

THE ROLE OF MAIN OLFACTORY AND VOMERONASAL SYSTEMS IN ANIMAL BEHAVIOUR AND REPRODUCTION

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ABSTRACT

In many terrestrial tetrapod, olfactory sensory communication is mediated by two anatomically and functionally distinct sensory systems; the main olfactory system and vomeronasal system (accessory olfactory system). Recent anatomical studies of the central pathways of the olfactory and vomeronasal systems showed that these two systems converge on neurons in the telencephalon providing an evidence for functional interaction. The combined anatomical, molecular, physiological and behavioural studies have provided new insights into the involvement of these systems in pheromonal perception and their influence on the neuroendocrine pathways. The olfactory and vomeronasal systems have overlapping functions and both are involved in responses to both pheromones and chemical odorants. Several studies in insects, amphibians, rodents and ungulates have established the importance of pheromones in the astonishing influence exerted by the male on the reproductive activity of the female. The great diversity of signals used in chemical communication indicates that this communication is not mediated exclusively by pheromones. A number of pheromonal responses are not dependent on the vomeronasal system, but on the main olfactory system. The dual olfactory systems also have overlapping functions. The importance of this organ in reproductive and social behaviours was the aim of carrying out the review on its basic morphology and functional correlations in order to encourage more future studies of this important organ of our local species and breeds of mammals.

Keywords: Main olfactory system, Vomeronasal system, Pheromones, Behaviour, Mammals

INTRODUCTION

The ability of mammalian olfactory and vomeronasal systems to detect an enormous array of structurally diverse volatile and non-volatile stimuli with extraordinary sensitivity and specificity has fascinated philosophers, writers and scientists since the previous century.

The current knowledge of how odor information from environment is perceived has greatly advanced since the discovery of about 1000 genes for odorant receptors in mammalian genome. From the combination of anatomic, molecular-genetic, electrophysiological and optical imaging studies, a better understanding of the sense of smell is emerging. The olfactory and vomeronasal system detects and discriminates among large number of structurally diverse odorant molecules that carry information about the environment and from amongst con-specific species. A pivotal event in understanding the mechanisms of olfaction came with identification of genes encoding odorant receptors (Buck and Axel, 1991). In the past dozen years, these receptors have created a new framework for anatomical and electrophysiological studies that have challenged long-held views and presented new puzzles on both

olfactory systems. The recent resurgence of interest in smells and scents has considerably expanded information and full understanding of the multiple chemoreceptive systems in the nose of mammals. New techniques and more systematic approaches have been steadily applied to this area of the chemical senses; olfactory and vomeronasal chemoreception (Evans, 2003). The main olfactory organ and vomeronasal organ have some common features, but also significant differences in neuron types, primary structures of receptor proteins and signal transduction (Firestein, 2001).

Pheromones are defined as those natural compounds secreted by one member of a social group that can influence the neuroendocrine mechanisms underlying behaviour, fertility or development of another group member, in which they release a specific reaction (McIntock, 2002). Pheromone modifies various physiological functions including the reproductive activity, after being processed by the vomeronasal system. Application of such actions of pheromones to the control of reproduction in domestic animals has long been desired. Pheromone research in rodents has made substantial advance, but is not the case for higher

mammals, especially domestic food animal (Okamura *et al.*, 2004).

Pheromones modify physiological functions including the reproductive activity after being processed through the vomeronasal system. The application of these effects of pheromone to the control of reproductive processes in domestic animals is quite important and is applied in biostimulation in several domestic food animals (Rekwot *et al.*, 2001). Chemosensory system and pheromonal research has not made a great advance in our domestic animals.

The aim of this article is to examine the role played by the two different but related olfactory systems in initiating several biological effects on mammals such as pheromonal effects, reproductive, parental, aggressive and marking behaviour, individual odor discrimination, prey trailing, flehmen behaviour and other responses to chemosignals. It is believed that these biological reproductive behaviours could help in the beneficial artificial management of reproductive processes.

MATERIALS AND METHODS

A comprehensive search was made from the Internet, various journal articles and textbook reports on the role of the olfactory and vomeronasal systems in animal behaviour and reproduction. Such articles were assembled and studied.

RESULTS AND DISCUSSION

Functional Anatomy of the Olfactory System:

The olfactory organ is situated in the nose. In animals with a well-developed sense of smell it consists of relatively large area of olfactory mucosa covering the lateral wall and ethmoidal concha (turbinates) in the caudal part of the nasal cavity. The olfactory region is said to be little more yellowish than the respiratory mucosa rostral to it. The olfactory region cannot be certainly identified by gross inspection. The olfactory neuroepithelium is a pseudostratified columnar epithelium. The specialized olfactory epithelial cells are the only group of neurons capable of regeneration. There six distinct cell types in the olfactory epithelium: bipolar sensory receptor neurons, microvillar cells, supporting cells, globose basal cells, horizontal basal cells, and cells lining the Bowman's glands (Jing and Ryan, 2003). The neuroepithelial cells are characterized by ciliated dendrites which protrude from the surface of the epithelium. The cilia are the site where interaction with odorant occurs. The sense of smell is much better developed in domestic animals than in humans, this is particularly true of dog, which can detect airborne substances in incredibly low

concentration. Each of the olfactory sensory neurons, which project to the main olfactory bulb, expresses a single receptor type from a large family of olfactory receptors. Also a second family of G-protein-coupled receptors, the trace amine associated receptors (TAARs), which recognize volatile amines present in urine, has also been shown to be expressed in olfactory sensory neurones (Liberias and Buck, 2006). The neurons in the main olfactory system use distinct signaling components unlike that of vomeronasal system. In the main olfactory, the binding of the odorant to one of as many 1000 different types of odorant receptors leads to activation of a second-messenger pathway involving olfactory-specific G-protein, which in turn activates adenylyl cyclase to produce cyclic adenosine monophosphate (cAMP). The cAMP opens a cyclic nucleotide-gated cation channel in ciliary membrane allowing cations to flow into the cell, resulting in gradual depolarization that travels down the dendrite to the cell body of the olfactory receptor neurones (Gold 1999; Lambrechts and Hossaert-Mckey, 2006). There is also evidence for another intracellular second messenger involving inositol 1,4,5-triphosphate (IP3). It is thought to act separately or with cAMP pathway. Current research supports a role for cyclic guanosine monophosphate and carbon monoxide in olfactory signal transduction (Simpson and Sweazey, 2006). In addition to differences in anatomical organization and transduction cascade, the molecular organization of the two chemosensory systems differ; Mice possess around 1000 olfactory receptors and around 300 vomeronasal receptors, but these two sets of receptors share little similarity (Zhang *et al.*, 2006).

In most vertebrates, the olfactory sensory neurons in the periphery are the primary sensing cells. They form a neuroepithelium that lines series of these conchas. The olfactory sensory neurones are bipolar neurons with a single dendrite that reaches up to the surface of the tissue and ends in a knob-like swelling from which project some 20 – 30 very fine non motile cilia. These cilia, which actually lie in the thin layer of mucous covering the tissue, are the site of sensory transduction apparatus. A thin axon from the proximal pole of the cell projects directly to the olfactory bulbs and to higher brain regions like the amygdala and hypothalamus. Other signals from the olfactory bulbs are passed via the entorhinal cortex to the hippocampus, which is associated with learning and memory (Deidre, 2001). The mucous layer of the olfactory epithelium is about 60 μm thick and is a lipid-rich secretion containing mucopolysaccharides, immunoglobins, proteins, that bathes the surface of the receptors at the epithelium surface. The mucous

layer is produced by the Bowman's glands which reside in the olfactory epithelium. The mucous layer assist in transporting the odorant molecule as only volatile materials that are soluble in the mucous can interact with the olfactory receptors and produce the signals that the brain interprets as odor.

Importance of Olfaction in Animal Production and Behaviour: Experimental removal of olfactory structures have widely assigned the role of olfactory system to the sense of smell, resulting in the detection of a large variety of volatile odorants, while the vomeronasal system is believed to mediate the detection of most gender and species-specific cues involved in the control of mating and aggressive behaviour (Dulac and Torello, 2003). Olfaction is defined as the capacity to detect airborne chemical compounds at a distance from their source (Lambrechts and Hossaert-Mckey, 2006). In mammals, olfactory cues play a preponderant role since they can mimic most of the behavioural and physiological changes provoked by social interaction. It has been reported in many species that chemical signals serve as sexual attractants, as well as inducing sexual arousal, appetitive and precopulatory postures, and mating behaviour in rat, mouse and elephant (Brown, 1977; Johnston and Bronson, 1982; Rasmussen *et al.*, 1996). These chemosignals can also modify the physiology and neuroendocrine state. However it is unclear whether the olfactory cues induce also behavioural changes (Gelez and Fabre-Nys, 2004).

Olfactory cues are used extensively in many aspects of maternal care to ensure the coordination of mother-infant interactions and consequently the normal development of the offspring. Outside the period of parturition and lactation, when the young are not a behavioural priority, olfactory cues play an inhibitory role on maternal responsiveness since in most mammalian species studied so far, non-pregnant females find the odor of young aversive. It is generally believed that recognition of opposite sex involves the main olfactory pathway, and this has been demonstrated to be the case in pigs, monkeys, ferrets and rodents (Kervene, 2004).

Apart from visual and auditory cues, the olfactory sense is the primary cue used by female animals to recognize their offspring during nursing (Horrel and Hodgson, 1985; Dunn *et al.*, 1987). Goats that are anosmic were unable to distinguish their own kids from alien kids even though great variations in coat colour were apparent (Romeyer *et al.*, 1994). Blindfolded goats were unable to distinguish their own offspring in a group of nonbleating kids (Klopfer *et al.*, 1964). These

recognition could not come from normal memorization of visual and or auditory cues (the paper). Also female goats required only 5 minutes of initial contact immediately after birth to discriminate their own kids from aliens after several hours of separation. Offspring recognition through olfaction in most female animals is believed to emanate from its body coat (Price *et al.*, 1984). The olfactory system also mediates responses to pheromones. Blockage of the vomeronasal duct has no effect on the behavioural detection of androstenone or elicitation of pheromone-induced mating postures (Dorries *et al.*, 1995) indicating that this well-characterized mammalian pheromonal effect is detected by the olfactory system.

Odours clearly play a role in food selection in several species of birds, such as kiwis, vultures, and shearwaters, and there are indications that some social behaviours of ducks may be influenced by odors. Olfaction is also used in birds to find food. For instance procellariiform seabirds (e.g. great shearwaters) have well developed olfactory apparatus used for detecting food on the sea in the absence of visual food cues (Verheyden and Jouventin, 1994). Olfaction in birds is also involved in courtship and mate recognition (Jacob *et al.*, 1979), nest building (Clark and Smeraski, 1990), nest relocation and discrimination (Walraff, 2001). That olfaction is involved in the control of reproduction is a long recognized fact with respect to sexual behaviour. This is well established in both invertebrates (e.g. with discovery of sexual pheromones such as bombycol and in vertebrates, there is an intimate embryological relationship between the olfactory and the GnRH systems (Schanzel-Fukuda and Pfaff, 1991), and the numerous modulations of sexual behaviours or sexual hormone responses mediated by olfaction.

Functional Morphology of the Vomeronasal Organ:

The presence of vomeronasal organ (VNO) has been confirmed in most mammals (Figures 1 and 2). It is also present in marsupials (It is well developed in some primates. The opinions concerning the presence and functioning of the organ in humans are controversial. The VNO is absent in fishes, birds, chameleons and crocodiles and most marine mammals. The receptors for the accessory olfactory system (vomeronasal system) are located within the vomeronasal organ (VNO). This organ consists of paired cigar-shaped structures that are located medially, usually along the anterior (rostral) portion of the nasal septum (Doving and Trotier, 1998). The VNO sensory epithelium consists primarily of three cell types; elongated cilia-like supporting cells, bipolar

sensory cells, called vomeronasal neurons, and basal stem cells. The vomeronasal neurons make up the majority of the cells in the sensory epithelium and are responsible for detection of chemostimuli. The VNO opens at one end and forms a blind sac at the other. The opening is variable. In rodents the opening is into the nasal cavity (Figure 1); in cats it is into the nasopalatine canal which connects with oral and nasal cavities; in cows it opens directly into oral cavity.



Figure 1: Histological section of VNO in African giant rat: N-nonsensory epithelium; S-sensory epithelium (Igbokwe, 2009)

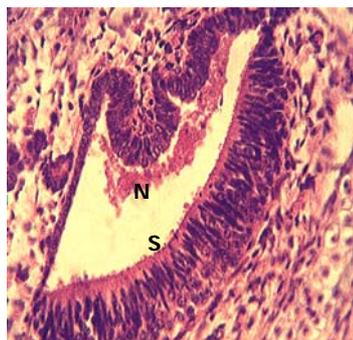


Figure 2: Histological section of VNO of the Red Sokoto goats N-nonsensory epithelium; S-sensory epithelium (Igbokwe, 2006)

The axons of the neuroreceptors of the VNO project to accessory olfactory bulb (AOB), which in turn projects to the media amygdala that has direct connections to the ventromedial hypothalamus and the preoptic area. The VNO neurons convey the pheromone signal directly to parts of the brain's limbic system-amygdala and several hypothalamic regions involved in primary motivated behaviour and neuroendocrinology (Von Campenhausen and Mori, 2000; Halpern and Martinez-Marcos, 2003).

Contrary to the accessory system, the main olfactory system is linked to several cortical areas: The main olfactory projects to the cortical amygdala, to the piriform cortex which is connected via the thalamus to the orbitofrontal and insular cortices, and to the entorhinal cortex which is connected to the

hippocampus (Jansen *et al.*, 1998). The organization of the vomeronasal system (VNS) is somewhat different from the main olfactory epithelium, as at least some vomeronasal sensory neurons express more than one receptor. Vomeronasal system projects their axons to a caudal region of the olfactory bulb known as the accessory olfactory bulb. VNS do not converge onto single glomeruli as the main bulb (Rodriguez *et al.*, 1999; Leiders-Zuffal *et al.*, 2000).

In mammals, the vomeronasal receptor neurons express genes encoding seven-transmembrane-domain receptors of either the V1R or the V2R family, which is coupled to different G proteins (Halpern and Martinez-Marcos, 2003). A low degree of sequence similarity suggests that genes encoding the olfactory, V1R and V2R receptors arose independently from within the larger family of G-protein coupled receptors evolved to detect different odorants from those detected by main olfactory system. Vomeronasal sensory neurons also have a different transduction mechanism from olfactory sensory neurons; this involves a diacylglycerol-activated cation channel, which depends in part on the transient-receptor potential channel 2 (Trpc2) genes (Lucas *et al.*, 2003). The Trpc2 channel is localized to the microvilli, the proposed site of pheromone transduction, suggesting the direct role in the VNO transduction cascade (Liman *et al.*, 1999). The vomeronasal system mediates responses to molecules of low volatility whereas the olfactory system mediates responses to more volatile molecules (Wysocki and Meredith, 1987). Vaginal discharge of estrous female hamsters contains both volatile compounds that signal the presence of female and nonvolatile compounds that elicit mating behaviours in males. In male hamsters lesions of the olfactory nerve reduce investigation of both females and vaginal discharge, suggesting that the olfactory system detects the volatile components; lesions of the vomeronasal nerve impair initiation of mating behaviour, suggesting that the vomeronasal system detects the components of lower volatility (O'Connell and Meredith, 1984).

Functions of the Vomeronasal Organ: The VNO plays a role in reproduction by detecting pheromones (Winnans and Powers, 1977). The VNO is widely referred to as being the primary system for sensory coding of pheromones. These chemical stimuli can induce hormonal changes, affect the success of pregnancy, alter the timing of puberty and female ovulation, elicit courtship and attraction, and modulate reproductive behaviour and aggression (Zuffal *et al.*, 2002). The central feature of

vomeronasal function is its ability to regulate the activity of the gonads; this it does through the neural pathway influencing hypothalamic control over gonadotrophin secretion (Hypothalamic-Pituitary-Gonadal axis) (Martinez-Marcos and Halpern, 1999). Mammalian pheromones have been shown to elicit both long-lasting effects that alter the endocrine state of recipient animal, and short-term effects on its behaviour. For example, detection of male pheromones by female mice results in an advance in the onset of puberty, induction of oestrus and termination of pregnancy, whereas detection of female pheromones causes a delay in the onset of puberty and suppression of oestrus. Modification of the hypothalamic-pituitary axis regulates the release of luteinizing hormone (LH) and prolactin (PRL), two hormones that are important for regulating these effects (Halpern, 1987). Most physiological responses to male pheromones seem to be linked to an increase in LH and a reduction in PRL, whereas physiological responses to female pheromones are usually associated with increase in PRL. Therefore the vomeronasal system provides a neural pathway that links the periphery to the hypothalamus, and modulation of LH and PR release through this pathway seems to provide the endocrine basis for 'primer effect' of mammalian pheromones (Dulac and Torello, 2003). The VNO by detecting mammalian pheromones also elicit behavioural responses. These include the regulation of inter-male aggression, courtship behaviours, aggressive responses in lactating females, initiation of male ultrasonic vocalizations and copulatory behaviour, reinstatement of lordosis in females, territorial marking, parental behaviour, individual odor discrimination and prey-trailing in snakes (Fernandez-Fewell and Meredith, 1995). These immediate behavioural responses are also modulated by the endocrine status of the animal, which is also under pheromonal control (Witt and Wozniak, 2006).

The experimental involvements of the VNO are in Bruce effect, Whitten and Vanderbergh effects (Aron, 1979). In Bruce effect, newly mated female mice return to estrus if exposed to strange males prior to embryo implantation. The Whitten effect is the induction of estrus in female mice made anestrus by group housing. This induction is caused by stimuli from males or their urine and is known to be dependent on a functional VNS. In Vanderbergh effect, there is puberty acceleration caused by exposure to male chemosignals during female development and occurs in several mammalian species.

The first experiments indicating that vomeronasal organ played a role in reproduction in

mammals were performed by Planel (Planel, 1953). He showed that when this organ in guinea pigs was impaired the males failed to mount. Females with impaired organs did not show lordosis, lost interest in their partner and seldom became pregnant. Peripheral differentiation of the vomeronasal system produces several sexual behaviour deficits in both male and female hamsters (Powers and Winnans, 1975). These authors found that the effects of removal or prevention of normal function of the vomeronasal organ were acute when the animal was sexually naïve, but if the animal had experienced a partner in sexual interplay, the effect of the removal of the vomeronasal organ was less dramatic. However injection of LHRH (gonadotrophin-releasing hormone) into experimental animals lacking a vomeronasal organ re-established sexual behaviour.

Most of the work on vomeronasal functions has been in rodents and snakes. Early experiments involve lesions (damage or removal) of the vomeronasal or olfactory systems in order to reveal deficits in behaviour or physiological function (Meredith and Fernandez-Fewell, 1994). More recently researchers have detected genes thought to be involved with vomeronasal function and looked for deficits (Dulac and Axel, 1995). In other experiments the activation of brain areas receiving central vomeronasal projections has been investigated with other techniques (Takigami *et al.*, 2000).

The vomeronasal system has been implicated in many behavioural/physiological responses to chemical signals in several species and both sexes. These responses may be of the type attributed to priming pheromones, where there is some delayed physiological effects usually mediated by hormonal change or they may be the type attributed to signaling pheromones, where rapid changes can be seen (Wysocki and Lepri, 1991). However not all putative pheromone communication is mediated by the vomeronasal system, nor is all vomeronasal chemosensory function necessarily related to pheromone communication. Communication between mother and young appears to be mediated by olfactory and not vomeronasal signaling. Vomeronasal organ removal did not disrupt odor-dependent nipple finding in young rabbits (Hudson and Distel, 1986). Also in pig, vomeronasal duct occlusion did not prevent female "standing" responses to male pheromone (Dorries *et al.*, 1995; 1997).

Priming-type responses that are dependent on an intact vomeronasal system in females are well documented. These include modulation of estrus in mice by urine signals from males and females, modulation of estrus in rats, the acceleration of

puberty in mice and voles and the block to pregnancy in mice produced by strange males (Bruce effect). All these effects are mediated by signals in male urine and all are prevented by lesions of the vomeronasal system. A similar dependence on intact vomeronasal organs is seen in the induction of estrus in prairie voles (but not in meadow voles), in monodelphic opossums and in induction of ovulation in light induced or estrogenized, persistence-estrus rats (Clancy *et al.*, 1994).

A signaling function is seen in lactating female mice, whose aggression toward intruders is reduced or eliminated by vomeronasal lesions, regardless of experience. Among males, there are clear examples of signaling functions mediated by vomeronasal organ but also examples of hormonal modulation by vomeronasal input. Golden hamsters, mice and prairie voles are particularly dependent on chemosensory input for normal reproductive behaviour.

Chemosignals and Flehmen Behaviour:

Chemosignals are usually volatile chemical compounds (odorants) that elicit signals finally transmitted to higher brain centres and they generate various cognitive and emotional responses, measured thoughts and behaviours. In contrast, pheromones lead to innate and stereotyped behaviours that may result from a non-conscious perception of this class of odours. Chemosignals which may be pheromones are obtained by touching, licking and or close-range sniffing and sometimes flehmen response. Chemosensory responses initiate sensory activity by sampling an odour source. Volatile chemosignals taken in with respiratory airstream will arrive at the main olfactory mucosa. Chemosignals are rarely advantageous to the sender, although predator urine odours can repel prey species, while prey scent-trails can betray them to a predator unless they too emit noxious odours (Cooper, 1997; Chizar *et al.*, 1999). The majority of the vomeronasal system usage is carried out in conjunction with the main olfactory system. Some pheromones operate via the vomeronasal system but some operate via the main olfactory system. Equally there also examples of VNO used for detecting nonpheromone chemicals in some species, particularly in snakes, which use the organ for prey-trailing (Meredith, 2002). This combination of information flow resulting from dual analysis of chemical input is bound to be advantageous in most circumstances. Flehmen which is the facial grin or grimace is a well known chemoreceptive investigative behaviour in terrestrial mammals. Flehmen is displayed by most ungulates. The behaviour is seen much more frequently in males than females,

particularly following olfactory investigation of the anogenital area or freshly voided urine of a female (Ladewig and Hart, 1980). The perceptive identification of flehmen as key element in oestrus detection was made by Estes (Estes, 1972). Intake of non-volatiles is considered to be function of flehmen. Flehmen is a vomeronasal-specific sampling mechanism for oral and/or nasal uptake into the opening of the vomeronasal organ. The use of urine as signal vehicle is prevalent in many mammals/skin gland secretions. Faecal products are also involved as is typical of South American ungulates and hyenas (Altman, 1969). During flehmen most mammals show jaw opening (gape or yawn) plus an elevated head posture and temporary stillness, there may also be specific respiratory and tongue movement plus a degree of nostril closure. Flehmen is conspicuous in ungulates and carnivores. The contribution of flehmen to fertility is bound up with the role of the vomeronasal system in reproductive patterns.

Conclusion: The advent of molecular studies has revealed enormous information about the structure and function of the main olfactory and vomeronasal systems particularly in small mammals. Vomeronasal (accessory) olfactory and main olfactory systems are related structurally and both play significant roles in detecting signals that have profound influence in behavioural and reproductive activities in mammals. It seems that the VNO plays a pivotal role in mediating pheromonal communication in mammals. The stimulation of this organ has profound influence on the endocrine system which in turn influences reproductive functions and behaviour. When the VNO fails to function in naive mammals, mating behaviour is affected, indicating the important role of this organ in some stages of reproduction. The main olfactory system is responsible for some pheromonal-triggered behaviour. The olfactory and vomeronasal systems have overlapping functions and these overlapping functions which are well studied in rodents may be applicable to several other mammals. There are limited molecular-genetic studies of the chemosensory systems in our domesticated food animals; perhaps vigorous attention on these species particularly the ungulates may reveal the diverging and complimentary roles of the dual olfactory systems reproductive behaviour.

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