynamic range at the extremes. A similar compression may occur in insects,

where LNs may provide presynaptic inhibition onto ORNs [49].

In insects, antennal lobe circuitry has been shown to construct invariant spatiotemporal representations of odors regardless of the temporal structure of the stimulus. Natural odor plumes can comprise a stream of rapid and nearly overlapping odor pulses. Each of these pulses can, in turn, elicit lengthy and complex responses in PNs. In a given PN, responses to one odor pulse can interfere with responses to subsequent pulses as periods of spiking and inhibition interact. However, invariant representations of the odor emerge when the responses of large numbers of PNs are integrated in a manner consistent with the anatomical convergence of PNs onto their follower neurons [40].

Thus, one function of the first-order inhibitory interneurons is to impose complex temporal structure onto the firing of principal neurons. Drawing analogies to the retina, where excitatory and inhibitory neurons form spatially-defined center-surround structures that enhance visual contrast, some researchers have hypothesized that inhibitory neurons enhance olfactory contrast: allowing responses to strong odors (the center) to activate principal neurons, while suppressing responses to weaker odors (the surround) that may simultaneously activate overlapping groups of ORNs. There is some evidence for this kind of inhibition in the responses of mitral cells to short series of odorants whose molecular structures differ stepwise by single carbon atoms [50,51]. Other results, however, highlight the difficulties of reconciling both the strict physical mapping requirements of center-surround processing with fragmented, overlapping odor maps, and of defining molecular neighbors (i.e. which odors constitute opposing pairs?) [8,52]. And, as discussed above, recordings from principal neurons, which can show broader selectivity than ORNs, suggest that a retina-like, center-surround form of contrast enhancement is probably not a general feature of antennal lobe or olfactory bulb information processing. This potential function for first-order inhibitory interneurons remains controversial.

4. Oscillatory synchrony

In both insects and vertebrates, odor stimulation elicits the oscillatory synchronization of responsive principal neurons. Intracellular recordings detect oscillatory fluctuations in the membrane potentials of lobe and bulb neurons. Oscillatory synchrony can be detected in paired intracellular recordings from lobe or bulb neurons, in local field potential (LFP) recordings from the vertebrate olfactory bulb, and from projection sites of insect PNs. In insects and vertebrates, these fast, odor-evoked oscillations appear to be generated by circuit interactions, driven by the reciprocal excitatory–inhibitory dendrodendritic synapse between principal neurons and local GABAergic interneurons [53–55] and phase locking of these neurons to the local oscillation [28,35,56].

5. Olfactory oscillations in insects

Odor-evoked neural oscillatory synchronization has been detected in most insects that have been tested (Fig. 3A and B). What olfactory functions, if any, might these oscillations serve?

In honeybees, as in other insects, the fast inhibition required for generating oscillations can be selectively abolished by injecting picrotoxin (a blocker of $GABA_A$ receptors) into the antennal lobe. Injected, desynchronized honeybees readily learned an olfactory conditioning task, and after conditioning, could behaviorally distinguish odorants having very different molecular structures. However, these honeybees could not distinguish molecularly-similar odorants, a task performed well by honeybees injected with saline. Thus, oscillatory synchronization is necessary for fine-grained odor discriminations [57]. Comparable results were obtained in an electrophysiological study in locusts. Beta lobe neurons (two synapses downstream from antennal lobe PNs) usually fire in temporal patterns that vary with the odorant. However, in locusts whose antennal lobes were injected with picrotoxin, these beta lobe neurons fired in patterns that were no longer distinct for different odors [58]. Thus, on behavioral and neural levels, oscillatory synchronization seems necessary for normal olfactory processing in insects.

What specifically does oscillatory synchronization contribute to odor processing in insects? Three general functions, which are not mutually exclusive, have been proposed. First, as clocks define arbitrary units of time, antennal lobe oscillations define sequences of time bins, with each bin defining a subgroup of principal neurons firing synchronously. From the perspective of downstream cells, PNs co-active during a given cycle of oscillation are synchronized. Because the subsets of transiently co-active PNs vary with odor (and over time) as a result of the temporal patterning of PN odor responses, these physiologically-defined activity "snapshots" provide informative representations of the odor. In the locust, odor-specific subsets of PNs have been shown to reliably synchronize during particular oscillatory cycles [59].

Interneurons immediately downstream from the antennal lobe, (Kenyon cells, KCs, in the mushroom body) are particularly sensitive to synchronous PN spiking [45,60]. This is for two reasons: first, KC intrinsic properties (high threshold for spiking, and conductance nonlinearities) favor temporally summing input; second, in addition to receiving direct oscillatory excitation from PNs, KCs also receive PN-driven, phase-delayed feed-forward inhibition via a population of GABAergic neurons (located in the lateral horn). With each oscillatory cycle, KCs receive alternating barrages of excitation and inhibition, resulting in a series of shutter-like narrow time windows that regulate when KCs can spike. Together, these observations support the idea that oscillatory synchronization defines odor-specific subgroups of co-active principal neurons in a way that can be decoded by follower neurons [61].

A second, related function for the periodic inhibition underlying oscillations is to make odor representations sparser. In the locust, for example, any given odorant elicits effusive bursts of spikes from a large percentage of PNs. Many of these PNs (probably more than 100) converge upon each follower KC. Yet, the intrinsic and network properties of KCs conspire to allow very

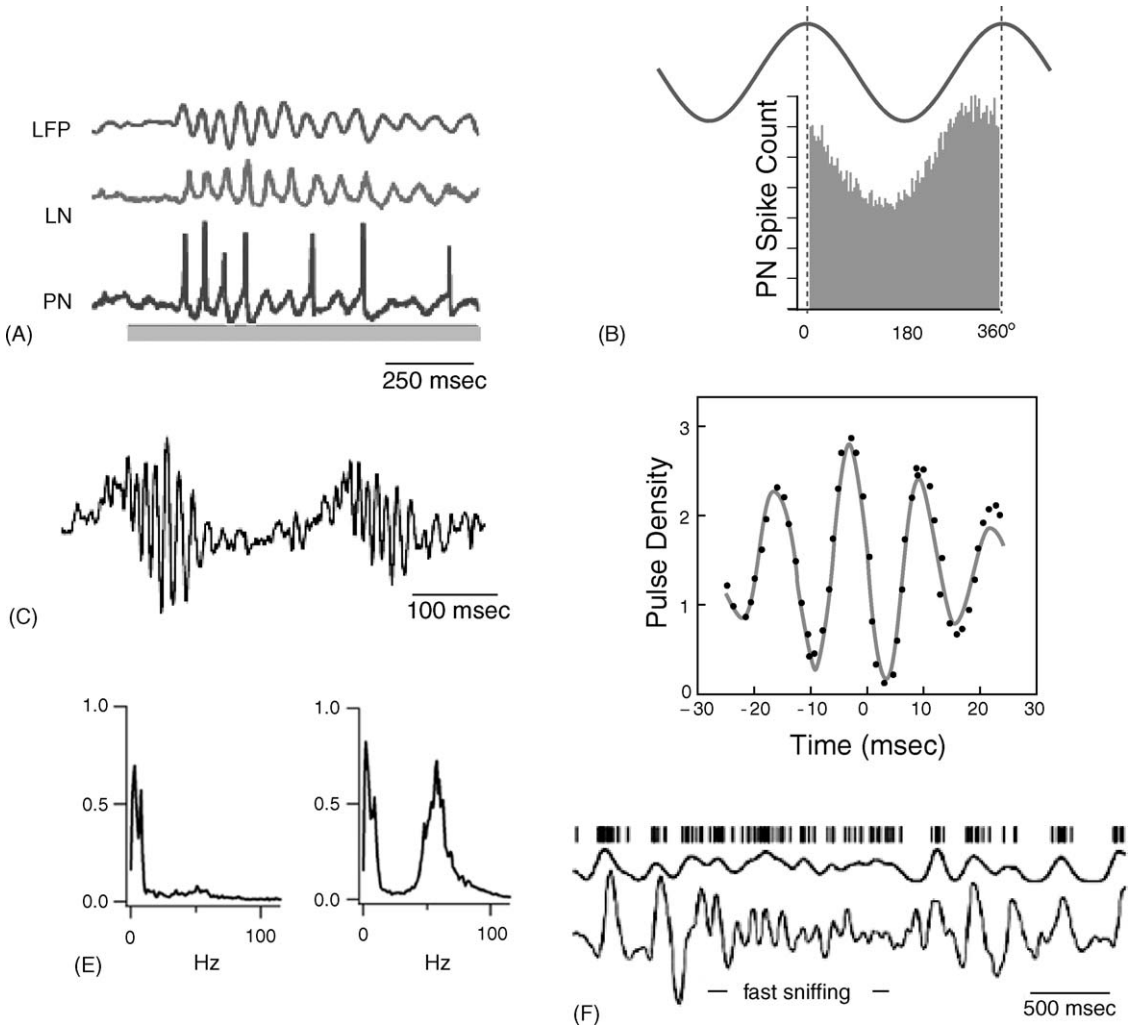


Fig. 3. Odor evoked oscillatory synchronization. (A) Antennal lobe circuitry in the locust generates odor-elicited oscillatory neural synchrony. Responding to afferent excitation, widely-branching inhibitory local neurons (LNs) provide to excitatory projection neurons (PNs) periodic inhibition (IPSPs, visible as negative-going, cyclic subthreshold activity). Responsive PNs tend to spike between IPSPs. The synchronized PN population gives rise to the local field potential (LFP), recorded in a PN projection site, the mushroom body. Gray bar: odor delivery. (B) Because of antennal lobe circuit interactions, PNs tend to phase-lock with each other (and therefore, to the LFP). Nevertheless, not all spikes are synchronized. This histogram shows the phase distribution of about 50,000 odor-elicited spikes from PNs in several experiments, plotted relative to the simultaneously-recorded LFP. (C) Inhalation cycle with superimposed gamma oscillations in an LFP recording from rat olfactory bulb. The gamma burst begins at the peak of the inhalation just prior to exhalation. (D) Mitral cell pulse density, relative to the gamma oscillation of the LFP. The peak of mitral cell firing is about 3 ms before zero, which is about 90 degrees before the peak of the local gamma oscillation. This phase is consistent across a range of frequencies and is similar to that of the insect and zebrafish (redrawn from [56], with permission from Elsevier). (E) Power spectra of LFP from normal (left) and beta3 knockout mice (right), measured from LFPs recorded during fast sniffing. Knockout mice have significantly stronger gamma oscillations during fast sniffing ([77]; Figure adapted from [74], with permission from World Scientific Publishing Co. Pte. Ltd, Singapore). (F) Mitral cells uncouple from the inhalation cycle during fast sniffing. Top trace: spike raster from a single mitral cell during odor sampling in a discrimination task. Middle trace: smoothed spike raster. Bottom trace: filtered theta band LFP recorded from an electrode near the mitral cell. In contrast to other times, the mitral cell fired relatively tonically during the fast sniffing, odor sampling period. (Figure adapted from [73]).

little spiking; a given odorant will often elicit zero or one spike from a given, normally silent KC. Sparser representations are easier to distinguish from one other. And, memory traces of sparse representations likely consist of relatively few modified neurons [61].

A third possible function for oscillatory synchrony is to standardize representations resulting from odor exposures of different durations. The antennal lobe's oscillatory mechanism may help provide invariant matches between memorized and incoming representations of odors encountered with different timing [40].

6. Olfactory oscillations in vertebrates

Odor-evoked neural oscillations have been detected in most olfactory animals. Several laboratories have studied mechanisms underlying fast, or "gamma" oscillations in mammals [54,62–65]. The gamma frequency in cats, rats, mice and rabbits ranges from 40–75 Hz, depending upon the species [62]. In zebrafish, the gamma-like oscillations resemble those seen in insects in both frequency and duration (20–30 Hz). Beta oscillations (15–30 Hz) have also been detected in the rat olfactory bulb in response to specific odorants [66], and have been correlated

with odor learning and expectation [67,68]. The sources of beta rhythms appear different from those of the gamma rhythm [54].

Several measures show that gamma oscillations reflect a form of large scale neuronal synchrony. Pulse probability density measurements, which gauge the probability of a neuron firing relative to the LFP, show that the distribution of spikes in mitral cells within a single burst tracks the local gamma oscillation (Fig. 3D) [69]. Furthermore, manipulations that decrease variance in the phase of mitral cell spikes relative to the gamma oscillation also increase gamma band power, consistent with a link between the extent of mitral cell spike synchrony and LFP amplitude. In anesthetized rabbits, mitral cells responding to a given odorant or odorant class fire spikes that are strongly coupled to the local gamma oscillation, and to each other [18]. Also, there is some evidence that mitral cells and external tufted cells display subthreshold membrane potential oscillations that guide the precise timing of action potentials [63,70], as in locusts (Fig. 3A) [59]. These results suggest that the olfactory bulb circuitry works to synchronize the spiking of populations of mitral cells. However, dramatic changes in both fast and slow oscillations and their underlying neuronal substrates with behavioral state complicate the analysis of these phenomena in waking animals.

When rodents are at rest, the respiratory rhythm in the olfactory bulb overlaps with low theta band oscillations (1–5 Hz), and is strongly correlated with odorized airflow in the nose. During this form of slow temporal synchrony, the majority of mitral cell spikes are restricted to a window of approximately 60–200 ms within the 200–1000 ms respiratory cycle (Fig. 3C and F). Different subgroups of mitral cells appear to spike together consistently at different phases of each inhalation cycle, forming a succession of synchronously firing principal neuron ensembles [71,72]. This odor-specific respiratory phase specificity develops after associative learning in waking animals, or after prolonged exposure to an odorant while under anesthesia, and is only manifest during slow breathing. Within these slow inspiratory cycles, gamma oscillations appear as brief bursts (6 or 7 cycles) at the peak of inhalation.

These well-defined oscillatory responses occur during slow respiratory behaviors. However, many types of olfactory information processing seem more likely to occur during periods of fast sniffing (6–12 Hz) associated with investigative behavior. Interestingly, measures of population synchrony decrease during fast sniffing. Mitral cells lose their strong coupling to the olfactory bulb's theta rhythm and airflow in the nose, firing more tonically [71,73,74]. Also, strong gamma oscillations diminish, giving way to relatively irregular, wide-band gamma power, suggesting wide-scale desynchronization (Fig. 3F) [67,68,75]. These results raise questions about the significance of fast oscillations in mammals for encoding odors during active behavioral states. Further, they suggest that understanding the role of synchronization in olfactory processing may require understanding mechanisms of desynchronization.

7. Modulating sensory processing

Two processes that desynchronize fast oscillatory activity in the mammalian olfactory bulb have been described. First, removing feedback to the olfactory bulb from more central brain areas greatly enhances olfactory bulb gamma oscillations in rabbits and rats, suggesting some feedback circuitry normally serves to desynchronize mitral cells [68,76]. Behavioral studies in rats show the period of apparent desynchronization begins with input from the entorhinal cortex to the olfactory bulb [67], and the onset of fast sniffing.

Second, a single mammalian study examined the role of intrinsic bulbar control in the reduction of gamma oscillations. In knockout mice, $GABA_A$ receptors on granule cells were selectively deleted from olfactory bulb circuitry [77]. These mice have significantly enhanced gamma oscillations in the olfactory bulb (Fig. 3E), suggesting that GABAergic drive to the inhibitory granule cell population normally serves to desynchronize the network. In behavioral experiments, knockout mice with abnormally large gamma oscillations (likely reflecting hypersynchronized mitral cells) were more successful than their control littermates at discriminating odorants with similar molecular structures.

The existence of multiple desynchronization mechanisms suggests that central influences on the olfactory bulb may modulate synchrony in a task-dependent fashion. What is needed is a test of whether and how synchrony is modulated while an animal performs easy and difficult odor discrimination tasks.

Together, studies on insects and mammals suggest that fast synchrony among principal neurons is important for achieving fine sensory discriminations (i.e., precisely identifying odors) but not coarse discriminations (i.e., roughly classifying odors). An animal may in one circumstance need to precisely identify an odor (e.g., "cherries"), while in another may need only to recognize that odor as a member of a general class (i.e. "food"). In fact, in the latter case, excessively fine discrimination may impede general classification performance. An interesting question is whether mechanisms for achieving fine discriminations and rough classifications are driven by the stimulus and hard-wired pathways, or rather are strongly shaped by intrinsic processes of learning and context association. The mammalian system has several candidate mechanisms for using immediate context to modulate synchrony, including systems associated with reward, affect and attention. These may use neuromodulatory drive, for example, to broadly change synaptic properties within the olfactory bulb. Recent computational models [60,78–81] explore these ideas.

Recently, Friedrich and colleagues have shown that the olfactory bulb of the zebrafish appears to encode both coarse categories and fine details simultaneously in a feat of multiplexing. By determining the phases of spikes in mitral cells with respect to simultaneously-recorded LFPs, the authors found tightly phase-locked spikes were elicited by broad classes of amino acid odorants, thus defining categories, while the remaining spikes from less-well synchronized mitral cells were elicited in a highly odor-specific manner, thus defining particular odorants [65]. It will be interesting to determine whether similar mechanisms are used by other systems, as well.

In both insects and vertebrates, slowly repeated odor pulses (e.g., 0.1 Hz) elicit increasingly strong oscillations: in insects, synchrony is not present at first, but increases over the course of

several repeated odor exposures; in rodents, large beta oscillations appear after several presentations [82,83]. The resulting odor specific, oscillatory state endures for about 10 min following withdrawal of the eliciting odor. This modulation of synchrony may be due to activity dependent facilitation among first-order interneurons [79], although the potential influences of neuromodulators have not been ruled out. Called "fast learning," this function increases the precision, and the signal-to-noise ratio, of representations of odors that are encountered repeatedly, and are thus potentially meaningful to the animal [79].

The olfactory systems of both insects and vertebrates are subject to change in other ways, as well. Both systems are richly endowed with feedback neurons bearing a variety of neuromodulators, and both support behavioral change when the meanings of odors are altered by conditioning paradigms.

8. Conclusions

Across broad swaths of phyla, several olfactory information processing motifs repeatedly appear. The odor world is sampled by huge numbers of ORNs, which converge type-wise upon a much smaller number of principal neurons within glomeruli. There, odor information is distributed and transformed by cross-glomerular circuit interactions mediated, in part, by inhibitory interneurons, which impose fast oscillations and slow temporal structures on the principal neuron firing patterns. Work from insects and vertebrates suggests that these transformations sparsen the neural representations of odors, improve signal-to-noise characteristics, define broad odor categories, achieve precise odor identification, extract invariant features, and prepare the representations for efficient memorization and recognition. By comparing common features and specializations across species, it should be possible to evaluate and expand these general principles, and to design studies that explore olfactory responses further along the olfactory pathway.

Acknowledgements

We thank Stacey L. Brown for extensive assistance with the text and figures, and Leonardo Belluscio and Kiriana Cowansage for valuable comments. M.S. is funded by an intramural grant from the National Institutes of Health, the National Institute of Child Health and Human Development. L.K. is funded by grants from NIDCD (R01DC00795-01) and the Brain Research Foundation.

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