Fine Structure of the Septal Olfactory Organ of Masera and its Associated Gland in the Golden Hamster

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ABSTRACT. Fine structures of the septal olfactory organ of Masera (MO) and its associated gland, a kind of olfactory glands, were examined in the golden hamster in comparison with those of the olfactory epithelium (OE) and vomeronasal organ (VNO) and their associated olfactory glands. Bipolar neurons of the MO were divided into two types according to their apical morphology, one similar to the receptors of the OE and the other to those of the vomeronasal sensory epithelium (VSE). The former was dominant and interpreted as main receptors of the MO. The other was less in number, but also regarded as a kind of olfactory receptors. The ultrastructural features of supporting cells of the MO were similar to those of the OE rather than to those of the VSE, while those of basal cells were almost in common in the OE, VSE and MO. The associated gland of the MO was positive to both PAS and alcian blue as the Bowman's gland of the OE. The fine structure of the associated gland of the MO was also similar to that of Bowman's gland. The present findings on the fine structure of the MO and its associated gland strongly suggest that the MO fulfills an olfactory function similar to that of the OE.—**KEY WORDS:** fine structure, olfactory epithelium, olfactory gland, septal olfactory organ of Masera, vomeronasal organ.

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In mammals can occur three different types of olfactory receptors, olfactory epithelium (OE), vomeronasal organ (VNO), and septal olfactory organ of Masera (MO) [18, 35, 42]. Thus, the OE exists in all mammals, and the VNO exists in most mammals with several exceptions, whereas the MO has been found only in a limited number of mammals [2, 9, 18, 22, 27, 35, 42]. This results in the meager knowledge of the fine structure of the MO, although structures of the OE and VNO are well documented [1, 3, 4, 7, 11, 14, 16, 17, 22, 25, 26, 29–31, 36, 38, 43, 45–47, 54]. The functional significance of the MO is still unclear. Besides, an associated gland of the MO, a kind of olfactory glands, is almost completely neglected in the previous reports and remains anonymous. As odoriferous molecules must be dissolved in the secretion of olfactory glands such as Bowman's and Jacobson's glands before they are perceived by olfactory receptors as olfactory stimuli [16, 18, 19, 31, 32], the knowledge of the structure of an associated olfactory gland is essential in addition to that of a receptor itself to assume the functional significance of an olfactory receptor. In the present study, therefore, the structure of the MO and its associated gland was examined by light and electron microscopy in comparison with that of the OE and VNO in the golden hamster to reveal the difference or similarity among them for the presumption of the

functional significance of the MO.

MATERIALS AND METHODS

A total of 20 adult golden hamsters of both sexes were used in the present study. For light microscopy (LM), 3 animals were anesthetized with ether and sacrificed by cardiac perfusion with the physiological saline followed by Bouin's solution. The OE, VNO and MO were removed as materials, immersed in the same fixative for 24 hr, dehydrated in a graded series of ethanol, and embedded in paraffin by the routine procedure. Paraffin sections were cut serially at 5 μ m, deparaffinized with xylene, and stained with hematoxylin-eosin, PAS-hematoxylin or alcian blue (pH 2.6)-hematoxylin.

For transmission electron microscopy (TEM), 7 animals were anesthetized as for LM, and perfused with the physiological saline followed by a modified Karnovsky's solution (2% glutaraldehyde and 2.5% paraformaldehyde in 0.05 M cacodylate buffer, pH 7.3). Materials were removed from the animals, immersed in the same fixative for 2 hr at 4°C, rinsed overnight at 4°C in 0.1 M cacodylate buffer (pH 7.3), and post-fixed for 1 hr at 4°C in 1% osmium tetroxide in the same buffer. Materials were then dehydrated as for LM, passed through n-butyl glycidyl ether (QY-1) at a room temperature, and embedded in Epon 812 by the routine procedure.

Ultrathin sections were cut on a Porter-Blum MT-2 ultramicrotome, stained with uranyl acetate and lead citrate and examined with a Hitachi H-800 electron microscope. Semi-thin sections were stained with Mallory's azur II-methylene blue for LM.

For scanning electron microscopy (SEM), materials were removed from 10 animals, fixed as for TEM, washed several times with the physiological saline to remove the excessive mucus, and then post-fixed and dehydrated as for TEM. Dehydrated materials were immersed in isoamyl acetate, critical point-dried in a Hitachi HCP-1 critical point dryer, coated with gold in a JEE-4C vacuum evaporator and examined with a Hitachi S-450 scanning electron microscope.

RESULTS

Although the OE, VNO and MO were simultaneously examined in the present study, the former two are referred to only in comparison with the MO in the following description, since they were detailed in our previous reports [46, 48]. The following description is valid for male and female animals because of the absence of the sex difference in the findings of the OE, VNO and MO.

Topography and histological structure of the MO and its associated gland: The MO was situated on the ventrocaudal side of the nasal septum slightly dorsal to the caudal end of the VNO and faced the common nasal meatus. The MO was a small patch of an epithelium, elliptically outlined, and surrounded by the respiratory epithelium of the nasal cavity. Its topographical relationship in the nasal cavity was schematically illustrated in Fig. 1.

Histologically, the MO (Fig. 2) consisted of receptor, supporting and basal cells as in the OE and vomeronasal sensory epithelium (VSE). Receptor and supporting cells were elongated and arrayed alternatively in the MO, while basal cells were small and were situated sporadically on the basement membrane. The superficial layer of the MO was formed by the distal prolongations of receptor and supporting cells. The upper third of the MO contained elliptical nuclei of elongated supporting cells. Middle and basal thirds were occupied by round nuclei of receptor cells arranged in several layers. The arrangement of the cells of the MO was conspicuously similar to that of the OE, although the MO was rather low in height. The height of the

Fig. 1. Schematic drawing of the parasagittal section of the nasal cavity and cranium. An arrow indicates the opening of the vomeronasal organ (VNO). AOB: accessory olfactory bulb, ET: endoturbinate, I: incisor, MO: septal olfactory organ of Masera, MOB: main olfactory bulb, NS: nasal septum.

Fig. 2. Light micrograph of the MO and its associated gland (AG). An arrow indicates the opening of the AG. B: basal cell, GL: gland in the deep layer of the lamina propria, R: receptor cell, S: supporting cell. H. E. staining. $\times 680$.

OE, VSE and MO was 80–90 μm , 160–180 μm and 40–50 μm , respectively.

The MO was occasionally penetrated by ducts of an associated gland. This gland was branched or unbranched simple tubulo-alveolar in type and possessed its small acinus in the superficial layer of the lamina propria of the MO. Acinar cells possessed a round nucleus in the middle of the cytoplasm and secreted materials positive to both PAS and alcian blue as those of Bowman's gland of the OE. Myoepithelial cells were not observed in

this associated gland. Small nerve bundles leaving the MO were occasionally encountered in the lamina propria.

Another gland was widely distributed in the deep layer of the lamina propria of the MO and neighboring respiratory epithelium. This gland was complex tubulo-alveolar in type and consisted of many acini and a poorly-developed ductular system. Myoepithelial cells were not observed in this gland. The opening of the duct into the nasal cavity was never observed in the posterior half of the nasal septum not to mention the MO and its adjacent regions, and seemed to be in the anterior part of the septum. Acinar cells possessed a round to oval nucleus in the middle to basal part of the cytoplasm. The acini were PAS-positive but alcian blue-negative as those of Jacobson's gland of the VNO.

Fine structure of the MO and its associated gland:

Fine structures of the cells of the MO were similar to those of the OE and VSE. The receptor cells of the MO were bipolar neurons and possessed a round nucleus with distinct nucleolus. Their cytoplasm was generally electron-lucent, but occasionally electron-dense. Electron-dense cells seemed to be in process of degeneration judging from their degenerative organelles and pyknotic features. The dendrites of the receptor cells usually displayed an aggregation of mitochondria below the apical part and many microtubules running parallel with the long axis of the dendrite below the aggregation area of mitochondria (Fig. 3). Their somata contained rough ER, Golgi apparatus, free ribosomes and lipofuscin granules other than nucleus. Smooth ER was occasionally encountered in the infranuclear cytoplasm. This organelle was usually well developed in the perinuclear cytoplasm of the receptor of the VSE, but hardly observed in that of the OE. Proximally, the cytoplasm of the receptor cell abruptly tapered and penetrated the basement membrane to leave the MO as an axon.

Receptor cells of the MO can be divided into two types according to their apical morphology. The first type of the receptor (Fig. 3) was dominant and possessed a structure similar to an olfactory vesicle of the OE. This structure bore cilia with basal bodies at their base, and displayed several pinocytic vesicles, mitochondria, and free ribosomes. The cilia extended radially at first from the structure and then ran parallel with the free surface of the apical cytoplasm of the MO cells. There was practically no difference in ultrastructural findings between this

structure and the olfactory vesicle. The second type of the receptor (Fig. 4) was occasionally encountered and possessed no such vesicle-like structure. Its apical cytoplasm protruded slightly, displayed numerous pinocytic vesicles and was covered with numerous microvilli, a little irregular in shape, on its free surface. These findings resembled those of the receptor cell of the VSE except that centrioles were hardly observed in the second type, because centrioles were characteristic in the receptor cell of the VSE in spite of the absence of cilia. There seemed to be almost no difference in fine structure between the two types of receptor cells of the MO except in their apical morphology.

The supporting cells of the MO (Fig. 3) were covered with a few microvilli on their free surface and possessed an elliptical nucleus (Fig. 5) with a peripheral deposition of chromatin materials. They were higher in electron density than the receptor cells, and displayed well-developed smooth ER and many mitochondria throughout the cytoplasm and less-developed rough ER and Golgi apparatus in the perinuclear cytoplasm. Smooth ER was also well developed in the supporting cells of the OE, but not in those of the VSE. The basal cells of the MO (Fig. 6) were small and amorphous, and lay sideways on the basement membrane. They were moderate in electron density and contained mitochondria, rough ER and free ribosomes. Their cytoplasm occasionally surrounded axonic processes of the receptor cells. Fine structures of supporting and basal cells of the MO displayed no remarkable difference from those of the OE or VSE except for smooth ER of the supporting cells.

The free surface of the MO was covered with a sheet of mucin as in the OE and VNO. This mucous sheet of the MO, different from that of the OE and VNO, was conspicuously resistant to several times of rinsing with physiological saline and hindered to obtain clear figures by SEM. Nevertheless, the free surface of the MO was composed of two regions. One region spread widely and occupied the central part of the free surface of the MO (Fig. 7). This region was covered with cilia running parallel with the free surface of the apical cytoplasm of the MO cells and resembled the surface of the OE in morphology (Fig. 8). The other region was situated in the periphery of the MO, where microvilli were dominant with occasional cilia protruding from structures similar to the olfactory vesicles (Fig. 9). The cilia in this region were shorter than those in the

Fig. 3. Transmission electron micrograph of the apical part of the MO in its central region. S: supporting cell, V: olfactory vesicle-like structure. $\times 6,000$.

Fig. 4. Transmission electron micrograph of the apical part of the MO in its peripheral region. An arrow indicates microvilli of a receptor cell. DR: degenerating receptor cell, DS: degenerating supporting cell, R: receptor cell. $\times 6,000$.

Fig. 5. Transmission electron micrograph of the middle part of the MO. G: Golgi apparatus, R: receptor cell, S: supporting cell. $\times 6,000$.

Fig. 6. Transmission electron micrograph of the basal part of the MO. Arrows indicate lipofuscin granules. B: basal cell, R: receptor cell. $\times 6,000$.

central region and extended only radially from the vesicle-like structures. The peripheral region displayed a surface morphology similar to that of the VSE (Fig. 10) except for the occasional vesicle-like structures. Outside of this region, the MO was completely surrounded and sharply demarcated

from the nasal respiratory epithelium exclusively covered with cilia. These cilia were usual in type, different from those of the OE and MO, and stood perpendicularly on the free surface of the respiratory epithelium.

The acinar cells of the associated gland of the MO

Fig. 7. Scanning electron micrograph of the surface morphology of the MO in its central region. C: cilia. $\times 6,000$.

Fig. 8. Scanning electron micrograph of the surface morphology of the OE. C: cilia. $\times 6,000$.

Fig. 9. Scanning electron micrograph of the surface morphology of the MO in its peripheral region. MV: microvilli, V: olfactory vesicle-like structure. $\times 6,000$.

Fig. 10. Scanning electron micrograph of the surface morphology of the VSE. MV: microvilli. $\times 6,000$.

(Fig. 11) were electron-dense, similar in fine structure to those of Bowman's gland of the OE, and contained numerous secretory granules. These granules were electron-lucent, 600–900 nm in diameter, and tended to aggregate in the apical part of the cytoplasm. The acinar cells also contained well-developed Golgi apparatus, rough ER, numerous free ribosomes, mitochondria, and occasional lipofuscin granules.

On the other hand, acinar cells of a gland (Fig. 12) situated in the deep layer of the lamina propria were moderate in electron density and contained numerous granules. These granules were round, electron-dense, 1,000–1,500 nm in diameter and tended to aggregate in the apical cytoplasm. The acinar cells also contained well-developed rough ER with dilated cisternae, mitochondria, Golgi apparatus, and occasional lipofuscin granules. The fine structure of

Fig. 11. Transmission electron micrograph of the associated gland of the MO. G: Golgi apparatus, L: lumen of the acinus. $\times 6,000$.

Fig. 12. Transmission electron micrograph of the gland in the deep layer of the lamina propria. Arrows indicate rER with distended cisternae. G: Golgi apparatus, L: lumen of the acinus. $\times 6,000$.

the acinar cells of this gland situated in the deep layer was similar to that of Jacobson's gland of the VNO.

DISCUSSION

The OE and VNO are in common derived from the embryonic olfactory placode, consisting of receptor, supporting and basal cells and undergoing some modifications during development [18, 19, 49, 50]. They project centrally via olfactory or vomeronasal nerves to the main olfactory bulb (MOB) and the accessory olfactory bulb (AOB), respectively, and constitute two distinct olfactory systems, OE-MOB and VNO-AOB [5, 13, 19–21, 32, 37, 40, 41]. These systems display functional specializations. The OE-MOB system takes charge of a usual olfactory perception, while the VNO-AOB system an olfaction related to reproductive and/or social behaviors [6, 10, 12, 15, 19, 24, 28, 39, 51, 52]. Receptors themselves respond differently to odoriferous molecules, and the OE and VNO are stimulated by volatile and non-volatile molecules, respectively [19, 32, 53].

On the other hand, there seems to be only a very limited knowledge concerning the MO. Its function, precise projection site and ontogeny are not established until now. Although Bojsen-Møller [9] re-

ported that nerves to the MO arise from the caudal part of the olfactory bulb, he did not discriminate as to whether this part belongs to the MOB or AOB. It can only be said at present that the MO is not an ectopic area of the OE or VNO, since bundles of axons originating in the MO are separate from those of the olfactory and vomeronasal nerves [9]. As for its function, Rodolfo-Masera [42] and Adams and McFarland [2] speculated that the MO is sampling olfactory stimuli during a period of rest to modify the function of the OE and VNO. Kratzing [27] made a similar suggestion that the MO could act to monitor the air flow in a quiet respiration, and further alluded its role in the appreciation of the direction from which the odour comes. Wysocki *et al.* [53] detected urine labelled with rhodamine in the VNO and MO but not in the OE after its application to the nose of a guinea pig, and suggested that the MO may be involved in the perception of pheromones and other non-volatile substances. On the other hand, Miragall *et al.* [35] caused the degeneration of receptor cells in the OE and MO but not in the VSE with a highly volatile compound, N-methyl-forminino-methylester, and suggested that the MO is also sensitive to volatile compounds. These different or conflicting findings stand independently upon their rights. According to the present results, however, the MO gives an

impression that it does not play at least a ruling role in the mammalian olfaction, since it was observed that the MO occupied only a small area in the nasal cavity and that its height was rather low in comparison with that of the OE and VSE. Such observation can strongly suggest that receptor cells of the MO are much smaller in number than those of the OE and VSE.

The fine structure of the MO was reported only by a few authors. Kratzing [27] examined the olfactory apparatus of the bandicoot by LM and TEM to note the presence of the MO, but did not find any difference in the fine structure between the OE and the MO. Consequently, she described their fine structure without distinction and reported the presence of pale cells and brush cells, though small in number, other than usual three cell types. Pale cells lack cilia or basal bodies, but occasionally possess centrioles towards the free surface, and are covered with microvilli irregular in shape. Pinocytic vesicles are observed at the base of the microvilli. Brush cells also lack cilia and are covered with a number of straight microvilli. She seemed to adopt a negative attitude to attribute a sensory function to any of these two cell types. On the other hand, Graziadei [18] described ultrastructural characteristics in the respective receptor cell of the OE, VSE and MO. According to him, the receptor of the OE is characterized by cilia, while that of the VNO bears microvilli instead of cilia and is characterized by smooth ER filling most of the perikaryon. The receptor of the MO is covered with cilia and contains characteristic smooth ER often taking an "onion ring" appearance in the infranuclear cytoplasm and preponderant Golgi apparatus in the supranuclear cytoplasm. By freeze-fracture electron microscopy, Miragall *et al.* [35] examined the plasma membranes of the MO and compared their findings with those of the OE and VNO obtained in their previous reports [33, 34]. They found that the olfactory border of the MO is mainly composed of the terminals of receptor cells covered with cilia and supporting cells covered with microvilli. A small number of cells with thick microvillus-like projections also contribute to the border. Olfactory vesicles show transitions between those displaying numerous cilia and those characterized by few or no cilia. According to the density and arrangement of the intramembranous particles, important similarities exist between the MO and the OE, whereas remarkable differences exist between the MO and

the VSE. They interpreted the cells with thick microvillus-like projections as typical brush cells described in the OE [4, 27] and mentioned their functional significance unclear.

In the present study, findings on the fine structure of the MO were partly similar to and partly different from previous findings described above. One type of the receptor cells with a structure similar to the olfactory vesicle was dominant and was observed in common in the previous reports [18, 27, 35] and the present study. The fine structure of this cell type was also in common and conspicuously similar to that of the receptor cell of the OE except for smooth ER, which was reported by Graziadei [18] and also observed in the present study. Although its functional significance in the olfaction is still unclear, smooth ER is also present in the receptor cells of the VSE [46–48]. Its presence in the receptor cells of the VSE and MO would not deny the olfactory function of these cells. This leads to the interpretation that the cells with an olfactory vesicle-like structure are the main olfactory receptors of the MO.

As for the cells lacking cilia, findings were different among previous reports [27, 35] and the present study. Kratzing [27] described two types of these cells, pale and brush, while Miragall *et al.* [35] reported only on brush cells and Graziadei [18] never mentioned such cells. On the other hand, only one type of such cells was observed in the present study. They seemed to correspond to pale cells of Kratzing [27] judging from their fine structure and were similar to receptor cells of the VSE [46–48] with a minor discrepancy. Although Kratzing was unwilling to regard them as olfactory receptors, they seemed to be equipped with almost all ultrastructural features of bipolar neurons. Therefore, they might be considered as one kind of olfactory receptors monitoring a similar kind of olfactory stimuli as perceived by the VSE.

The present findings on the fine structure of supporting cells of the MO agreed well with those of the previous reports [27, 35]. The supporting cells were covered with microvilli and characterized by the presence of smooth ER in the cytoplasm. Since smooth ER was well developed in the supporting cells of the OE but almost absent in those of the VSE [4, 11, 16, 46], and since the other ultrastructural features of supporting cells were almost common in all of the OE, VSE and MO [27, 35, 46, 48], there existed no morphological evidence to distinguish supporting cells of the MO from those of the OE.

This strongly suggests that they play at least a similar role in the olfactory function of the OE and MO.

There is no report on the fine structure of basal cells of the MO, while Kratzing [27] reported two types of basal cells in the OE and MO. The first type is more numerous and described as a typical basal cell, while the second type of a basal cell is rarer and less differentiated and may act as an olfactory stem cell to serve either a newly differentiating olfactory cell or a more differentiated basal cell. In the present study, however, there was no morphological necessity to divide basal cells into two or more types. The present findings on basal cells agreed well with those of typical basal cells of the OE and VSE in the previous reports [4, 11, 16, 46, 48]. Since new receptors are thought to develop from basal cells of the epithelium [4, 16, 19], it seems unnecessary to distinguish basal cells from stem cells. As Kratzing [27] reported that the second type of a basal cell resembles a light olfactory cell, it might be considered as a newly developing receptor cell at a very early stage of differentiation.

As described in the introduction, there is no report on the fine structure of the associated gland of the MO. In the present study, this gland was positive to both PAS and alcian blue as Bowman's gland of the OE [8, 22]. This suggests that this gland secretes both neutral and acid mucopolysaccharide. The fine structure of this gland was also similar to that of Bowman's gland [4, 11, 16]. Since Jacobson's gland of the VNO was positive only to PAS to suggest the secretion of neutral mucopolysaccharide and was different from the gland of the OE and MO in fine structure [31, 46], the MO would be covered with a mucous sheet, which seems to be similar to that of the OE and to be different from that of the VNO. This seems to suggest that the MO perceives odoriferous molecules similar to those perceived by the OE, since the molecules must be dissolved in the mucus before they reach receptors as olfactory stimuli. Details in the chemical or histochemical properties of secretions from the associated gland of the OE and MO are further to be investigated.

The other gland located in the deep layer of the lamina propria cannot be interpreted as an associated gland of the MO, since openings of ducts of this gland were not present in the posterior part of the nasal septum adjacent enough for its secretion to cover the MO. Since this gland was positive to PAS and negative to alcian blue as was Jacobson's gland of the VNO and similar to the latter gland in fine

structure, the nature of its secretion may also be similar to that of Jacobson's gland. According to its location, secretion and fine structure, however, this gland seemed to correspond to the PAS-positive nasal gland of Katz and Merzel [22] which was reported elsewhere as the anterior medial gland [23, 44]. This would not conflict with its similarity to Jacobson's gland, because Jacobson's gland is also thought to be a kind of nasal glands [8, 22]. The anterior medial gland is thought to secrete substances serving for the cleaning of the inner surface of the nasal cavity or to function for warming and moistening of the inhaled air [22, 23, 44]. However, there remains a minor possibility that the secretion of this gland is flown back from the openings in the anterior part of the nasal septum to reach at least the peripheral part of the MO by the ciliary movement of the nasal respiratory epithelium, because the MO is located in the ventral part of the septum. No information is so far available on the participation of the secretion of this gland in the formation of the mucous sheet covering the MO, although the secretion of this gland may be mixed with that of the associated gland of the MO and may make the mucous sheet resistant to several times of rinsing with physiological saline. The significance, if any, of the secretion of the anterior medial gland in the olfaction is further to be investigated.

In conclusion, the MO is similar to the OE in fine structure of the epithelium and its associated gland in spite of the minor modification of the surface morphology in a part of receptors, and also similar to the OE in nature of the secretion of the gland. This seems to suggest that the MO plays a role in the olfactory function similarly to the OE.

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