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Preliminary results on the role of the vomeronasal organ in modulating the response to the buck effect in does

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Abstract

The vomeronasal organ (VNO) consists of paired, blind ending tubes on either side of the nasal septum. The VNO lumen connects to the nasopalatine canal and also to the oral and nasal cavities. The vomeronasal sensory epithelium is connected to the accessory olfactory bulb (AOB). The AOB in turn has a direct link to the hypothalamus. If the VNO and the accessory olfactory system do play a role in the detection of pheromones, females with a non-functional VNO would not be able to detect male pheromones. Therefore, theoretically, no or a very poor endocrine response should be detected in does after the introduction of males during the non-breeding season, while does with a functional VNO are expected to show an endocrine response. The aim of this study was evaluate the role of the VNO in the reproductive responses of does in terms of oestrus behaviour and conception rates subsequent to the introduction of bucks. The preliminary results, although not statistically significant, support this hypothesis. Only 20% of does with a non-functional VNO was pregnant while 56% of does with a functional VNO was pregnant after the introduction of bucks during the non-breeding season. Lower concentrations of oestradiol and LH were also observed in treated does compared to the controls.

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Introduction

The vomeronasal organ (VNO) consists of a pair of blind ending tubes, situated on either side of the nasal septum (Kratzing, 1971). A neuro-anatomical pathway linking the VNO, accessory olfactory bulb and the hypothalamus has been described (Raisman, 1972; Scalia & Winans, 1975; Kevetter & Winans, 1981). This pathway is distinct from the neural pathway of the main olfactory system, which does not connect to the hypothalamus. The receptors of the sensory epithelium of the VNO seem to be more sensitive to non-volatile substances. This is in contrast with olfactory receptors that show more sensitivity to volatile substances (Wysocki, 1980, Keverne *et al.*, 1986). Vomeronasal and olfactory receptors also differ in certain biochemical and functional aspects, which indicates a fundamental difference between odour and pheromone reception (Liman, 1996a; Tirindelli, 1998). Pheromone receptors have only been identified in the VNO, and not in the nasal cavity (Dulac & Axel, 1995; Tirindelli, 1998).

When a ram or buck is introduced to a group of females, the reproductive cycles of these females tend to synchronize. During the non-breeding season some females may even be stimulated to ovulate and express oestrus. This effect is known as the "buck effect", and is mediated by male pheromones. The physiological effects of the "buck effect" have been extensively investigated and described by various authors, but the exact mechanism by which the male stimulus is delivered to the female neuro-endocrine system remains to be accurately described (Over *et al.*, 1990; Rosa & Bryant, 2002).

Flehman has been indicated as a possible mechanism by which stimuli can be delivered to the VNO. It is postulated that during Flehman, airflow over the nasal opening of the nasopalatine canal is manipulated to draw fluids from the nasopalatine canal and the vomeronasal lumen into the nasal cavity through a venturi-effect. This is supported by a pumping mechanism within the VNO lumen, which expels vomeronasal fluids into the nasopalatine canal. These fluids are then sucked into the nasal cavity and are replaced by fluids from the oral cavity (Bailey, 1977).

Evidently the accessory olfactory system (AOS), with the VNO as its primary sensory apparatus, seems to be well equipped to receive and transfer male sensory cues to the female endocrine system. The introduction of bucks to a group of does is known to synchronize their oestrus cycles during the breeding

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season. This is known as the "buck effect" and is mediated through male pheromones and does in the non-breeding season can also be stimulated to ovulate and exhibit oestrus subsequent to the introduction of males. Luteinizing hormone (LH) is responsible for inducing ovulation. The hypothalamus controls the secretion of LH through the pulsatile release of GnRH, which mediates the secretion of LH from the adenohypophysis. Since the "buck effect" modulates the oestrous cycle in does and stimulates ovulation, it appears that the "buck effect" facilitates the secretion of LH. The "buck effect" is probably mediated through sensory stimuli via the VNO's neural link to the hypothalamus in the doe. If the VNO and the accessory olfactory system do play a role in the detection of pheromones, females with a non-functional VNO would not be able to detect male pheromones. Therefore, theoretically, no endocrine response should be detected in the female after male introduction during the non-breeding season. In contrast, females with a functional VNO would be expected to show an endocrine response to male introduction. An endocrine response can be characterised in the blood levels of LH, follicle-stimulating hormone (FSH) and estradiol, and in the conception rate.

Materials and Methods

Nineteen, indigenous does were randomly assigned to a treatment (n = 10) and a control group (n = 9). The vomeronasal organ of treated does was rendered non-functional by means of cauterisation of the nasopalatine canal. The treated and control or normal does were not separated, but housed away from the bucks. The does were synchronized with two injections of Estrumate (Scherring-Plough Animal Health) 10 days apart. The bucks were introduced on day 32 of the experiment for five days. Blood sampling was done by jugular venipuncture and commenced on day 27 of the experimental period and continued for 10 days. Blood samples were collected twice daily, while samples were collected at 2 hourly intervals for 48 hours around the expected time of oestrus. Blood samples were analysed for estradiol and LH.

Conception rates were used as a preliminary, indirect parameter to assess the response of the does subsequent to the introduction of bucks during the non-breeding season. The does were scanned for pregnancy 10 weeks after the bucks were introduced. The data was analysed by means of the ANOVA procedure on SAS (SAS®, 2001). Categorical data was analysed by means of log-linear analysis and multiple comparisons tested by means of the Bonferroni technique for unbalanced data.

Results and Discussion

In the treatment group 20% of the does conceived, while 55.6% of the does in the control group conceived. Although the difference in conception rates only tended towards significance ($P < 0.07$), these preliminary results support the hypothesis that the VNO plays an important role in modulating the buck effect, which stimulates oestrus behaviour and ovulation in does. Estradiol concentrations in blood samples from does in the control group (78.5 pmol/L) were numerically higher compared to those in the treated does (75.3 pmol/L), while LH concentrations were higher ($P = 0.1$) in the control (0.372 IU/L) compared to the treated does (0.289 IU/L).

These results agree with the initial observations just after the introduction of the rams, suggesting a difference in reproductive behaviour between normal does and does with a non-functional VNO. Most of the control does expressed interest in the males immediately after being introduced, while the vomero-ectomised does did not express any interest in the males. Therefore, signs of overt oestrus activity were more pronounced for does in the control group compared to the treated does, which coincides with the hormone profiles obtained. Similarly, the results of the pregnancy diagnosis at 60 days suggest that animals with a non-functional VNO showed less of a response to the buck effect compared to those with a functional VNO in terms of conception rates.

Although rare, spontaneous ovulation in some individuals will occur in seasonal breeders during the non-breeding season, particularly in South African indigenous goats that tend to breed all year round (Webb *et al*., 1998). Also, the animals used were sexually experienced and it is possible that odour (stimuli perceived by the main olfactory system) of the males provided adequate stimulus to induce oestrus in certain experienced individuals. However, if this affected the does in the present study, a higher conception rate was to be expected in the does with a non-functional VNO. The only difference between these does was the functionality of the VNO. So, it follows that this organ probably contains receptors that mediate the buck effect.

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Conclusions

The preliminary results suggest that the VNO plays a role in modulating oestrus in does, in response to the introduction of bucks or the so-called "buck effect".

References

Bailey, K., Flehman in the ring tailed lemur (*Lemur catta*). Behaviour LXV, 309-319.

Dulac, C. & Axel, R., 1995. A novel family of genes encoding putative pheromone receptors in mammals. Cell 83, 195-206.

Kratzing, J., 1971. The structure of the vomeronasal organ in the sheep. J. Anatomy 108, 247-260.

Kevetter, G.A. & Winans, S.S., 1981. Connections of the corticomedial amygdala in the golden hamster. I. Efferents of the "Vomeronasal Amygdala". J. Comp. Neur. 197, 81-98.

Kevetter, G.A. & Winans, S.S., 1981. Connections of the corticomedial amygdala in the golden hamster. II. Efferents of the "Olfactory Amygdala". J. Comp. Neur. 197, 99-111.

Over, R., Cohen-Tannoudji, J., Denhard, M., Claus, R. & Signoret, J.P., 1990. Effect of pheromones from male goats on LH-secretion in anoestrus ewes. Physiology & Behaviour 48, 665-668.

Liman, E.R., 1996. Pheromone transduction in the vomeronasal organ. Current Opinion in Neurobiology 6, 487-493.

Raisman, G., 1972. An experimental study of the projection of the amygdala to the accessory olfactory bulb and its relationship to the concept of a dual olfactory system. Exp. Brain Res. 14, 395-408.

Rosa, H.J.D. & Bryant, M.J., 2002. The "ram-effect" as a way of modifying the reproductive activity in the ewe. Small Rumin. Res. 45, 1-16.

SAS, 2001. Statistical Analysis Systems user's guide (V 6). SAS Institute Inc., Cary, North Carolina, USA.

Scalia, F. & Winans, S.S., 1975. The differential projections of the olfactory bulb and accessory olfactory bulb in mammals. J. Comp. Neur. 161, 31-56.

Tirindelli, R., Mucignat-Caretta, C. & Ryba, N.J.P., 1998. Molecular aspects of pheromonal communication via the vomeronasal organ of mammals. Trends in Neurosciences 21 (11), 482-486.

Webb, E.C., Mamabolo, M.J., Du Preez, E.R. & Morris, S.D., 1998. Research and training strategies for goat production systems in South Africa. Proc. workshop held on 22-26. November, 1998. Eds. Webb, E.C. & Cronje, P.B. pp. 81-87.