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Research report

Female recognition and assessment of males through scent

Jane L. Hurst*

Mammalian Behaviour & Evolution Group, Department of Veterinary Preclinical Science, University of Liverpool, Leahurst, Neston CH64 7TE, UK

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ABSTRACT

Scents play key roles in mediating sexual behaviour in many vertebrates, both in the recognition of opposite sex conspecifics and in assessing the suitability of different individuals as potential mates. The recognition and assessment that underlies female attraction to male scents involves an important interaction between the main and accessory (vomeronasal) olfactory systems. Female mice gain information through the vomeronasal system on nasal contact with a scent source that is essential to stimulate attraction to an individual male's scent. Three highly polymorphic multigene families contribute involatile proteins and peptides to mouse scents that are detected through specific vomeronasal receptors during contact with scent. Major urinary proteins (MUPs) provide an individual genetic identity signature that underlies individual recognition and assessment of male competitive ability, kin recognition to avoid inbreeding, and genetic heterozygosity assessment. Familiar mates are recognised in the context of pregnancy block using MHC peptides, while exocrine-gland secreting peptides (ESPs) are likely to play additional roles in sexual assessment. By associating this involatile information in individual male scents, gained on initial scent contact, with the individual male's airborne volatile signature detected simultaneously through the main olfactory system, females subsequently recognise and are attracted by the individual male's airborne volatile signature alone. This allows much more rapid recognition of scents from familiar animals without requiring physical contact or processing through the vomeronasal system. Nonetheless, key information that induces attraction to a male's scent is held in involatile components detected through the vomeronasal system, allowing assessment of the genetic identity and attractiveness of each individual male.

1. Introduction

Scents play an integral role in mediating reproductive interactions in many vertebrates including mammals. Initial attention focused largely on the scents that prime reproductive physiology according to the social environment, particularly among laboratory mice. These can have a wide variety of affects, including the acceleration or delay of reproductive development among young animals, the synchrony or inhibition of oestrus among females, interruption of pregnancy establishment and, among males, modulation of luteinizing hormone levels, sperm density, sperm motility and spermatogenesis [25,77]. Scents also play key roles in mediating sexual behaviour itself. Research into the olfactory and neural pathways underlying sex-biased responses to conspecific scent signals has focused on the pathways underlying sex recognition and the control of sexual behaviour. However, there has been relatively little consideration of the complexity of the scent signals used in sexual signalling, particularly on the need to assess the suitability of potential mates beyond simple sex recognition. Here I will argue that to understand the pathways underlying reproductive behaviour, we must consider the functional significance of the information that is being processed and its importance for individual reproductive success, both to guide and to interpret investigations of the signals and the neural pathways that are involved. Laboratory rodents play a key role in these investigations because they are easily manipulated and bring advantages of genetic homogeneity and targeted manipulation. However, this homogeneity introduces its own complications which need to be taken into account when interpreting the responses of laboratory animals, as explained below.

2. Interaction between the main and accessory olfactory systems

Much research to date has addressed the separate roles of the main and accessory olfactory system in sex recognition and the control of sexual behaviour (recent reviews by [19,72,113]). The main olfactory system detects airborne scents (volatile chemical components and small airborne peptides) via receptors in the main olfactory epithelium (MOE) and can thus detect scents at some distance from their source. By contrast, the accessory olfactory system detects volatile and involatile molecules that are pumped to the vomeronasal organ (VNO) when animals make nasal contact with a

* Tel.: +44 151 794 6100; fax: +44 151 794 6107.
E-mail address: jane.hurst@liv.ac.uk.

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scent source [16,47,89]. Although these two systems detect partially overlapping sets of chemosignals, each system appears to mediate different social and sexual responses [113,134]. Because the main olfactory system can detect scents in the air, this system is key in allowing animals to detect the presence of scents in the environment. This may stimulate animals to approach the source to gain further information, particularly if the volatile scent detected is unfamiliar or has not been encountered recently. Once animals are in close nasal contact with the scent source, the VNO pump is activated to gain additional information through the accessory olfactory system.

Attempts to understand the different roles of these two systems generally involve debilitation of one system to see what responses are controlled by the system remaining intact, or are disrupted presumably because responses depend on processing through the debilitated system. This approach provides very useful information, but there are significant limitations that need to be considered when interpreting responses. Detection of airborne scents through the main olfactory system may be necessary to activate delivery of scent to the VNO for example [61,71]. Thus, deficits caused by removal of MOE input may be due to the absence of information detected through the main olfactory system, the accessory olfactory system, or both. Another major limitation is that disruption of one system fails to take into account any important interaction between the systems. The functional importance of this interaction is illustrated by the effect of sexual experience on sexual responses when the VNO is removed. When male mice or hamsters have had no prior sexual experience with females, ablation of the VNO eliminates normal sexual behaviour towards females even if the main olfactory system remains intact. However, if males have sexual experience prior to VNO ablation, they learn to associate airborne volatiles detected through the MOE with scents detected through the VNO. Airborne odours processed through the main olfactory system then are sufficient to stimulate normal sexual responses towards females even if the VNO is ablated [88,99,145]. Females similarly learn to recognise airborne volatiles from males detected through the MOE by association with involatile scent information gained through the VNO during nasal contact with scents. When naïve to adult male scents, females show an inherent attraction to adult male compared to either female scents [92,93] or to castrated male scents [84], but only if they are able to contact the scent source and gain information through the VNO [85]. Once females have had repeated nasal contact with male scents, they become attracted to the airborne volatiles emanating from male scents that were not previously attractive [85,92,93].

Based on studies of laboratory mice, these findings initially suggest that animals have to learn to recognise airborne scents representing the opposite sex through the main olfactory system by association with opposite sex scents that can be inherently recognised through vomeronasal inputs without any prior experience. Such associations could be learnt through contact with scents from adult conspecifics during development in juvenile and prepubertal mice, but a need to learn such sex-specific airborne odours would be somewhat surprising. There are substantial differences in the airborne odours of male and female mice that are readily detected even by the human nose. Why then should animals have to learn to recognise the difference between male and female airborne volatile profiles through association with scents detected on contact? Our recent studies of genetically heterogeneous wild mice reveal that animals do not learn to discriminate between sex-specific airborne scents, but instead they learn the airborne scent profiles of individual mice whose scent they have previously contacted. Thus, the association learnt between contact and airborne scents is for individual recognition rather than for sex recognition [112]. When female mice are able to contact scents from individual wild-derived adult males or females, they show a consistent attraction to spend

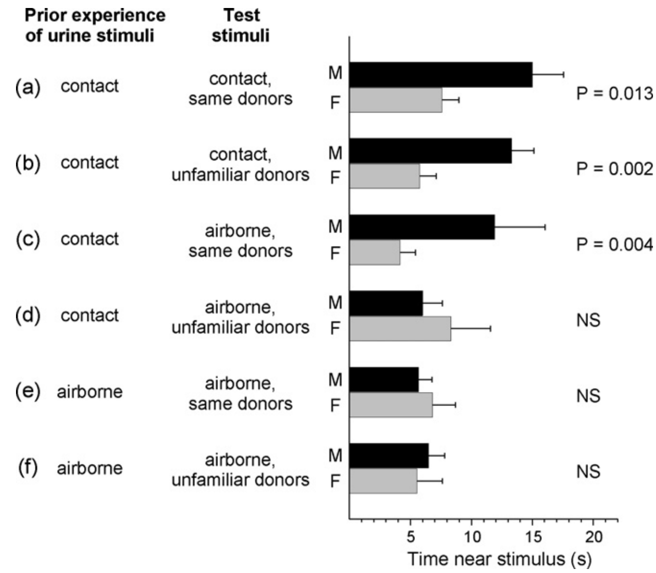

Fig. 1. Preference for male (M, black bars) over female (F, grey bars) urine according to prior experience of urine from the same or different individual donors and whether female mice can contact the stimuli before or during the test. Females spend more time near male urine if they can contact stimuli during the test (a and b). They only spend more time near airborne odours from male urine if they have had prior contact with urine stimuli from the same individual donors (c–f). *p*-values indicate Wilcoxon signed ranks tests. Total time near a stimulus (mean ± S.E.M.) involves two components. First, females spend more time sniffing closely at male than at female scents, a difference that might simply reflect greater processing time required to interpret information in male scents which are more dissimilar from their own. However, females also spend more time in the vicinity of male scents even when not sniffing [112], reflecting attraction that is not likely to be due to scent processing. Under free-ranging conditions, attraction to spend more time near male scents will increase the chances of encountering a male, as male mice scent mark their territories extensively [61]. Adapted from [112].

more time near to male scents regardless of whether or not they have met scent from particular individual donors before (Fig. 1a and b). When unable to contact the scent source, females are only attracted to airborne scents from individual males whose scent they have previously contacted (Fig. 1c–f). This is the case regardless of the prior sexual and social experience of females—even those that have natural social experience of many different males and females in semi-natural populations fail to learn a generalised attraction to airborne volatiles from unfamiliar males whose scent they have not contacted [112]. When experiments are carried out with inbred laboratory mice, by contrast, males or females within the same strain are genetically identical. Thus, it is not surprising that responses to one individual often generalise to other individuals of the same strain and individual-specific responses are not apparent. Even mice from so-called 'outbred' laboratory strains are still likely to share key individual genetic identity signatures (see below) because all classical laboratory strains derive from the same very small gene pool and originate from a single female ancestor [6,33,41,44]. This is clearly not a natural situation and wild mice have much more distinct scent signatures of individual genetic identity. Instead of learning an attraction to 'male' volatile scents, females learn an attraction to the volatile profile of an individual male after direct contact with that male's scent. Familiarity with an individual male's airborne volatile profile *per se* does not make that individual's scent attractive if the female has been unable to contact the scent directly (Fig. 1e). The implication is that females gain essential information about the suitability, and thus attractiveness, of a particular individual male as a potential mate through direct contact investigation of his scent, which allows detection of information through the VNO. Without this information, females do not find a male's scent attractive.