Review

Olfactory oscillations: the what, how and what for

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Olfactory system oscillations play out with beautiful temporal and behavioral regularity on the oscilloscope and seem to scream 'meaning'. Always there is the fear that, although attractive, these symbols of dynamic regularity might be just seductive epiphenomena. There are now many studies that have isolated some of the neural mechanisms involved in these oscillations, and recent work argues that they are functional and even necessary at the physiological and cognitive levels. However, much remains to be done for a full understanding of their functions.

Introduction

The various types of oscillations seen in the olfactory bulb (OB; see Glossary) local field potential (LFP) differ in frequency and in the circuits and behavioral circumstances that produce them. The best studied are gamma oscillations, which occupy the higher end of the olfactory LFP frequency range (~70 Hz in rats and mice), are evoked by sensory stimulation and are initiated at the end of the inhalation cycle, riding the crest of the respiratory (theta) wave [1]. The power of odor-evoked gamma oscillations is associated with successful discrimination of closely related odorants [2–4]. Both odor-evoked gamma and beta (~20 Hz in rats) oscillations have been associated with odor learning [2,5], and there is some evidence that the oscillation type and circuit could depend on the cognitive task [2,6]. There are many questions remaining to be answered about olfactory theta (~1–12 Hz), beta (~15–30 Hz) and gamma (~40–100 Hz) frequency bands.

Oscillations in these frequency bands have been associated with sensory processing in other systems and with network properties in the hippocampus. However, frequencies can be deceiving, with even odor-evoked gamma oscillation frequencies varying widely across species [1]. Translating what has been learned about olfactory oscillations to other cortical systems, we argue that oscillations must be defined by multiple factors to make similarity arguments across systems and species.

What are the different rhythms?

A power spectrum of the rat OB LFP shows three distinct frequency bands corresponding to three classes of behavioral phenomena (Figure 1). Theta oscillations, so named because they overlap in frequency with hippocampal theta oscillations, are driven by sensory input and are also called respiratory oscillations [7]. Gamma oscillations are the

Glossary

Beta oscillations: in waking rodents, these oscillations occur in the 15–30 Hz band. They are seen in all parts of the olfactory and hippocampal systems in response to odor learning in a Go/No-Go task and with sensitization to some types of odorants.
Current source density: method by which voltage at successive defined depths is converted to current sources and sinks, via a spatial derivative across successive sets of three equally spaced locations. New linear silicon probes have made this procedure feasible within cortical areas that are easily accessible. This remains one of the best and only ways of determining, in waking mammals, which cortical layers contribute to an identifiable phenomenon such as an oscillation. See Ref. [65] for an excellent review of the method and the physics associated with it.
Gamma oscillations: in rodents, gamma ranges from ~40–100 Hz, but it can be as low as 10–30 Hz in some species and as low as 30–35 Hz in urethane anesthetized rodents. Gamma1 oscillations occupy the upper range of the gamma band (>60 Hz in rodents), are associated with odor processing within the OB and arise at the transition from inhalation to exhalation. Gamma2 oscillations occupy the lower end of the gamma band (~40–60 Hz) and are seen only in waking animals during grooming or attentive behaviors.
Go/No-Go task: operant responding task in which subjects respond with a particular behavior (e.g. lever press) for one or more stimuli and avoid responding for one or more stimuli. Usually, only a correct 'Go' response is rewarded, and often an incorrect No-Go response is punished (e.g. longer delay to the next trial).
Local field potential (LFP): summed extracellular voltage in a local area of (usually) cortical tissue. It is the measure of coherent activity within a small to large population of cells, depending on electrode size and impedance.
Olfactory bulb (OB): the first stage of olfactory processing in vertebrate brains. Olfactory receptor neurons in the epithelium project their axons directly onto mitral cells in the OB, which themselves send axons directly to piriform cortex, entorhinal cortex and many other limbic areas.
Piriform cortex (PC): this is commonly referred to as the primary olfactory cortex, although there are some disagreements as to whether the OB, anterior olfactory nucleus or anterior PC is primary olfactory cortex [66].
Theta oscillations: in rodents, theta is a broad band (4–12 Hz), which is often divided into theta1 (8–12 Hz) and theta2 (4–7 Hz). In the olfactory system, theta oscillations track the respiratory cycle and range in waking rodents from 2 Hz to 12 Hz, with frequencies above 4 Hz defined usually as sniffing. These numbers are somewhat different in head-fixed rodents [8].
Two-alternative choice task: operant-responding task in which subjects respond with two slightly different behaviors (e.g. lever press right, lever press left) for two different stimuli. Usually, correct responses to both stimuli are rewarded.

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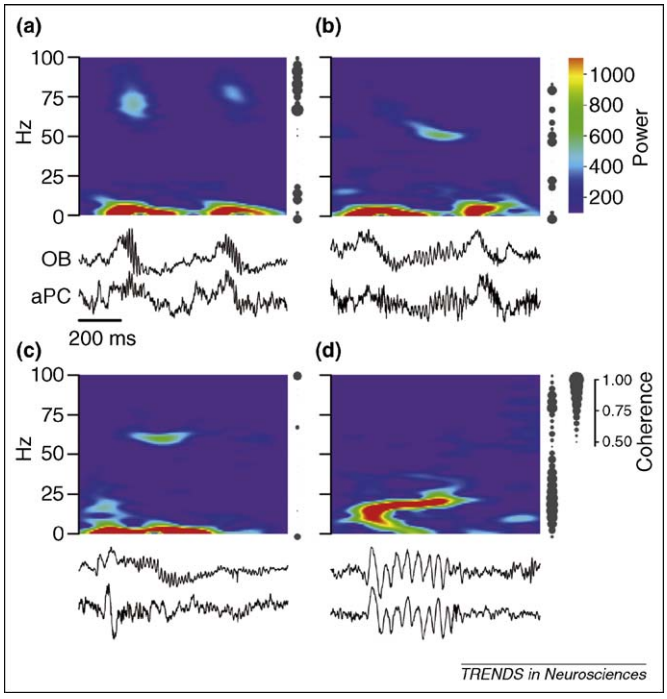

Figure 1. The range of oscillation types in the rat OB (top trace) and anterior piriform cortex (aPC; bottom trace); above each one the second LFP trace is a sonogram representation of the frequency structure from the OB segment. Coherence between the two traces is shown to the right of each sonogram, with the smallest dot representing the cutoff for significance (0.55) and values below that blank. **(a)** Rat attentive and breathing at a resting frequency (2 Hz). LFP shows a prominent theta oscillation coincident with inhalation cycle and gamma1 bursts initiating at the peak of inhalation. The theta frequency appears in dark red at the bottom. Because of the asymmetry of the respiratory wave, it shows a sweep between 5 and 1 Hz (over many inhalations, the 2 Hz frequency will survive the averaging). The two bursts are centered at 71 Hz (1st burst) and 78 Hz, with considerable spread in frequency within each burst. Coherence is high at gamma and respiratory frequencies. **(b)** Lower amplitude gamma1 bursts during grooming behavior; gamma2 episodes are evident between inhalations. Gamma2 bursts have a more consistent oscillation frequency (variable across individuals) than gamma1 bursts: 52 Hz here. Coherence is significant in the gamma2 frequency range. Very high frequency activity in the PC trace is from jaw movement electromyogram (EMG). **(c)** Extended gamma1 burst seen during odor sampling in criterion performance of a fine discrimination task (heptanone–octanone discrimination; the response to heptanone is shown). Coherence with PC is very low in the gamma1 range, indicating a decoupling of the normal oscillatory drive seen in part (a). **(d)** Beta oscillations recorded during odor sampling in a Go/No-Go task. The frequency of this oscillation begins low (probably owing to an underlying sensory evoked potential) and ends at ~20 Hz. Beta oscillation frequencies, like gamma2, are less variable within an animal than for gamma1. Coherence is very high in the beta band, with lower coherence in the respiratory frequency range. Data were digitized at 2016 Hz (Neuralynx Cheetah 32, Bozeman, MT, USA; NB Laboratories headstage; 1–475 Hz analog filter). Sonograms were made using a Gabor taper on a 2016 point window (padded with zeroes when necessary), stepped by 1 time point (Igor Pro 6.03- Wavemetrics, Lake Oswego, OR, USA). Power is dimensionless because data are normalized to zero mean and unit standard deviation and all four plots use the same power and coherence scales.

fastest oscillations described in the olfactory system and are evoked by sensory input within a single inhalation–exhalation cycle. Beta oscillation episodes can last much longer than gamma oscillations, on the scale of 2–4 inhalation cycles, and have been associated with some types of odor learning and odor sensitization.

Respiratory (theta) oscillations

The basic processing unit in olfaction is the respiratory cycle. In rodents and other small mammals, waking-state respiratory rates are 1–4 Hz, transitioning to as high as 12 Hz as animals explore novel odorants or perform odor discriminations. In the OB, a slow LFP oscillation tracks

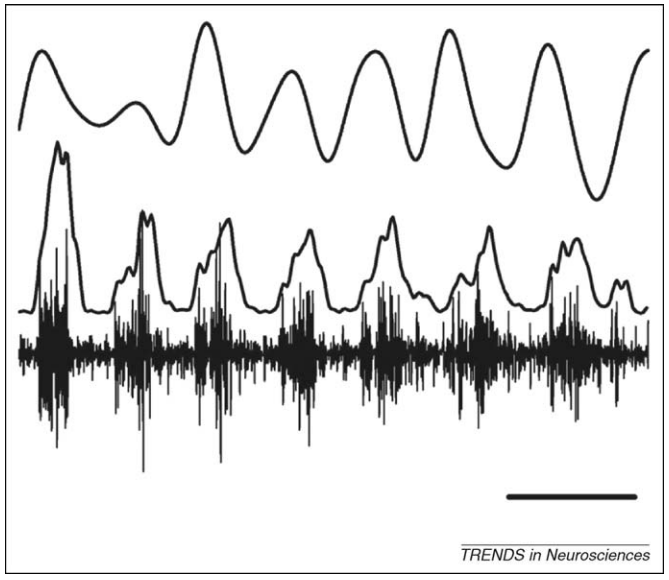

Figure 2. OB theta oscillations track the respiratory cycle during fast sniffing. The top trace is the theta band (low pass digital filter at 12 Hz) from the OB LFP; the bottom trace is EMG from the diaphragm; and the middle trace is a smoothed version of the EMG. One second of data sampled at 2016 Hz is shown.

the respiratory cycle [7] (Figure 2). Specific glomeruli are activated during inhalation by the incoming sensory nerve, supporting the inhalation–exhalation cycle as the principal sensorimotor process in OB circuitry [8]. Although we know how the theta rhythm follows the respiratory cycle, we know little about how it relates to sensory input directly. It would be informative to couple the LFP theta rhythm to sensory stimulation with a method such as calcium imaging of glomerular activation [8].

The closely connected piriform cortex (PC) also has theta oscillations, which can be strongly coupled to OB rhythms during rest states and when animals sniff odorants [9] (Figure 1a). The OB and PC go through coupled and uncoupled states at theta frequency under the influence of ketamine–xylazine anesthesia reminiscent of transitions between coupled and uncoupled states in thalamocortical networks during sleep [10]. Little else is known about sources of theta in the PC.

Most of the data on respiratory oscillations comes from anesthetized or slowly breathing animals. When a waking animal transitions to fast sniffing, the LFP still seems to track the respiratory cycle (Figure 2). However, mitral cells uncouple from their normal respiratory burst pattern in this state and fire more or less tonically [7,11].

Gamma oscillations

Odor-evoked gamma oscillations (~40–100 Hz, depending on the species and presence or absence of anesthesia; ~60–90 Hz in waking rats) represent the best studied olfactory oscillations [1]. These sensory-associated oscillations are linked strongly with the respiratory rhythm, beginning at the end of the inhalation cycle and persisting into the expiratory period (Figure 1a,c). Correlated oscillations can be seen in the PC during exploratory behavior, particularly when OB gamma is large (Figure 1a). Homologous and analogous oscillations at 10–30 Hz have been noted in many vertebrate and invertebrate species such as frogs, fish, locusts and honeybees [4,7,12,13].

A second gamma oscillation band occupies the lower end of the gamma spectrum in waking rats (~50–60 Hz) and is associated with alert immobility and behaviors such as grooming [1] (Figure 1b). They are present at low respiratory rates between inhalations during long expiratory or non-breathing periods, are strongly coupled with similar oscillations in the PC (Figure 1b) and have not been observed under anesthesia. These oscillations have been labeled gamma2, with odor-evoked gamma described before being gamma1.

Beta oscillations

Beta oscillations (~15–30 Hz) are seen in waking rats in the OB, PC, entorhinal cortex and hippocampus during exposure to highly volatile odorants [14,15]. They are amplified in response to all odorants when rats learn some odor associations [5] (Figure 1d) and are involved in entorhinal drive to the OB in anticipation of odor stimuli [7]. Coherence in this band between the OB and hippocampus accompanies odor learning and transfer of a learned response to new odor sets [6].

The roles of beta and gamma oscillations in odor learning and discrimination are ambiguous because different reports conflict on whether gamma or beta has a bigger role. As we show in the following sections, olfactory gamma and beta oscillations are not just different frequencies but rely on different networks and behaviors.

How do the rhythms come about?

Frequencies are only useful for assigning an identity to oscillatory phenomena within a species and often within a single individual because numbers vary across species and between individuals. Therefore, it is important to know the underlying mechanisms, sources and associated behavioral markers of oscillations, in addition to their relative frequency bands. This enables us to transition from a simple number-based taxonomy to a functional representation of oscillatory events.

Theta oscillations

Low-frequency burst firing of external tufted cells in the glomerular layer can support theta oscillations [16]. There are also central components to the respiratory rhythm even in urethane-anesthetized animals, because bypassing the nasal epithelium with tracheal breathing maintains a portion of mitral cell respiratory patterning [17]. Little else is known about what circuits contribute to centrifugal theta drive. In some circumstances OB and hippocampal theta rhythms are coherent, and phase relationships indicate that hippocampal theta might drive some portion of OB theta during fast sniffing [9]. More research is needed to determine what the central sources of OB theta might be. Current source-density analysis of LFP from animals engaged in odor-discrimination tasks can be a powerful tool to determine in what layers other sources of theta might appear. If substantial sources of current are seen in deep layers of the OB, this would support a central role to the rhythm because centrifugal inputs to the OB arrive primarily to the deeper granule cell layer.

Gamma oscillations

Gamma1 oscillations have been shown by many different methods to be supported by the reciprocal excitatory–inhibitory synapse between mitral and granule cells in the external plexiform layer of the OB [18–21]. Mitral cells have background firing rates of ~5–20 Hz, although the rates can be higher or lower during odor presentation, with higher rates occurring sometimes under anesthesia [11,22]. Thus, gamma1 oscillations do not predict the instantaneous firing rate in a given cell, but they do represent probabilistic firing patterns during a gamma1 oscillation. Mitral cells typically fire ~90 degrees from the peak of the gamma1 oscillation. Thus, a larger oscillation represents a more coordinated mitral cell assembly near the electrode, whereas a smaller oscillation represents either a smaller or less precise assembly. Mechanisms for PC gamma1 oscillations are similar to those in the OB. The oscillatory evoked potential is driven by interactions between excitatory pyramidal cells and inhibitory interneurons, and pyramidal cell spikes predict the PC gamma1 oscillation [23,24].

Similar odor-evoked oscillations occur in some non-mammalian vertebrates and invertebrates [7,13,25]. For example, zebrafish show a prominent 20–30 Hz oscillation in the OB (supported by reciprocal interactions between mitral and granule cells) and similar oscillations in frogs are ~10 Hz. Locusts and honeybees show an odor-evoked gamma-like ~20 Hz oscillation that is supported by interactions between excitatory projection neurons and inhibitory local neurons in the antennal lobe, the insect analog of the OB. This oscillation is best recorded in the mushroom body, but it can be seen in membrane oscillations of the antennal lobe neurons.

Computational models of gamma1 oscillations have focused on the OB and began with the oscillatory evoked potential [1]. The dendrodendritic synapse between mitral and granule cells takes center stage [26]. A unique feature of some models is that granule cells do not have to spike to help coordinate the assembly of mitral cells; subthreshold granule cell oscillations are enough [27]. One model has argued that granule cells provide noisy input to mitral cells and that coordination happens at the level of the mitral cells [28], but a recent report does not support this mechanism [19].

Gamma1 oscillations can be modified by several mechanisms. Removing centrifugal input to the OB, and thus to granule cells, causes a large increase in gamma1 power [29]. The β3-knockout mouse lacks a functional γ-aminobutyric acid $(GABA)_A$ receptor β3 subunit; in the OB this knocks out the $GABA_A$ receptors only on granule cells. $\beta3^{-/-}$ mice have larger than normal gamma1 oscillations and lack gamma2 oscillations, which indicates mutual inhibition between granule cells as a source of the gamma2 oscillation [1,3]. In locusts and honeybees, blocking the $GABA_A$ receptors in the antennal lobe with picrotoxin results in a selective ablation of the odor-evoked gamma-like oscillation, leaving projection neuron slow temporal patterns intact [4,13].

We do not know what mechanisms modulate the network dynamically to increase or decrease gamma1 oscillations. A recent publication examines in detail multiple

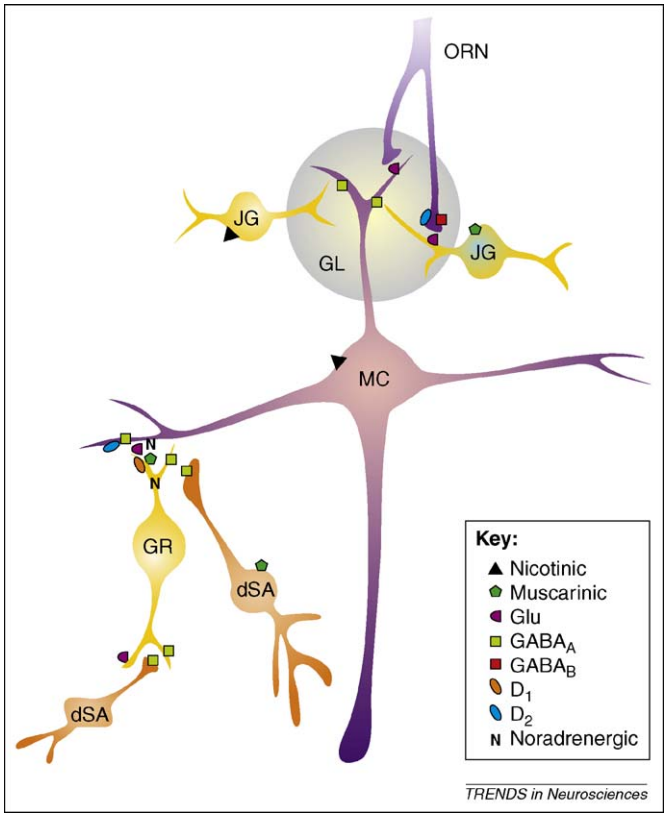

Figure 3. Basic OB circuit, including points at which neuromodulators might affect oscillations (not all types and locations of receptors are shown here). Since we know most about the circuits involved in the gamma1 rhythm, the figure concentrates on the mitral–granule cell reciprocal synapse, which supports this oscillation. Receptors at the receptor neuron to mitral cell and juxtaglomerular cell synapses might affect the strength of the respiratory rhythm, input or sensory evoked potentials. Dopaminergic D_1 and D_2 receptors regulate the strength of inhibition at the reciprocal synapse and the strength of sensory input [67,68]. Noradrenergic receptors of several types at this synapse affect the excitability of both mitral and granule cells and the strength of inhibition, and they affect discrimination of closely related odorants [48,57]. Cholinergic action on granule cells decreases their firing rates but increases the release of GABA [69]. Glutamate receptors are of both AMPA and NMDA types (metabotropic receptors not shown). Abbreviations: dSA, deep short axon cell (GABAergic); GL, glomerulus; GR, granule cell (GABAergic); JG, juxtaglomerular cells (yellow is GABAergic and blue and yellow is both dopaminergic and GABAergic); MC, mitral cell (glutamatergic); ORN, olfactory receptor neuron axon (glutamatergic) [30].

deep short-axon cell types, some of which form reciprocal GABAergic synapses with granule cells that could modulate the strength and synchrony of inhibition [30]. Neuromodulators might also play a large part in modulating gamma1 oscillations because dopamine, norepinephrine and acetylcholine receptors are situated where they can affect either inhibition strength at the reciprocal synapse or centrifugal or intrinsic GABAergic inputs to granule cells (Figure 3). Excitatory and inhibitory centrifugal inputs to granule cells also represent mechanisms by which cognitive processes associated with higher brain areas could manipulate circuits within the OB and modify temporal precision momentarily.

Beta oscillations

What we do not know about the mechanisms of beta oscillations in olfactory circuits exceeds what we do know. We do not know the cellular or synaptic origins of beta oscillations, but studies in anesthetized rats lend some insight. Urethane anesthetized rats show increased levels of granule cell firing in the OB during beta oscillations [31], and a recent report links beta oscillations to differences in respiratory phase dependent on odor class [32]. However, odor-evoked beta oscillations in anesthetized animals show differences from those in waking animals [14]. At the systems level, beta oscillations show strong coherence with similar oscillations in all parts of the olfactory system and the hippocampus during odor learning and odor sensitization [5,6,14]. Gamma1 oscillations are generated locally and show much lower levels of coherence with downstream structures [2,14]. OB beta oscillations require an intact network between the OB and the rest of the brain [20,29]. Thus, the evidence indicates that olfactory beta and gamma1 oscillations emerge from different underlying networks.

Because beta oscillations are a network phenomenon, it is necessary to look at more central areas to understand them. We do not know the relationship between OB mitral and granule cells or PC pyramidal cell firing patterns and beta oscillations. Recording single or multi-unit firing patterns from these cells coincident with local field recordings in waking animals will help to determine which cell populations participate in the beta oscillation. Current source-density analyses in both the OB and PC in waking animals performing odor-discrimination tasks will help determine what synaptic layers support beta oscillations. These experiments will enable a more precise comparison of gamma and beta networks within olfactory circuits.

There are no published models of beta oscillations in the olfactory system, but the relationships between beta and gamma oscillations in neocortical models might provide some clues for the olfactory system. There are multiple mechanisms that can produce a beta rhythm; some of these involve intrinsic currents in pyramidal cells, whereas others seem to be network phenomena in which other rhythms are transformed into beta rhythms [33–37]. For example, in somatosensory cortical slices strengthening connections between deep-layer intrinsically bursting cells causes a change from gamma and high-frequency beta oscillations to a unified low-frequency beta [35]. Thus, it is reasonable to associate at least some forms of the beta rhythm with either a learning process or its accomplishment. This is supported by *in vivo* experiments that show that beta oscillations often occur after a bout of gamma [38]. In the case of olfactory beta oscillations, the fact that they require an intact bulb-PC loop and appear during the learning process indicates that they are also a network phenomenon produced plastically.

What might the oscillations be good for?

Functional studies of cortical oscillations are more difficult than those that address their mechanisms, often requiring ablation of the oscillatory mechanism in awake-behaving animals. Many of these ablations interrupt more than the oscillation so the data must be interpreted with caution. However, in a few circumstances a strong functional argument can be made (see gamma oscillation section later). The remaining functional arguments for olfactory oscillations are still in the early stages and consist primarily of behavioral correlations and analogies with other systems.

Theta: sensorimotor processing

OB theta oscillations provide an internal representation of the sensorimotor act of sniffing, and also of breathing. Because it is not obvious how the theta rhythm can be removed without removing circuits and behaviors necessary for sensory sampling, functional studies of this rhythm have, so far, only used correlational measures to assess the role that theta rhythms could have in odor processing.

Because the olfactory system is so closely connected with the hippocampal system, it is natural to ask whether these oscillations are coupled in some way with hippocampal theta activity. Coherence between sniffing and dorsal hippocampal theta rhythms is observed when the positive (reward) and negative (no reward) associations of a known odorant pair are reversed [39]. The strength of this association decreases as learning progresses, indicating a negative correlation between theta coherence and task performance. The opposite relationship is seen during performance of a sensorimotor odor-discrimination task in which rats keep track of inter-trial timing in the absence of outside cues [9]. In this case, coherence between OB and hippocampal theta rhythms during odor sniffing is positively correlated with performance on the task. These two studies present opposite results that could be dependent on the type of task in which the rats were engaged. At the single unit level, during low respiratory rates mitral cells fire at specific phases of the theta rhythm, dependent on the odorant and its association [40]. However, at higher respiratory rates, these relationships become unreliable as mitral cells uncouple from the respiratory cycle and fire tonically [11,41].

These few correlational studies indicate that olfactory system theta oscillations might be more than an internal register of the inhalation–exhalation cycle; they could also be part of a cognitive network involving other olfactory areas and the hippocampus. OB theta rhythms represent at least two distinct processes. Inhalation corresponds to sensory acquisition and occurs in the earlier part of a theta cycle. The later phases of the respiratory cycle seem to contain most of the higher frequency phenomena, with gamma1 at the transition between inhalation and exhalation, beta in anesthetized animals initiating in early exhalation [31] and gamma2 in the late expiratory phase or between inhalations [1]. Thus, exhalation occupies the later part of the cycle during which information acquired in the early part of the oscillation is processed, reminiscent of a hippocampal model [42].

In hippocampal circuits it has been suggested that theta oscillations coordinate cell assemblies [43,44]. Interneurons could support this process because they have resonant properties fostering a theta rhythm and can rhythmically inhibit both pyramidal and basket cells [45,46]. OB theta is inherited from respiration as a drive to inhibitory interneurons in the glomeruli and might involve central inputs to inhibitory granule cells. These common rhythmic inhibitory inputs to mitral cells might also help to coordinate outputs of cell assemblies.

Gamma: local discrimination of sensory stimuli

As described earlier, manipulations of the circuitry involved in the gamma1 oscillation have led to reliable increases or decreases in gamma1 oscillation power. A few studies have linked these manipulations to changes in odor-discrimination performance. Blocking the $GABA_A$ receptors in the locust antennal lobe ablates gamma-like odor-evoked LFP oscillations, and the responses of downstream neurons are changed, indicating that temporal precision in projection neuron responses is essential to activating appropriate responses in target neurons [13]. The same treatment to honeybees impairs discrimination of similar, but not dissimilar, odors [4]. Increases in gamma1 oscillations are associated with the opposite behavioral effects in β3-knockout mice [3]. Thus, the fine temporal precision associated with sensory-evoked gamma1 oscillations indicates that this activity supports disambiguating overlapping input patterns.

What was missing from these studies was evidence that animals can adjust the level of gamma1 online in response to the demands of an odor-discrimination task. A recent study addressed this question and found that gamma1 oscillations are specifically enhanced in the OB of rats when they reach criterion performance on discrimination of similar odorants in a two-alternative choice task [2]. The increase in gamma1 power is restricted to the OB, with no increase in PC. The mechanism for this online change in gamma1 power is unknown, but a cholinergic process was suggested (Figure 3).

We do not know whether all increases in discrimination of similar odorants are accompanied by increases in gamma1 oscillations, or if any increase in gamma1 oscillations will enhance odor-discrimination performance. Several behavioral studies have shown that manipulations of neuromodulator circuits in the OB and odor enrichment lead to enhanced discrimination of similar odorants [47–49]. What is needed is concurrent recording of LFP and/or mitral cell activity during these treatments to determine whether behavioral differences are also accompanied by gamma1 oscillation changes.

The questions naturally arise: why oscillations and why gamma? In other sensory systems gamma rhythms have been cited as markers for cell assemblies [50,51]. Although much has been written on the association of gamma rhythms with cell assemblies, less has been done showing why the biophysics of the gamma rhythm is a natural substrate for the formation of cell assemblies. This issue has been addressed for neocortical gamma [37] and is closely related to the dependence of the gamma rhythm period on the decay time of $GABA_A$-induced inhibition [52]. In this model, the period of the gamma rhythm is determined by when the inhibition wears off sufficiently to enable pyramidal cells to spike. Pyramidal cells with the most drive cause local interneurons to fire; this depresses firing of other pyramidal cells, creating a cell assembly. This gamma rhythm is labeled PING (pyramidal-interneuron gamma). The underlying biophysics of the PING gamma rhythm gives clues to how cell assemblies might be dynamically modulated. In the aforementioned mechanism, the boundary between cells that are included and those that are excluded from an assembly depends on multiple factors, including the inhibition strength onto pyramidal cells and excitation onto inhibitory cells. Thus, any neuromodulation that changes these factors or other

sources of inhibition onto the excitatory cells can be expected to affect which cells participate in an assembly, as has been described in computational models [53,54].

The biophysical properties of downstream targets might also be important for supporting the oscillation period. PC pyramidal cells are sensitive to a few spikes arriving in a 5–10 ms time window [55], and these same neurons show enhanced odor selectivity in a window <50 ms long at a latency of <100 ms after odor onset in rats performing a two-alternative choice odor-discrimination task [56].

Beta: completing a cognitive circuit

As described before, beta and gamma1 oscillations rely on different anatomical networks. Do these different networks imply different functions? A closer look at the behaviors used to evaluate odor discrimination provides some insight.

We have seen beta and gamma1 oscillations in different cognitive tasks. Beta oscillations seem to be elicited in behavioral circumstances in which a rodent identifies a distinct behavior or reward valence with an odorant [5,6]. In Go/No-Go tasks, each odorant has a unique behavior with which it is associated (i.e. respond or refrain from responding) and a unique reward association (i.e. reward or no reward). By contrast, gamma1 oscillations seem to be elicited in conditions in which an animal responds with a single type of behavior (e.g. lever press left or right) and receives the same reward in either case, such as in a two-alternative choice task [2]. A recent study has reported beta oscillations in a slightly different two-alternative choice task, indicating that it is not gross differences between Go/No-Go and two-alternative choice that determine the network differences [57,58].

Go/No-Go tasks are usually easier for animals to learn than two-alternative choice tasks, and in the former we see no difference in learning time or difficulty for overlapping versus non-overlapping odorant input patterns. Rats and mice are usually more accurate in Go/No-Go than two-alternative choice tasks [59]. Olfactory behaviors that exhibit rule learning are supported by long-term changes in the OB and hippocampus [6,60], and differential reinforcement is associated with strengthened input to anterior PC from the OB and orbitofrontal cortex [61]. The system-wide involvement of beta oscillations might, thus, underlie cognitive advantages of some tasks. Beta oscillations are associated with motor models, favoring this oscillation as a good substrate for long-distance communication [62–64].

We do not yet know whether disrupting the beta oscillation network impairs odor-discrimination performance. Depending on the site of the lesion, would odor discrimination be affected wholesale, would only rule learning be affected or would the animals simply lose the advantage in learning speed provided by the cognitive structure of a Go/No-Go or other task? There are still many unanswered questions.

Conclusions

It has been nearly seventy years since the first publication describing odor-evoked OB oscillations, and in that time we have made substantial progress in understanding the various oscillatory modes and their mechanistic and functional roles. We do not yet know whether all increases in gamma1 relate to increased discrimination ability, nor do we know the mechanisms for changing the strength of gamma1 oscillations online; neuromodulators and centrifugal synaptic input from other olfactory areas are likely to have an important role. Open questions that remain regarding theta rhythms are what the central sources of drive to the OB might be and whether the inhalation and exhalation phases of theta oscillations represent separation between sensory acquisition and processing as hippocampal rhythms might. More work is needed to understand the functional roles and mechanisms of gamma2 and beta oscillations because we have little more than phenomenology for these rhythms. One of the most interesting open questions is what are the cognitive factors and mechanisms that determine a neural processing strategy, in which very different oscillatory modes are seen? The next seventy years should bring us a deeper understanding of more types of oscillations and their cognitive roles.

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