Chapter 4
Odor Maps in the Olfactory Bulb

Kensaku Mori

Abstract The olfactory bulb is the first relay station of the central olfactory system in the mammalian brain and contains a few thousand glomeruli on its surface. Individual glomeruli represent a single type of odorant receptor, and the glomerular sheet of the olfactory bulb forms odorant receptor maps. This chapter summarizes the spatial organization of the odorant receptor-representing glomerular maps of the rodent olfactory bulb, focusing on (1) the domain organization of each glomerular map, (2) "intrabulbar projections" of tufted cell axons that precisely and topographically connect the lateral and medial maps, (3) molecular feature clusters of glomeruli in the olfactory bulb, and (4) functional compartmentalization of the glomerular maps.

Keywords Clusters • Domains • Glomeruli • Intrabulbar projections • Odor map • Odorant receptor • Olfactory bulb • Two mirror-symmetrical glomerular maps

4.1 Glomerular Modules

As shown in Chap. 3, axons of olfactory sensory neurons (OSNs) expressing a given odorant receptor (OR) converge to a fixed projection site, forming a glomerulus in each of two olfactory maps in the olfactory bulb (Imai and Sakano 2007; Mombaerts 2006; Mori and Sakano 2011). Thus, an individual glomerulus in the olfactory bulb represents a single OR species. Within each glomerulus, OSN axons form excitatory synapses on the terminal tufts of primary dendrites of projection neurons, the tufted cells and mitral cells (Mori 1987; Shepherd et al. 2004). Because each tufted or mitral cell projects a single primary dendrite to a single glomerulus, an individual glomerulus together with its associated tufted and mitral cells form a

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single structural and functional module (glomerular module or glomerular unit) (see Fig. 7.1 in Chap. 7). In the mouse, each olfactory bulb contains approximately 1,800 OR-representing glomerular modules that are arranged at stereotypical positions and thus form glomerular maps (Mori and Sakano 2011; Mori et al. 2006). In this sense, the olfactory bulb resembles primary sensory areas of the neocortex in which functional columns are spatially arranged in a modality-specific manner and form sensory maps.

4.2 Each Olfactory Bulb Has Two Mirror-Symmetrical Glomerular Maps That Are Connected Precisely with Tufted Cell Axon Collaterals

In the mouse olfactory bulb, an individual OR is typically represented by a stereotypic pair of glomeruli located at two different sites, one at the rostrodorsolateral half and the other at the caudoventromedial half of the olfactory bulb (Mombaerts et al. 1996; Ressler et al. 1994; Vassar et al. 1994). Because of the dual representation, each olfactory bulb has two mirror-symmetrical glomerular maps: a lateral map and a medial map (Figs. 4.1b, 4.2) (Nagao et al. 2000). The lateral map receives olfactory axon inputs from OSNs distributed in the rostrodorsolateral part of the ipsilateral olfactory epithelium, whereas the medial map receives olfactory axon inputs from those in the caudoventromedial part of the olfactory epithelium (Astic and Saucier 1986; Saucier and Astic 1986; Schoenfeld et al. 1994).

Each functional pair of glomerular modules is precisely and reciprocally linked via the axon collaterals of tufted cells (external, middle, and internal tufted cells), which are called intrabulbar projections (Fig. 4.3) (Belluscio et al. 2002; Cummings and Belluscio 2010; Igarashi et al. 2012; Liu and Shipley 1994; Lodovichi et al. 2003; Schoenfeld et al. 1985; Zhou and Belluscio 2008). For example, tufted cells associated with a given glomerular module (glomerulus A or B in Fig. 4.3) in the lateral map extend axon collaterals through the internal plexiform layer (IPL) to the dendrites of granule cells located beneath the isofunctional glomerular module (glomerulus A′ or B′ in Fig. 4.3) in the medial map. It can be speculated that these granule cells are tufted cell-targeting granule cells that form dendrodendritic reciprocal synaptic connections with tufted cell dendrites (Fig. 4.3, see also Chap. 7). Because sister tufted cells belonging to a particular glomerulus and tufted cell-targeting granule cells form local tufted cell circuits (see Chap. 7), tufted cell circuits in the glomerular module A or B may interact preferentially with tufted cell circuits of the isofunctional glomerular modules A′ or B′, respectively, via the precise “intrabulbar projections.” In striking contrast, intrabulbar axon collaterals of mitral cells do not participate in the precise “intrabulbar projections.”

The “intrabulbar projections” of tufted cell axon collaterals are thought to coordinate responses of two mirror-symmetrical glomerular maps, but detailed functional roles of the precise reciprocal connections are not well understood

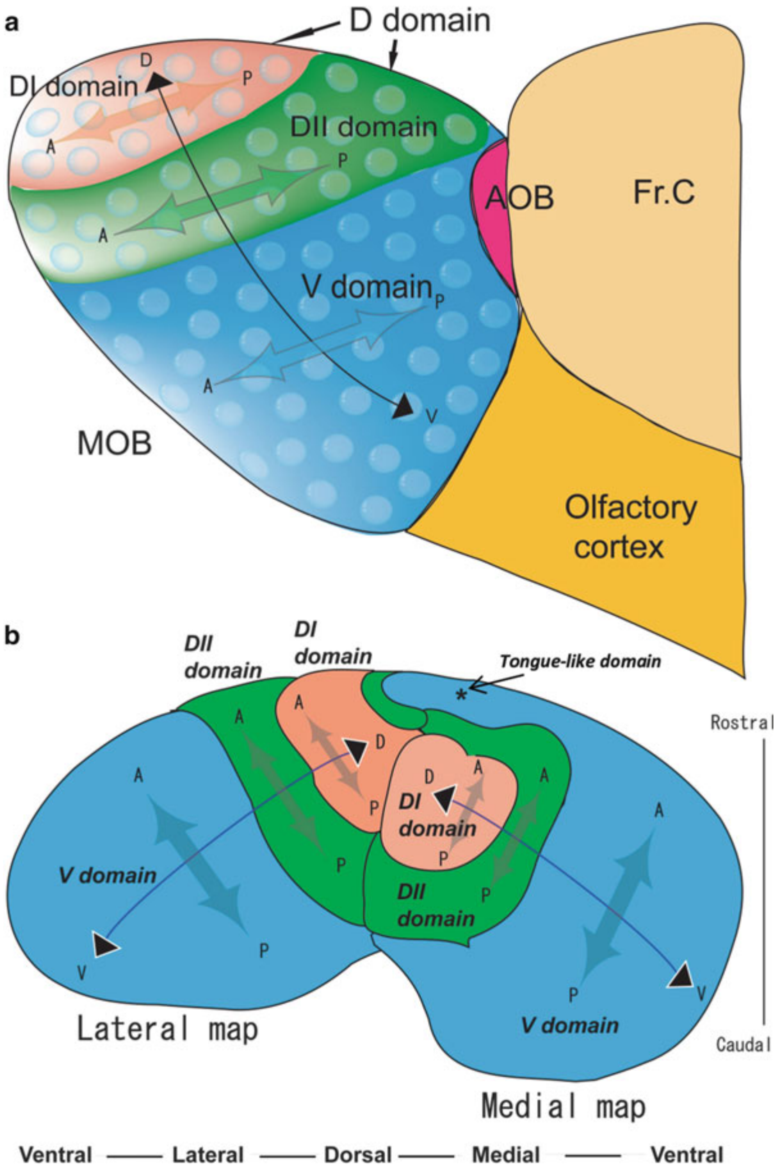

Fig. 4.1 Glomerular map of the olfactory bulb. (**a**) *Lateral view* of the domain organization of glomeruli in the lateral map of the rodent main olfactory bulb (*MOB*). *Double-headed colored arrows* indicate the anterior-posterior (anteroposterior, A-P) axis of each domain; *black arrows* indicate the dorsal-ventral (dorsoventral, D-V) axis of the lateral map. *AOB* accessory olfactory bulb, *DI* class I part of the dorsal (D) domain, *DII* class II part of the D domain, *Fr.C* frontal cortex. (**b**) A dorsal centered view of an unrolled flattened map of glomerular layer of the MOB. *Double-headed gray arrows* indicate the A-P axis of each domain of the lateral and medial maps; *black arrows* indicate the D-V axis of the lateral and medial maps. In mice, an individual OR is typically represented by a pair of glomeruli: one in the lateral map and the other in the medial map. However, for a small subset of ORs, each OR is represented only by a single glomerulus. Some of these glomeruli are located in the *tongue-like domain* (*asterisk*). (Modified from Mori and Sakano 2011)

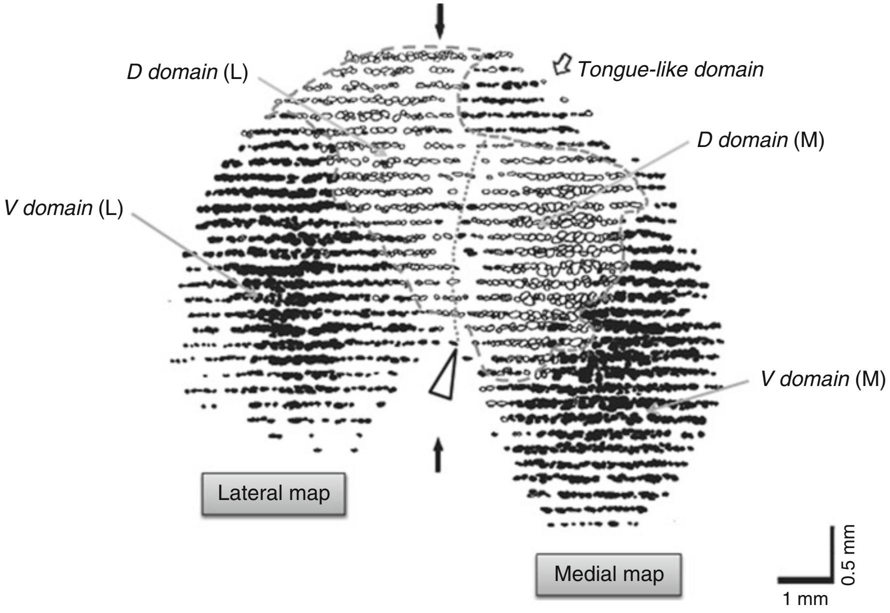

Fig. 4.2 Unrolled flattened maps of glomeruli showing OCAM-positive domain (V-domain) and OCAM-negative domain (D-domain) in the mouse olfactory bulb. The flattened glomerular layers with OCAM-positive glomeruli (*filled spots*) and OCAM-negative glomeruli (*open spots*) were aligned from rostral to caudal using the dorsal edge (*filled arrows*) of the frontal sections of the olfactory bulb. A *dotted line* with an *open triangle* indicates a possible dorsal boundary between the lateral (*L*) and medial (*M*) maps. *Open arrow* indicates the tongue-like domain. Unit length along the rostrocaudal axis is twice that of the circumferential to better illustrate the organization of glomeruli in the unrolled map. (Modified with permission from Nagao et al. 2000)

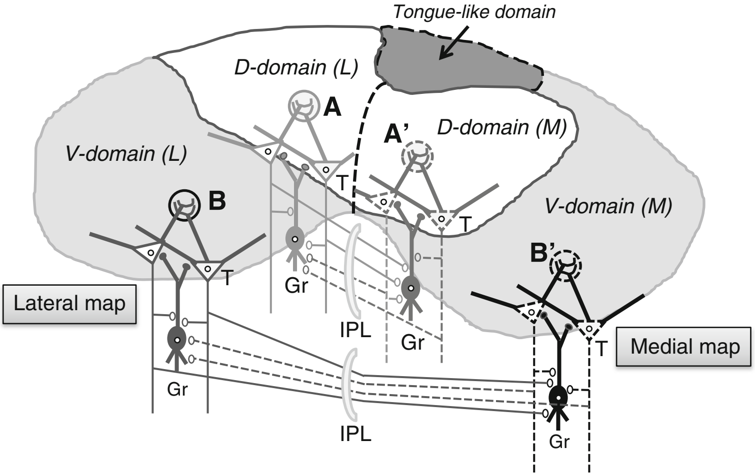

Fig. 4.3 Intrabulbar projections of tufted cell axon collaterals. Tufted cells associated with a given glomerular module (glomerulus *A* or *B*) in the lateral map extend axon collaterals through the internal plexiform layer (*IPL*) to the dendrites of granule cells (*Gr*) located beneath the isofunctional glomerular module (glomerulus *A′* or *B′*) in the medial map. The intrabulbar projection of tufted cell axon collaterals reciprocally connects isofunctional glomerular modules in the lateral and medial maps. Axons of tufted cells whose somata are in the lateral map are shown by *solid lines*; those in the medial map are illustrated by *dashed lines*

(Cummings and Belluscio 2008). Because tufted cell circuits in each glomerular module are thought to be responsible for the generation of sniff rhythm-paced early-onset fast gamma oscillations (see Chap. 7), one possible functional role of the "intrabulbar projections" is the coordination of fast gamma oscillations between isofunctional glomerular modules. It has been shown that the precise intrabulbar projections of tufted cell axon collaterals are achieved during postnatal development and undergo olfactory activity-dependent refinement during both development and adulthood (Cummings and Belluscio 2010; Marks et al. 2006). Olfactory deprivation by naris closure disrupts the intrabulbar projection, and reopening of the naris recovers the precise intrabulbar projection. These results suggest that the intrabulbar projections of tufted cells maintain a continuous level of activity-dependent plasticity throughout life.

In addition to the intrabulbar projections, each tufted cell projects axons to focal targets in the pars externa of the anterior olfactory nucleus (AONpE) (Igarashi et al. 2012; Schoenfeld and Macrides 1984). The axonal projection of tufted cells to the AONpE is organized in a topographic fashion such that the dorsoventral axis of the glomerular map in the olfactory bulb is conserved precisely in the dorsoventral axis of the axonal targets in the AONpE (Schoenfeld and Macrides 1984; Yan et al. 2008). As is described in Chap. 7, each tufted cell also projects axons to focal targets in the pars principalis of the anterior olfactory nucleus, the rostroventral part of the anterior piriform cortex, and the rostrolateral part of the olfactory tubercle. Each tufted cell may send specific OR information to focal targets both in the olfactory bulb and in the olfactory peduncle areas of the olfactory cortex.

4.3 Domain Organization of Glomerular Map

Based on the OR species (Zhang and Firestein 2002), glomeruli are grouped into specific compartments, such as domains at stereotypical positions in the olfactory bulb. Figure 4.1a shows the domain arrangement in the lateral view of the olfactory bulb. Glomeruli in the main olfactory bulb are grouped into two domains, dorsal and ventral, arranged in parallel with the anteroposterior axis of the olfactory bulb. Glomeruli in the dorsal domain (D domain) receive olfactory axon inputs from OSNs in the dorsal zone of the olfactory epithelium. Therefore, D-domain glomeruli represent dorsal-zone ORs. Glomeruli in the ventral domain (V domain) receive olfactory axon inputs from OSNs that are distributed in the ventral zone of the olfactory epithelium (Yoshihara et al. 1997). Glomeruli in the V domain therefore represent ventral-zone ORs. Olfactory axons that project to the V domain express olfactory cell adhesion molecule (OCAM), whereas those that project to the D domain lack OCAM expression (Fig. 4.2). Over the course of embryonic development, the D-domain glomeruli are formed first in the olfactory bulb, and the glomerular map expands ventrally (Takeuchi et al. 2010).

As shown in Fig. 4.1, the D-domain glomeruli are further grouped into two domains, DI and DII, according to the expressed OR species (Bozza et al. 2009; Kobayakawa et al. 2007; Tsuboi et al. 2006). The DI domain occupies the rostrodorsal part of the D domain and the DII domain surrounds the DI domain (Fig. 4.1b). Glomeruli in the DI domain represent class I (fish-type) ORs, whereas DII glomeruli represent class II (terrestrial-type) ORs. OSNs expressing class I ORs and those expressing class II ORs are intermingled in the dorsal zone of the olfactory epithelium. However, the two subsets of OSNs project their axons to separate dorsal domains in the olfactory bulb.

Trace amine-associated receptors (TAARs) are a small family of evolutionally conserved ORs (Liberles and Buck 2006). A majority of olfactory TAARs are represented by a cluster of glomeruli located in the caudal part of the D domain near the boundary between DI and DII domains (Pacifico et al. 2012). The cluster of TAARs-representing glomeruli is referred as the DIII domain.

As described earlier, each of the lateral and medial maps is divided into DI, DII, and V domains arranged in parallel to the anteroposterior axis. A comparison between the lateral and medial maps using the unrolled flattened maps indicates that each map has its own anteroposterior–dorsoventral axis coordinates, although the two maps are arranged in roughly a mirror-symmetrical manner (Fig. 4.1b).

A majority of ORs are represented by a pair of glomeruli in the mouse olfactory bulb. However, a small subset ORs is represented only by a single glomerulus. The rostromedioventral domain (so-called tongue-like domain shown in Figs. 4.1b, 4.2, and 4.3) of the glomerular map is unique in that it contains glomeruli representing the single glomerulus ORs. For example, OSNs expressing a given member of OR37 family genes converge axons only to a single glomerulus, and glomeruli for the different OR37 subtypes are grouped together in the rostromedioventral domain (Bader et al. 2012). Interestingly, mitral/tufted cells associated with the OR37 glomeruli show a unique pattern of axonal projection. They project axons directly to the medial amygdala, paraventricular nucleus, and supraoptic nucleus of the hypothalamus (Bader et al. 2012).

4.4 Molecular Feature Clusters of Glomeruli

Glomeruli in the olfactory bulb can also be grouped into subsets by the odorant selectivity, or molecular receptive range (MRR) property, of individual glomeruli. Mapping the odor-induced glomerular activity and the MRR properties of glomeruli demonstrated that (1) individual glomeruli typically respond to a range of odorants that share a specific combination of molecular features, and that (2) each glomerulus appears to be unique in its MRR property (Kikuta et al. 2013; Mori et al. 2006). In addition, glomeruli with similar MRR properties tend to gather and form molecular feature clusters at stereotypical positions in the glomerular map (Johnson and Leon 2007; Johnson et al. 2009; Matsumoto et al. 2010; Mori et al. 2006; Takahashi et al. 2004).

Figure 4.4a shows molecular feature clusters of glomeruli superimposed on the domain organization at the dorsal surface of mouse olfactory bulb (Matsumoto et al. 2010). Fatty acids, aliphatic aldehydes, and amines have distinct unpleasant

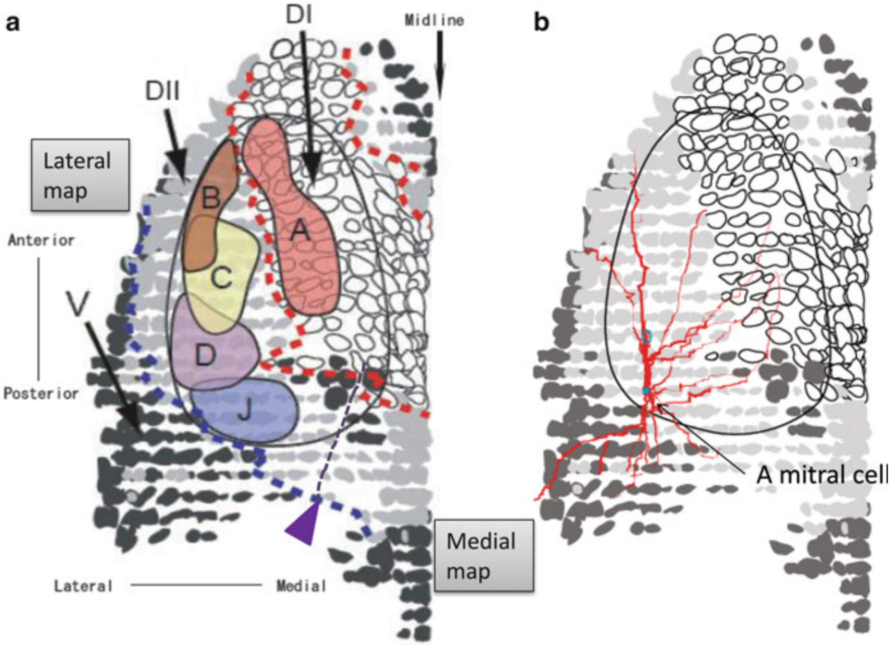

Fig. 4.4 Reconstructed glomerular map of the dorsal part of the mouse olfactory bulb. (**a**) Molecular feature clusters *A–J* are superimposed on the domain organization of the standard glomerular map. The *large black contour line* indicates the optically imaged region for determining the molecular feature clusters. *DI* DI domain (glomeruli shown by *open spots*), *DII* DII domain (glomeruli shown by *light gray spots*), *V* V-domain (glomeruli shown by *dark gray spots*). The boundaries between the DI and DII domains and between the DII and V domains are indicated by *red* and *blue dotted lines*. A *purple broken line* with *purple triangle* indicates a possible boundary between the lateral and medial maps. (**b**) Reconstructed dendritic tree of a single mitral cell (shown by *red*) whose soma is located in the DII domain is superimposed on the standard glomerular map to estimate the spatial distribution of the lateral dendrites of a single mitral cell in reference to the domain organization of glomerular maps. The standard map and the mitral cell were obtained from different mice. (Modified with permission from Matsumoto et al. 2010)

odors that characterize spoiled foods. Glomeruli in cluster A respond to fatty acid and aliphatic aldehyde odorants. The cluster A glomeruli also respond to alkyl amine odorants that contain an amino group ($-NH_3$) and are located in the lateral part of the DI domain adjacent to the DII domain.

A small cluster of glomeruli located caudomedially to the cluster A respond to amine odorants including trimethylamine but not to fatty acids (this cluster is not shown in Fig. 4.4a; cf. posteromedial amine-selective cluster in Takahashi et al. 2004). The amine-selective cluster of glomeruli appears to correspond to the TAARs-representing cluster of glomeruli (in DIII domain) (Pacifico et al. 2012).

Cluster B, which responds to aliphatic alcohol odorants and a wide range of aliphatic ketone odorants, is located in the anterior part of the DII domain. It should be noted that the aliphatic alcohols and ketones do not activate cluster A glomeruli.

Glomeruli in cluster C, which respond to phenol odorants (e.g., cresol and ethyl phenol) and phenylethyl odorants (e.g., guaiacol and creosole) are located in the DII domain just posterior to cluster B.

Cluster D glomeruli are activated by aliphatic and aromatic ketone odorants and are located posterior to cluster C. Cluster J glomeruli that respond to thiazole and thiazoline odorants (including the fox odor tri-methyl-thyazoline) are located in the caudal part of the DII domain in the lateral map. Thus, clusters B, C, D, and J are invariably arranged from the anterior to the posterior region in the DII domain. Molecular feature clusters are also found in the V domain of the olfactory bulb (Igarashi and Mori 2005). The spatial arrangement of the molecular feature clusters A–D and J appears to be conserved between rats and mice (Matsumoto et al. 2010).

In human sensory psychophysical studies, a variety of correlations have been reported between the molecular features of odorants and their perceived "odor quality" (Amoore et al. 1964; Beets 1970; Moncrieff 1967; Mori et al. 2006; Rossiter 1996). Although the molecular structure–odor relationships are complex and cannot be explained in simple terms, it can be speculated that the molecular feature clusters of glomeruli might be part of the neural representation of basic odor quality. In addition, the molecular feature maps provide a basis for understanding how the olfactory cortex read the odor maps in the olfactory bulb.

4.5 Functional Compartmentalization in the Olfactory Map

Odors emitted by predators signify danger and induce fear responses such as freezing in rodents (Dielenberg and McGregor 2001; Hebb et al. 2002, 2004). Trimethyl thiazoline (TMT) is a fox odor known to induce a freezing response in mice and rats. TMT activates glomeruli in cluster J of the DII domain and many glomeruli in the V domain. Ablation of glomeruli in the D domain including the DII domain abolishes the TMT-induced fear response in mice (Kobayakawa et al. 2007), suggesting that TMT-responsive glomeruli in the DII domain are responsible for the TMT-induced fear responses.

Spoiled foods produce amines and fatty acids, and these odors induce innate aversive responses in rats and mice (Dielenberg and McGregor 2001) and activate multiple glomeruli in various areas of the olfactory bulb. However, only cluster A glomeruli in the DI domain are responsible for fatty acid-induced aversive responses (Kobayakawa et al. 2007).

These results raise the possibility of functional compartmentalization of the glomerular map of the olfactory bulb: TMT-responsive glomeruli and other predator odor-responsive glomeruli in the DII domain might be specialized for inducing fear responses to the predator odors, and fatty acid and amine-responsive glomeruli in the DI domain might be specialized for inducing aversive responses to spoiled foods.

A single glomerular module consists of a glomerulus together with sister tufted cells and mitral cells. Each granule cell also might mainly associate with a single glomerular module (Willhite et al. 2006). Mitral and tufted cells belonging to a particular glomerular module extend lateral dendrites in the external plexiform layer and thus can interact with mitral and tufted cells belonging to other glomerular modules via dendrodendritic reciprocal synaptic connections with granule cell inhibitory interneuron (Migliore et al. 2010) (see Chap. 7). To estimate the extent of dendritic projection of a single mitral cell in reference to the glomerular maps, we superimposed the dendritic tree of a mitral cell (whose soma was located in the DII domain) on a standard glomerular map of the dorsal surface of the mouse main olfactory bulb (Fig. 4.4b). It can be seen that a single mitral cell extends a lateral dendrite widely covering not only wide areas of the DII domain but also DI and V domains. Thus, a number of glomerular modules can interact globally across wide areas of the olfactory bulb via the long lateral dendrites of mitral cells.

In contrast, external tufted cells and middle tufted cells extend shorter lateral dendrites, suggesting that interactions among glomerular modules via these tufted cell dendrites are more spatially restricted. Therefore, tufted cells and mitral cells appear to read the glomerular OR maps in a different manner, as is discussed in more detail in Chap. 7.

References

Amoore JE, Johnston JW Jr, Rubin M (1964) The sterochemical theory of odor. Sci Am 210:42–49

Astic L, Saucier D (1986) Anatomical mapping of the neuroepithelial projection to the olfactory bulb in the rat. Brain Res Bull 16:445–454

Bader A, Klein B, Breer H, Strotmann J (2012) Connectivity from OR37 expressing olfactory sensory neurons to distinct cell types in the hypothalamus. Front Neural Circuits 6:84

Beets MG (1970) The molecular parameters of olfactory response. Pharmacol Rev 22:1–34

Belluscio L, Lodovichi C, Feinstein P, Mombaerts P, Katz LC (2002) Odorant receptors instruct functional circuitry in the mouse olfactory bulb. Nature (Lond) 419:296–300

Bozza T, Vassalli A, Fuss S, Zhang J, Weiland B et al (2009) Mapping of class I and class II odorant receptors to glomerular domains by two distinct types of olfactory sensory neurons in the mouse. Neuron 61:220–233

Cummings DM, Belluscio L (2008) Charting plasticity in the regenerating maps of the mammalian olfactory bulb. Neuroscientist 14:251–263

Cummings DM, Belluscio L (2010) Continuous neural plasticity in the olfactory intrabulbar circuitry. J Neurosci 30:9172–9180

Dielenberg RA, McGregor IS (2001) Defensive behavior in rats towards predatory odors: a review. Neurosci Biobehav Rev 25:597–609

Hebb AL, Zacharko RM, Dominguez H, Trudel F, Laforest S, Drolet G (2002) Odor-induced variation in anxiety-like behavior in mice is associated with discrete and differential effects on mesocorticolimbic cholecystokinin mRNA expression. Neuropsychopharmacology 27:744–755

Hebb AL, Zacharko RM, Gauthier M, Trudel F, Laforest S, Drolet G (2004) Brief exposure to predator odor and resultant anxiety enhances mesocorticolimbic activity and enkephalin expression in CD-1 mice. Eur J Neurosci 20:2415–2429

Igarashi K, Mori K (2005) Spatial representation of hydrocarbon odorants in the ventrolateral zones of the rat olfactory bulb. J Neurophysiol 93:1007–1019

Igarashi KM, Ieki N, An M, Yamaguchi Y, Nagayama S et al (2012) Parallel mitral and tufted cell pathways route distinct odor information to different targets in the olfactory cortex. J Neurosci 32:7970–7985

Imai T, Sakano H (2007) Roles of odorant receptors in projecting axons in the mouse olfactory system. Curr Opin Neurobiol 17:507–515

Johnson B, Leon M (2007) Chemotopic odorant coding in a mammalian olfactory system. J Comp Neurol 503:1–34

Johnson B, Xu Z, Ali S, Leon M (2009) Spatial representations of odorants in olfactory bulbs of rats and mice: similarities and differences in chemotopic organization. J Comp Neurol 514:658–673

Kikuta S, Fletcher ML, Homma R, Yamasoba T, Nagayama S (2013) Odorant response properties of individual neurons in an olfactory glomerular module. Neuron 77:1122–1135

Kobayakawa K, Kobayakawa R, Matsumoto H, Oka Y, Imai T et al (2007) Innate versus learned odour processing in the mouse olfactory bulb. Nature (Lond) 450:503–508

Liberles SD, Buck LB (2006) A second class of chemosensory receptors in the olfactory epithelium. Nature (Lond) 442:645–650

Liu WL, Shipley MT (1994) Intrabulbar associational system in the rat olfactory bulb comprises cholecystokinin-containing tufted cells that synapse onto the dendrites of GABAergic granule cells. J Comp Neurol 346:541–558

Lodovichi C, Belluscio L, Katz LC (2003) Functional topography of connections linking mirror-symmetric maps in the mouse olfactory bulb. Neuron 38:265–276

Marks CA, Cheng K, Cummings DM, Belluscio L (2006) Activity-dependent plasticity in the olfactory intrabulbar map. J Neurosci 26:11257–11266

Matsumoto H, Kobayakawa K, Kobayakawa R, Tashiro T, Mori K, Sakano H (2010) Spatial arrangement of glomerular molecular-feature clusters in the odorant-receptor class domains of the mouse olfactory bulb. J Neurophysiol 103:3490–3500

Migliore M, Hines ML, McTavish TS, Shepherd GM (2010) Functional roles of distributed synaptic clusters in the mitral-granule cell network of the olfactory bulb. Front Integr Neurosci 4:122

Mombaerts P (2006) Axonal wiring in the mouse olfactory system. Annu Rev Cell Dev Biol 22:713–737

Mombaerts P, Wang F, Dulac C, Chao SK, Nemes A et al (1996) Visualizing an olfactory sensory map. Cell 87:675–686

Moncrieff RW (1967) The chemical senses. Leonard Hill, London

Mori K (1987) Membrane and synaptic properties of identified neurons in the olfactory bulb. Prog Neurobiol 29:275–320

Mori K, Sakano H (2011) How is the olfactory map formed and interpreted in the mammalian brain? Annu Rev Neurosci 34:467–499

Mori K, Takahashi Y, Igarashi K, Yamaguchi M (2006) Maps of odorant molecular features in the mammalian olfactory bulb. Physiol Rev 86:409–433

Nagao H, Yoshihara Y, Mitsui S, Fujisawa H, Mori K (2000) Two mirror-image sensory maps with domain organization in the mouse main olfactory bulb. Neuroreport 11:3023–3027

Pacifico R, Dewan A, Cawley D, Guo C, Bozza T (2012) An olfactory subsystem that mediates high-sensitivity detection of volatile amines. Cell Rep 2:76–88

Ressler KJ, Sullivan SL, Buck LB (1994) Information coding in the olfactory system: evidence for a stereotyped and highly organized epitope map in the olfactory bulb. Cell 79:1245–1255

Rossiter KJ (1996) Structure–odor relationships. Chem Rev 96:3201–3240

Saucier D, Astic L (1986) Analysis of the topographical organization of olfactory epithelium projections in the rat. Brain Res Bull 16:455–462

Schoenfeld TA, Macrides F (1984) Topographic organization of connections between the main olfactory bulb and pars externa of the anterior olfactory nucleus in the hamster. J Comp Neurol 227:121–135

Schoenfeld TA, Marchand JE, Macrides F (1985) Topographic organization of tufted cell axonal projections in the hamster main olfactory bulb: an intrabulbar associational system. J Comp Neurol 235:503–518

Schoenfeld TA, Clancy AN, Forbes WB, Macrides F (1994) The spatial organization of the peripheral olfactory system of the hamster. Part I: receptor neuron projections to the main olfactory bulb. Brain Res Bull 34:183–210

Shepherd G, Chen WR, Greer CA (eds) (2004) Olfactory bulb. Oxford University Press, New York, pp 165–216

Takahashi Y, Kurosaki M, Hirono S, Mori K (2004) Topographic representation of odorant molecular features in the rat olfactory bulb. J Neurophysiol 92:2413–2427

Takeuchi H, Inokuchi K, Aoki M, Suto F, Tsuboi A et al (2010) Sequential arrival and graded secretion of Sema3F by olfactory neuron axons specify map topography at the bulb. Cell 141:1056–1067

Tsuboi A, Miyazaki T, Imai T, Sakano H (2006) Olfactory sensory neurons expressing class I odorant receptors converge their axons on an antero-dorsal domain of the olfactory bulb in the mouse. Eur J Neurosci 23:1436–1444

Vassar R, Chao SK, Sitcheran R, Nunez JM, Vosshall LB, Axel R (1994) Topographic organization of sensory projections to the olfactory bulb. Cell 79:981–991

Willhite DC, Nguyen KT, Masurkar AV, Greer CA, Shepherd GM, Chen WR (2006) Viral tracing identifies distributed columnar organization in the olfactory bulb. Proc Natl Acad Sci USA 103:12592–12597

Yan Z, Tan J, Qin C, Lu Y, Ding C, Luo M (2008) Precise circuitry links bilaterally symmetric olfactory maps. Neuron 58:613–624

Yoshihara Y, Kawasaki M, Tamada A, Fujita H, Hayashi H et al (1997) OCAM: A new member of the neural cell adhesion molecule family related to zone-to-zone projection of olfactory and vomeronasal axons. J Neurosci 17:5830–5842

Zhang X, Firestein S (2002) The olfactory receptor gene superfamily of the mouse. Nat Neurosci 5:124–133

Zhou Z, Belluscio L (2008) Intrabulbar projecting external tufted cells mediate a timing-based mechanism that dynamically gates olfactory bulb output. J Neurosci 28:9920–9928