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The Vomeronasal Organ: Still Many Questions Remain

El Órgano Vomeronasal: Aún Quedan Muchas Preguntas

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SUMMARY: The vomeronasal organ (VNO), also known as Jacobsen's organ, is a specialized chemosensory structure located in the nasal cavity of various vertebrates including mammals, amphibians, reptiles and birds. It is responsible for detecting non-volatile chemical signals known as pheromones that play a crucial role in social, reproductive and behavioral processes. The VNO plays an important role in mediating these responses, influencing mating behaviors, aggression, territoriality and social bonding in animals. However, its role and functionality in humans remains a subject of debate. Some researchers suggest that the VNO may be vestigial in humans, while others argue that it may still play a functional role in detecting chemical cues that influence human social behavior. In this systematic review, we will gather all the available scientific information on the vomeronasal organ and the influence of pheromones on it. We will analyze existing theories in order to use this information in the future for medical purposes. The aim of this review is to draw the attention of medical professionals from various fields to the study of this important organ.

KEY WORDS: Vomeronasal organ; Vertebrate sensory systems; Morphological adaptations; Functional relevance.

INTRODUCTION

The initial depiction of the VNO is attributed to Frederic Ruysch, a Dutch anatomist, who pictured it in a drawing of a young man's nasal septum in 1703 (Bhatnagar & Smith, 2003). Approximately a century later, Samuel Semmering also described the human VNO. However, this text will focus solely on the VNO in non-human animals (Bhatnagar & Smith, 2003; D'Aniello *et al*., 2017).

Danish physician and anatomist Ludvig Levis Jacobson is widely recognized for discovering the VNO. His groundbreaking paper detailing this new organ was published in Danish in 1813. An English translation, based on both the original Danish text and Jacobson's own French translation, is available. Notably, Jacobson described the VNO in a wide range of mammals, including rodents, ruminants, horses, pigs, dogs, and cats (Stoyanov *et al*., 2018).

Jacobson's initial description of the VNO encompassed most of its essential macroscopic characteristics known to modern scientists: a cartilaginous capsule situated in the nasal septum, a crescent-shaped internal receptacle (VNO lumen) visible in coronal section, associated secretory apparatus comprised of VNO glands and cavernous tissue, an exit duct (VNO duct), abundant blood supply, innervation from the trigeminal nerve, and neural connection with the olfactory bulb (Jacobson *et al*., 1998). While Jacobson proposed a secretory role for the VNO, he also hypothesized a sensory function, suggesting that secretions from the VNO glands were crucial for sensation (Jacobson *et al*., 1998; Bhatnagar & Smith, 2003). Later in the 19th century, the Golgi technique enabled researchers to demonstrate the morphological similarities between neurons in the olfactory and vomeronasal epithelia of snakes (Retzius, 1894), thus confirming the sensory function of the VNO. A comprehensive review of 19th-century knowledge regarding the VNO can be found in von Mihalkovics' work (von Mihalkovics, 1898).

Research conducted in the early 20th century revealed the presence of the VNO in amphibians, suggesting its evolutionary origins within this class. Conversely, the VNO

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was found to be absent in fish and birds. Early hypotheses proposed that the VNO functioned as a pump, circulating either air or fluid through its vascular structures (Broman, 1920; Hamlin, 1929).

Mid-century studies by Negus (1956) suggested that the VNO likely detected airborne odor molecules related to dietary preferences rather than immediate food detection. A significant breakthrough in understanding VNO function occurred in the 1970s and 1980s with the establishment of a strong link between the VNO and sexual behavior in animals (Wysocki, 1979). Studies demonstrated that the VNO played a crucial role in reproductive behaviors, such as ovulation induced by urine in rats (Powers & Winans, 1975).

Prior research had already established the influence of urinary substances on reproductive physiology in mice, including delayed puberty onset, estrus induction, pregnancy prevention, and accelerated puberty (Van der Lee & Boot, 1955). This led to the hypothesis that the VNO detects pheromones, airborne chemical signals secreted by individuals for communication within a species (Karlson & Lüscher, 1959).

By the late 20th century, comprehensive reviews summarized current knowledge about the VNO, its evolutionary patterns, and functional characteristics in mammals. Key findings included: the VNO's role in detecting non-volatile pheromones; the presence of two distinct receptor types coupled to specific signaling pathways; the activation of hypothalamic functions through the accessory olfactory bulb and amygdala, influencing reproductive, defensive, and ingestive behaviors; and the possibility of additional, non-pheromonal functions (Meredith, 1998; Keverne, 1999).

Phylogenesis

The vomeronasal system (VNS) is considered a derived character in tetrapods, indicating its presence in early vertebrates, including larval amphibians, and suggesting it did not arise solely as a terrestrial adaptation (Takami, 2002). The genetic components of the VNS, such as vomeronasal type 1 receptors (V1Rs) and Trpc2, were present in the common ancestor of all extant vertebrates, as evidenced by their presence in early diverging lineages like the sea lamprey and elephant shark. This suggests that the VNS has ancient origins, with its genetic components predating the morphological structures found in tetrapods. The VNO has been independently lost in several taxa, including crocodilians, some bats, cetaceans, and certain primates, often coinciding with the degeneration of the organ in these groups. In birds, the VNO is absent, and fishes lack vomeronasal receptors (VRs) and a VNO, yet they can still detect pheromones through olfactory receptors. In bats, the presence and development of the VNO vary significantly, with some species exhibiting a rudimentary or absent organ, particularly in those with a disrupted TRPC2 gene. The V1R genes, part of the pheromone receptor family, show significant variability among mammals due to gene gain and loss, with a conserved ancient V1R gene (ancV1R) found across most Osteichthyes, from ray-finned fishes to mammals (Halpern & Martínez-Marcos, 2003). The loss of this gene in some tetrapods aligns with the degeneration of the VNO, highlighting the dynamic evolutionary history of the VRs in vertebrates. Morphological studies in squamates and bats reveal diverse adaptations and evolutionary changes in the VNO and its associated structures, reflecting the organ's varied roles and significance across species. The vomeronasal organ's phylogenesis illustrates a complex evolutionary trajectory marked by ancient origins, significant variability, and independent losses across different vertebrate lineages. Its study provides valuable insights into the evolution of vertebrate sensory systems and the genetic and morphological adaptations that have occurred over millions of years (González *et al*., 2010).

Human vomeronasal organ

The existence and functionality of the VNO in humans remains a point of contention within the scientific community. During fetal development, the VNO originates as paired thickenings of epithelial tissue in the nasal septum, termed the vomeronasal primordium (McGann, 2017). This structure then invaginates to form a tubular shape between 37 and 43 days of gestation. The VNO undergoes three distinct developmental stages: initial formation (early morphogenesis), transformation of its cellular lining (epithelium), and growth (Trotier, 2011).

While structurally similar to VNOs found in other mammals, the human VNO's position shifts and varies during embryonic development. The presence of luteinizing hormone-releasing hormone (LHRH) within the VNO during specific prenatal stages suggests a potential role in early neuroendocrine system development (Singh & Groves, 2016). However, by 12 to 14 weeks of gestation, the VNO may lose its specialized sensory receptor cells and transition into a ciliated pseudostratified epithelium.

The connection between the neuroepithelium and structures within the central nervous system typically deteriorates before the 28th week of gestation. While some studies suggest the persistence of the vomeronasal nerve and its associated Go- and Gi-positive epithelial cells until later fetal development, the absence of other crucial

components likely renders these structures nonfunctional (Ikeda *et al*., 2010).

Observations indicate the presence of the vomeronasal nerve up to the sixth month of gestation, with occasional reports of "vestigial remains" detected as late as week 18. Although the closure of the vomeronasal duct has been historically interpreted as a sign of degeneration, it often persists to varying degrees in most individuals (Ikeda *et al*., 2007; Katreddi & Forni, 2021).

The precise timing of nerve detachment from epithelial cells within the vomeronasal organ remains unclear. Current research on the neural pathways connecting accessory olfactory bulbs in humans is limited. In contrast, animal studies have clearly established these connections extending to the hypothalamus and amygdala (Osakada *et al*., 2018). These brain regions play crucial roles in regulating neurohormonal functions, as well as behaviors related to reproduction and feeding. Notably, these structures are integral components of the limbic system, which is heavily involved in emotional processing. However, unlike in animals, there is no evidence suggesting connections between accessory olfactory bulbs and the neocortex in humans. This absence of connectivity implies that signals originating from these bulbs cannot be consciously processed or integrated into higher cognitive functions (Dulac & Wagner, 2006; Yang *et al*., 2013).

While some studies using electrovomeronasography suggest that the VNO functions as a receptor organ, genetic evidence indicates that genes responsible for key components of the VNO's signaling pathway are mutated and non-functional in humans. The ongoing debate surrounding this issue is intensified by apprehensions within the field of rhinology. These concerns stem from the possibility that surgical interventions in close proximity to Jacobson's organ, the site where the VNO is located, could have unintended consequences for an individual's sexual behavior (Foltán & Sed‡, 2009).

The discovery that neurons within the terminal nerve, connected to the VNO, release gonadotrophin-releasing hormone upon VNO stimulation adds another layer of complexity. Despite extensive research in non-primate species, the structure and function of the terminal nerve in humans remain poorly understood. Recent studies suggest a potential link between the accessory olfactory system, of which the VNO is a part, and post-traumatic stress disorder (Baum & Bakker, 2013).

The presence of ectopic esthesioneuroblastoma, a rare malignant tumor originating from olfactory neuroepithelial cells, has been reported in the area of Jacobson's duct, suggesting that the VNO may indeed represent an accessory nasal structure in humans (Caldwell & Sato, 2019). Further support for this theory comes from the hypothesis that pneumatization of the vomer bone is driven by a "pumping" mechanism involving the vomeronasal duct. Despite these intriguing findings, definitive answers regarding the function of the VNO in humans and its role in sexual and social behavior remain elusive (Stoyanov *et al*., 2018).

Scientific research using electrophysiology has demonstrated that the VNO is activated by exposure to urine. In addition, scientific studies have shown that participants in the experiment experience mood changes when exposed to androstanedione and estratetraenil. These chemicals cause a noticeable electrophysiological response in the vomeronasal region, called an electrovomeronasogram. Notably, this effect is not observed with conventional odors (Moss *et al*., 1998).

Furthermore, numerous indirect studies suggest the presence of pheromone-like substances influencing human behavior (Meredith, 2001). A prominent example is the tendency for menstrual cycles to synchronize among women living in close proximity (McClintock, 1971). This phenomenon may have evolutionary roots, similar to the Lee-Boot effect observed in mice, where females housed together suppress estrus cycling to conserve energy when pregnancy is unlikely (Van der Lee & Boot, 1955). Conversely, exposure to male pheromones can restore estrus cycling in group-housed females, known as the Whitten effect (Whitten, 1959).

The results of the study tell us that pheromone interactions in humans can convey information that can change the likelihood of a person's response without necessarily causing immediate changes in behavior.

During psychiatric evaluations, many sexual aggressors attribute their actions to an uncontrollable impulse and attraction towards the victim. They suggest this is triggered by the victim's stress response during the attack, leading to the activation of the sympathetic nervous system and perspiration. Aggressors are then purportedly influenced by pheromones present in sweat (Loos *et al*., 2025).

This connection between olfaction and reproduction has been studied since the late 19th century, with researchers observing physiological changes in women during menstruation linked to smell. More recent studies have explored the influence of pheromones on menstrual cycles, demonstrating that exposure to certain axillary secretions can either lengthen or shorten the cycle (Burger & Gochfeld, 1985; Jacob *et al*., 2004).

Furthermore, research indicates a strong correlation between pheromones and sexual attraction. The studies we selected showed that exposure to androstenone, a pheromone found in male sweat, can increase men's perception of the attractiveness of members of the opposite sex (Lanfranchi, 2021; Loos *et al*., 2025).

The VNO, which is responsible for detecting pheromones, plays a significant role in maternal behavior. Stimulation of the VNO has been linked to the release of hormones that promote maternal care and bonding in animals. Disruption of the VNO in sheep, for instance, resulted in impaired maternal recognition and milk sharing behaviors (Van der Lee & Boot, 1955).

Pheromones are released from human skin through both volatile emission and a natural delivery system for non-volatile compounds. Surveys suggest a significant proportion of individuals experience sexual stimulation through their partner's scent, highlighting the ongoing relevance of olfactory cues in human intimacy (Burger & Gochfeld, 1985).

Research has demonstrated that pheromones can induce hormonal changes and activate brain regions associated with reproductive behavior.

There are publications that suggest that pheromones can also influence the timing of menopause. Thus, it has been established that married women experience menopause later. This conclusion was reached by scientists from the University of Massachusetts, who studied the lifestyle of a large group of women aged about fifty. It turned out that married women experience menopause on average at 50 years and 3 months, while unmarried women experience it at 48 years (Sievert *et al*., 2001). The authors of the study believe that odorous substances, pheromones, released with male sweat stimulate the production of female sex hormones and prolong a woman's childbearing age. The difference in the timing of menopause could not be explained by other lifestyle features of the individuals examined (Stern & McClintock, 1998).

In 2019, nature prepared a new test for humanity. Severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), the virus responsible for COVID-19, is structurally composed of spike, membrane, and envelope proteins. Typically, odorant molecules bind to proteins released by sustentacular cells, enabling detection by olfactory receptor neurons. Loss of smell, known as anosmia, is a prominent symptom of COVID-19. Anyway, further research is needed to fully understand the mechanisms by which SARS-CoV-2 infection leads to anosmia (Las Casas Lima *et al*., 2022). The SARS-CoV-2 virus uses ACE2 and TMPRSS2 receptors, which are located on human cells, to penetrate the body. Since these receptors are predominantly located on the cells of the olfactory epithelium, it is hypothesized that anosmia is caused by damage to non-neuronal cells in this area. This cellular damage leads to impairment of olfactory function. Magnetic resonance imaging studies have been conducted. And they have revealed a correlation between the reduction of neuronal epithelium and atrophy of the olfactory bulb (Butowt *et al*., 2023). These data support the theory of non-neuronal cell involvement. The most common recovery period of several weeks is consistent with the regeneration cycle of these non-neuronal cells. However, an overly aggressive immune response may develop. Spread to neuronal cells and stem cells may worsen the damage. Persistent anosmia may develop due to more severe cell destruction. It is important to point out that simple conduction blockade of the olfactory pathways does not explain most cases of olfactory loss caused by COVID-19. Studies examining the effects of COVID-19 infection, including its association with the development of olfactory loss, have provided conflicting results and have not provided a comprehensive analysis of its impact on sexual behavior (Finlay *et al*., 2022; Al-Ani & Acharya, 2022).

Current studies that examine the neural pathways connecting the accessory olfactory bulbs in humans are not as extensive. In comparison, animal studies have found that these connections extend to the hypothalamus and amygdala. These brain regions play an important role in regulating behaviors related to reproduction and feeding. It should also be noted that these structures are important components of the limbic system, which is heavily involved in emotional processing (Zharova *et al*., 2025). However, there is no evidence that indicates connections between the accessory olfactory bulbs and the neocortex in humans. The lack of this connection indicates that the signals emanating from these bulbs cannot be consciously processed (Burger & Gochfeld, 1985; Meredith, 2001).

CONCLUSIONS

Despite the studies of the vomeronasal system in animals and humans, there remains a real prospect of studying the human body's responses to both the stimulation of the VNO receptors and the method of transmitting the stimulation to the brain and managing these processes for the benefit of humans. In our opinion, the practical prospects of further research into the vomeronasal complex in humans are difficult to overestimate. This opens up broad opportunities for research by specialists in various medical fields. There are no recommendations in the literature regarding Jacobson's organ during rhinosurgical

interventions. Statistics indicate that about 20 % of the population requires surgical correction of nasal breathing disorders. Therefore, the question of whether to take the vomeronasal complex into account during surgical interventions in the nasal cavity is very relevant and requires scientific justification.

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RESUMEN: El órgano vomeronasal (OVN), también conocido como órgano de Jacobson, es una estructura quimiosensorial especializada ubicada en la cavidad nasal de varios vertebrados, incluidos los mamíferos, anfibios, reptiles y aves. Es responsable de detectar señales químicas no volátiles conocidas como feromonas que desempeñan un papel crucial en los procesos sociales, reproductivos y de comportamiento. El OVN juega un papel importante en la mediación de estas respuestas, influyendo en los comportamientos de apareamiento, agresión, territorialidad y vínculos sociales en los animales. Sin embargo, su función y funcionalidad en humanos sigue siendo un tema de debate. Algunos investigadores sugieren que el OVN puede ser vestigial en humanos, mientras que otros argumentan que aún puede desempeñar un papel funcional en la detección de señales químicas que influyen en el comportamiento social humano. En esta revisión sistemática, reunimos toda la información científica disponible sobre el órgano vomeronasal y la influencia de las feromonas en él. Analizmos las teorías existentes para utilizar esta información en el futuro con fines médicos. El objetivo de esta revisión fue llamar la atención de los profesionales médicos de diversos campos sobre el estudio de este importante órgano.

PALABRAS CLAVE: Órgano vomeronasal; Sistemas sensoriales de vertebrados; Adaptaciones morfológicas; Relevancia funcional.

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