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REVIEW

Controversies on the human vomeronasal system

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SUMMARY

Most vertebrates possess an accessory olfactory system parallel to the olfactory system. The most peripheral structure of the accessory (or vomeronasal) system is the vomeronasal organ, located at the base of the nasal septum. From the vomeronasal organ, vomeronasal sensory neurons project to the accessory olfactory bulb, which in turn projects to the vomeronasal-recipient structures in the basal telencephalon. The vomeronasal system detects pheromones (substances generally emitted by conspecifics) or prey chemicals, which have been demonstrated to be critical for sexual behaviors and foraging, respectively. In humans, the existence and functionality of the vomeronasal system has been debated for the last three centuries. Recent anatomical, histological, behavioral and physiological studies have reached very different conclusions on this issue, leaving an old controversy unresolved. A review of the literature indicates that most of evidence for a functional human vomeronasal system has been provided by physiological studies conducted by a single research group. Since current anatomical evidence does not support the existence of neural substrates for these physiological effects, the functionality of the human vomeronasal organ awaits further independent confirmation.

Key Words: Accessory olfactory system – Chemosensory – Human – Pheromone – Vomeronasal

INTRODUCTION

Most vertebrates interact with their chemical environment primarily through their olfactory and vomeronasal systems. Anatomically, these two chemosensory systems are similar. Chemical information follows parallel pathways in the main and accessory (or vomeronasal) olfactory systems, being relayed from the olfactory and vomeronasal epithelia to the main and accessory olfactory bulbs and from there to olfactory- and vomeronasal-recipient structures in the basal telencephalon, respectively. Functionally, the olfactory system is able to detect a number of volatile odorants, whereas the vomeronasal system is specialized for the detection of substances with high molecular weight usually emitted by conspecifics, e.g., pheromones, or prey (see Halpern, 1987; Wysocki and Meredith, 1987; Keverne, 1999, for reviews). Pheromone effects have been demonstrated to be critical for the execution of species-typical behaviors, such as mating and foraging. In rodents, dramatic effects such as implantation failure in a mated female after exposure to a male different from her mate has been reported to be under vomeronasal influence (the Bruce effect) (e.g., Bellringer et al., 1980; Lloyd-Thomas and Keverne, 1982).

In mammals, the olfactory epithelium covers turbinates at the dorsal posterior aspect of the nasal cavity where airborne odorant molecules can readily gain access. Embryologically, the vomeronasal epithelium derives from the olfactory placode, but becomes separated from the olfactory epithelium and is sequestered in the developed vomeronasal organ, a paired, cigar-shaped structure located at the base of the nasal

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septum. The surface of the vomeronasal organ is covered by a bony capsule. The vomeronasal lumen communicates anteriorly with the nasopalatine duct. This allows access of pheromones through the oral and/or nasal cavities. The vomeronasal lumen separates chemosensory and non-chemosensory epithelia (see Halpern, 1987; Wysocki and Meredith, 1987; Keverne, 1999, for reviews).

Olfactory and vomeronasal sensory epithelia are composed of supporting, basal and sensory cells. The cell bodies of supporting cells are situated in the apical portion of the epithelium, but cell processes extend to the luminal and basal surfaces. Adjacent to the basal lamina, basal cells give rise to cells that migrate vertically to replace apoptotic sensory cells (e.g., Martínez-Marcos et al., 2000a, b). Olfactory and vomeronasal sensory cells display an apical dendrite directed toward the luminal surface, where sensory transduction takes place, and a basal axon that pierces the basal lamina to reach the glomeruli of the main and accessory olfactory bulbs, respectively. Within the glomeruli, axons of olfactory and vomeronasal sensory cells establish synaptic contacts with apical dendrites of mitral cells. The mitral cells of the main and accessory olfactory bulbs, in turn, send their axons mainly to the pyriform and entorhinal cortices and olfactory amygdala, and to the vomeronasal amygdala, respectively (e.g., Martínez-Marcos and Halpern, 1999; see Halpern, 1987, 1998a, b, for reviews).

The vomeronasal system has been considered an acquisition of terrestrial vertebrates and it was thought to be absent in aquatic animals (Bertmar, 1981). Its recently demonstrated presence in aquatic salamanders (Eisthen, 1997, 2000) has led to the hypothesis that the origin of the vomeronasal system goes back to aquatic tetrapods. Accordingly, the vomeronasal system does not appear to be an adaptation to terrestrial life, which has important implications for the widely accepted idea that the vomeronasal system is specialized for detection of non-volatile compounds. Among tetrapod vertebrates, the development of the vomeronasal system depends on the relationships with the ecological substrate, being severely reduced or nonexistent in adult forms of arboreal or aerial species. Regarding primates, prosimians display a well-developed vomeronasal system, whereas there is significant variation in anthropoids. Most platyrrhini have a reduced but functional vomeronasal system, while it appears to be absent in adult catarrhini studied to date (Maier, 1980; Hunter et al., 1984; reviewed in Halpern, 1987). The presence of a functional vomeronasal organ in humans is still controversial, as demonstrated by the fact that recent reviews on this issue (McClintock, 1998a; Monti-Bloch et al., 1998a; Trotier et al., 2000; Wysocki and Preti, 2000; Meredith, 2001) have reached very different conclusions. The aim of the present review is therefore to critically analyze the literature on the anatomy and function of the human vomeronasal system.

Anatomical and histological observations

Early descriptions of the human vomeronasal organ date back to 1703, when Ruysch reported and illustrated a vomeronasal organ in his *Thesaurus Anatomicus tertius,* the *canalibus nasalibus*, considering it as a mucus-secreting structure. It was a century later, however, when Jacobson (1811) described in different species the main anatomical features of the vomeronasal organ, since then also known as Jacobson's organ. The exact position (Kölliker, 1877) and length (Potiquet, 1891) of the human vomeronasal organ was subsequently addressed in detail (see Zuckerkandl, 1910, for a review).

Two findings, one anatomical, the other physiological concerning the mammalian vomeronasal system reignited interest in this system in the early seventies, i.e., the demonstration of parallel pathways from the main and accessory olfactory bulbs to the basal telencephalon and demonstration of the critical nature of sexual pheromones for reproduction (reviewed in Halpern, 1987). The dual olfactory hypothesis that derived from these two findings stated that parallel, non-overlapping pathways from the olfactory and vomeronasal epithelia through the olfactory bulbs and basal telencephalon to the hypothalamus subserved different reproductive functions (Winans and Scalia, 1970; Raisman, 1972; Scalia and Winans, 1975).

In the 1970's and 1980's, in contrast with earlier ideas, it was generally accepted that the human vomeronasal organ was present in early fetal life but degenerated thereafter (e.g., Bossy, 1980; Kreutzer and Jafek, 1980; Nakashima et al., 1985; see Wysocki, 1979; Halpern, 1987; Wysocki and Meredith, 1987, for reviews). New data on fetuses and adult humans, however, indicate that the human vomeronasal organ persists until birth and is present during adulthood. Kjaer and Hansen (1996), after examining 49 normal human prenatal specimens, report that the vomeronasal organ was present in 8-16 week old fetuses, apparently regressed at 11-16 weeks, and was not observable at 17-19 weeks of gestational age. Conversely, several studies have described linear increases in length and logarithmic increases in volume of the vomeronasal organ and vomeronasal epithelium through 30 weeks of postmenstrual age (Smith et al., 1996; 1997; Sherwood et al., 1999; Smith and Bhatnagar, 2000). Regarding histological observations, silver-stained receptor-like cells have been described at 11-18 weeks of prenatal age (Ort-

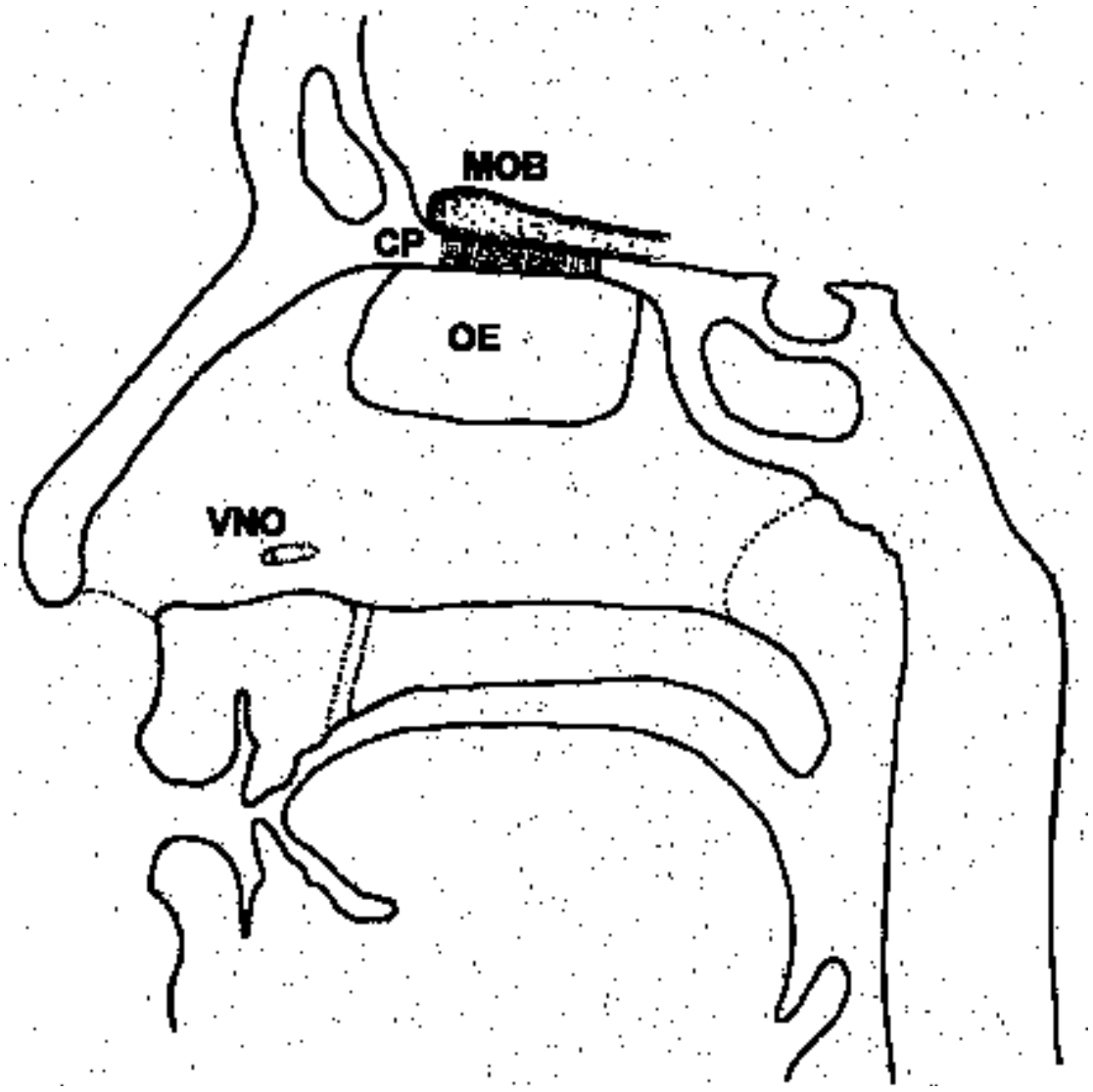

Fig. 1.- Schematic drawing of the adult human nasal septum showing the approximate location of the vomeronasal organ (VNO) and olfactory epithelium (OE). CP: cribiform plate; MOB: main olfactory bulb.

mann, 1989). Neural markers, such as neuron-specific enolase, have revealed positive cells in fetuses younger than 23 weeks but not in older specimens (Boehm and Gasser, 1993).

A number of recent anatomical descriptions have identified a vomeronasal pit in adult human beings (Fig. 1). However, the frequency of occurrence varies greatly between observations performed on cadavers as compared to living patients, and between examinations using anterior rhinoscopy *vs*. nasal endoscopy. The incidence of vomeronasal pits using anterior rhinoscopy varies from 6% (Zbar et al., 2000) to 16% (Gaafar et al., 1998) to 39% (Johnson et al., 1985) to virtually 100% of patients examined (Moran et al., 1991; Garcia-Velasco and Mondragon, 1991; Stensaas et al., 1991; Garcia-Velasco and Garcia-Casas, 1995), whereas using microscopic examination of septa in cadavers an incidence of 70% has been reported (Johnson et al., 1985). Using rigid nasal endoscopes, frequencies of occurrence vary from 28.2% (Won et al., 2000) to 76% (Gaafar et al., 1998) in living subjects, and 59.1% in cadavers (Won et al., 2000). Magnetic resonance imaging studies also report a high variability of occurrence of the vomeronasal duct (Abolmaali et al., 2001). Two factors could explain such variability. The presence of vomeronasal structures does not appear to be a constant feature throughout life since repeated examinations of previously identified vomeronasal pits have only confirmed 65.3% of initial observations (Trotier et al., 2000). Another source of variability could arise from the fact that a second opening at the base of the nasal septum, the nasopalatine duct, is frequently present in adult humans and it could be misidentified as a vomeronasal aperture (Maier, 1997; Jacob et al., 2000). Finally, no accessory olfactory bulb has been demonstrated in humans (Meisami et al., 1998), which is a major argument against the idea of a functional human vomeronasal system.

Using presumptive vomeronasal material obtained from humans, a number of histological and immunocytochemical studies have been performed with different conclusions. Gaafar and

colleagues (1998) describe a pseudostratified columnar epithelium composed of two cell types, while Moran and colleagues (1991) describe three cell types, including dark-staining columnar cells, light-staining columnar cells, and basal cells, and Smith and colleagues (1998) described columnar, basal and goblet cells. Furthermore, Smith et al. (1998) described ciliated epithelia on both medial and lateral luminal surfaces, which is unusual since in most animals the vomeronasal sensory epithelium is not ciliated. Trotier et al. (2000) state that the epithelium lacks the appearance of a typical functional vomeronasal epithelium as described in other species. Likewise, histological observations have found a number of glandular elements associated with the human vomeronasal organ, whose specific function remains to be elucidated (Roslinski et al., 2000).

Most immunohistochemical studies have attempted to demonstrate the presence of neurons by using different neural markers such as neuron-specific enolase (NSE), protein gene product 9.5 (PGP) or olfactory marker protein (OMP) (reviewed by Johnson, 1998). In the human vomeronasal epithelium, NSE- and PGP 9.5-positive neurons have been identified that bear a striking morphological similarity to OMP-positive neurons located in the olfactory epithelium (Takami et al., 1993). Similarly, Trotier et al. (2000) found some NSE-positive cells, but no OMP- or S-100-positive cells. Since S-100 is expressed in Schwann cells, this indicates a lack of nerve bundles communicating with the olfactory bulbs. Since both OMP- and S-100-positive cells have been observed in the human olfactory epithelium, Trotier and colleagues (2000) concluded that the vomeronasal epithelium is not a sensory organ in adult humans. Nitric oxide synthase- and NADPH-diaphorase-immunoreactive elements have been found in the adult human olfactory epithelium (Kulkarni et al., 1994) and main olfactory bulb (Briñón et al., 1998), but not in the vomeronasal mucosa (Kulkarni et al., 1994). Calbindin-D28k-immunoreactive cells have been reported in both newborn and adult material, although the absence of identifiable axons has lead to the conclusion that the labeled cells are not sensory neurons (Johnson et al., 1994; Johnson, 1998). Although some positive cells for neural markers have been identified in the vomeronasal epithelium, the lack of immunoreactivity for OMP (a specific marker for mature olfactory and vomeronasal neurons) as well as the lack of anatomical evidence for neural connections between the vomeronasal epithelium and the accessory olfactory bulb do not support the idea of functional sensory neurons in the human vomeronasal epithelium.

In agreement with light microscope observations, electron microscopy studies report three cell types, including basal, and dark and light columnar cells displaying microvilli on the apical surface (Moran et al., 1991; Stensaas et al., 1991; Jahnke and Merker, 2000). Myelinated and unmyelinated axons were observed in the basal membrane, particularly in the lamina propia, although their origin, destination or function remain elusive (Stensaas et al., 1991; Jahnke and Merker, 2000).

While data are controversial among morphological studies, most observations do not provide anatomical substrates for a human functional vomeronasal system.

Pheromonal communication in humans

As discussed in the introduction, the vomeronasal system is not the only pheromone-detecting system. Some pheromone-triggered behaviors have been demonstrated to be under olfactory control. Nipple search in newborn rabbits, for instance, does not depend on a functional vomeronasal system, but instead is mediated by olfactory cues (Singh et al., 1976; Hudson and Distel, 1986, reviewed in Halpern, 1987). Nevertheless, a number of groups have emphasized the importance of human pheromonal communication, although the involvement of the vomeronasal system is unclear at present (e.g., Weller, 1998; McClintock, 1998a; Wysocki and Preti, 2000). Menstrual synchrony of females grouped together (McClintock, 1971; 1998b) and regulation of ovulation by axillary compounds are among the most remarkable pheromone effects reported in humans (Stern and McClintock, 1998; reviewed in Weller, 1998). In this latter study, axillary secretion from female donors in the follicular phase of the menstrual cycle applied to the upper lip of recipients shortens their cycle. In contrast, when donors are in the ovulatory phase, the cycle is significantly longer for recipients. Recipients stated that they did not consciously perceive such compounds (Stern and McClintock, 1998). However, nothing in this study suggests that the vomeronasal system would be mediating this effect (Wysocki and Preti, 2000).

Functional magnetic resonance imaging has been also used to address the issue of pheromonal communication in humans. Using a putative skin-derived «pheromone» (oestra-1,3,5(10),16-tetraen-3yl acetate), functional magnetic resonance imaging and behavioral studies have reached different conclusions (Sobel et al., 1999). Subjects were able to discriminate the higher but not the lower concentration among two different dilutions of the putative pheromone. Subjects, however, did not report perceiving any odor. These experiments, includ-

ing both concentrations, induced brain activation, primarily in the anterior medial thalamus and inferior frontal gyrus. Since presentation of the stimulus was not restricted to the vomeronasal organ, no vomeronasally-induced brain activation can be concluded. Functional magnetic resonance imaging studies specifically focused on the vomeronasal system could help to shed light on the issue of the functionality of this system.

Behavioral and physiological studies

Most data reviewed in the previous sections are inconclusive regarding a functional human vomeronasal system. A number of behavioral and physiological studies reported by Monti-Bloch and associates (see below) provide data that support the notion of the existence of a functional vomeronasal system in humans. However, since this is the only research group reporting activation of the presumptive human vomeronasal organ using skin-derived compounds, their data must be taken with special caution.

Monti-Bloch and Grosser (1991) recorded in humans the summed receptor potential in the vomeronasal and olfactory epithelia after administering putative human pheromones. Local stimulation of the vomeronasal organ produced negative potentials showing adaptation, whereas no responses were obtained when the electrode was placed in the nasal respiratory mucosa. Furthermore, two different compounds gave rise to sexually dimorphic responses. A potent olfactory stimulant, clove oil, depolarized the olfactory, but not the vomeronasal epithelium. Subsequently, Monti-Bloch and co-workers (1994) using different chemosensory substances, named vomeropherins, achieved not only sexually dimorphic negative potentials in the vomeronasal epithelium, but sexually dimorphic autonomic responses, such as changes in skin resistance. Presumptive vomeronasally-triggered autonomic responses were further explored by applying steroids to the vomeronasal epithelium. The steroidal vomeropherin, pregna-4,20-diene-3,6-dione, applied to the human vomeronasal organ resulted in changes of serum levels of luteinizing and follicle-stimulating hormones as well as changes in cardiac and respiratory frequencies and alpha brain waves (Berliner et al., 1996). This same vomeropherin also affects vagal tone and serum levels of testosterone (Monti-Bloch et al., 1998b). Androstadienone, an androstene present on male axillary secretions, produces a significant reduction in nervousness, tension and other negative feeling states in females (Grosser et al., 2000). This latter experiment has been partially replicated (Jacob and McClintock, 2000), although the authors conclude that it is «premature to call these steroids human pheromones».

Since virtually all evidence regarding vomeronasal responses using skin-derived human compounds have been reported by the same research group, and since no neural substrates subserving such effects have been convincingly demonstrated, independent confirmation of these experiments is required before stating that the human vomeronasal system is functional. Future directions would include anatomical and physiological studies using G proteins, which have been shown to be critical for sensory transduction in mammalian vomeronasal neurons. Identification of neural connections from the vomeronasal epithelium to the telencephalon and, particularly, identification of the human accessory olfactory bulb still constitute major issues prior to definitively validate functional studies.

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XX CONGRESO DE LA SAE
SALAMANCA
19, 20 Y 21
DE SEPTIEMBRE
DE 2001
Salamanca 2002
Ciudad Europea
de la Cultura
DEPARTAMENTO DE ANATOMÍA E HISTOLOGÍA HUMANAS
FACULTAD DE MEDICINA - UNIVERSIDAD DE SALAMANCA

Sociedad Anatómica Española

XX CONGRESS OF THE SPANISH ANATOMICAL SOCIETY

Place an Date: Salamanca, Spain, 19-21 September, 2001

Venue: Historical Building, University of Salamanca.
Patio de Escuelas, s/n. 37008 Salamanca, Spain

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Ana Sánchez Fernández
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Preliminary Program

Wednesday, Thursday and Friday (19, 20 and 21 September)

Oral communications on Embryology, Neuroanatomy, Neuroregeneration, Clinical and Macroscopic anatomy, Neuroendocrinology, Teaching in anatomy and free communications.
Poster display on these topics.
Invited Speakers:

— Prof. Luis Puelles López: University of Murcia.
— Prof. Manuel Nieto Sampedro: Instituto Cajal (CSIC), Madrid.
— Prof. José M. García Verdugo: University of Valencia.
— Prof. Pedro Guembe: Hospital Gregorio Marañón, Madrid.
— Prof. Gustav F. Jirikowski: University of Jena, Germany.
— Prof. Reinhardt Putz: University of München, Germany.
— Prof. Vicent Delmas: Université René Descartes, Paris, France.
— Prof. Domingo Ruano Gil: University of Barcelona.
— Prof. Luciano Muñoz Barragán: University of Salamanca.
— Prof. A. Javier Puerta Fonollá: Complutense University, Madrid.
— Prof. Juan Jiménez Collado: Complutense University, Madrid.

Fryday (21 September)
17:00 h.: General Assembly of the Spanish Anatomical Society.
22:00 h.: Closing Dinner (Colegio Mayor "Arzobispo Fonseca").