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BRAIN RESEARCH

Research Report

The main and accessory olfactory systems of female mice are activated differentially by dominant versus subordinate male urinary odors

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ABSTRACT

Previous studies have shown that female preferences for male pheromones depend on the female's reproductive condition and the dominance status of the male. However, it is unknown which olfactory system detects the odors that result in a preference for a dominant male. Therefore, in the present study, we asked whether dominant versus subordinate male urinary odors differentially activate the main and accessory olfactory systems in female (*C57Bl/6j*) mice by monitoring the induction of the immediate early gene, c-fos. A more robust induction of Fos was observed in female mice which had direct nasal contact with dominant male urinary odors in four specific segments of the accessory olfactory system, i.e., the posteroventral part of the medial amygdala, the bed nucleus of the stria terminalis, the medial part of the preoptic nucleus and the ventrolateral part of the ventromedial hypothalamus, compared to females that were exposed to subordinate male urine. This greater activation of the accessory olfactory pathway by dominant male urine suggests that there are differences in the nonvolatile components of dominant versus subordinate male urine that are detected by the vomeronasal organ. By contrast, subordinate male urinary odors induced a greater activation in the piriform cortex which is part of the main olfactory system, suggesting that female mice discriminate between dominant and subordinate male urine using their main olfactory system as well.

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1. Introduction

In rodent species, body odors provide essential information about the sex, social and reproductive status of conspecifics (Brown, 1979). They induce hormonal changes and play a key role in mate recognition and partner preferences (reviewed in Bakker, 2003; Keller and Bakker, 2009; Keller et al., 2009). For instance, male urinary pheromones induce sexual maturation (Lombardi and Vandenbergh, 1977) and pregnancy block (Bruce, 1959; Lloyd-Thomas and Keverne, 1982) in female mice. These physiological effects of male pheromones are mediated through the vomeronasal organ (VNO) and subsequently the accessory

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olfactory system since lesions of the VNO prevented the occurrence of pregnancy block in female mice when exposed to an unfamiliar male (Lloyd-Thomas and Keverne, 1982). Furthermore, female mice must make direct nasal contact with non-volatile male body odors first before later showing any recognition/attraction to volatile components of male body odors. This suggests a role for the VNO and the accessory olfactory system in mate recognition (Hurst et al., 1998; Martinez-Garcia et al., 2009). However, it should be noted that odor-experienced female mice might use volatile odors alone to discriminate between different males, which would implicate the main olfactory system in odor preferences. Indeed, lesions of the main olfactory epithelium (MOE) by bilateral infusion of zinc sulfate into the nares disrupted male odor preferences and mate recognition in odor-experienced female mice whereas lesions of the VNO had no such effect (Keller et al., 2006a, b). These results suggest that mate recognition likely depends on a combination of MOE and VNO input.

Studies of wild-caught house mice living in seminatural enclosures have shown that females' male odor preferences are based on the females' reproductive condition (estrous or nonestrous) and the dominance status of the male (Mossman and Drickamer, 1996). Thus in dominance odor tests, estrous females preferred odors from dominant males whereas nonestrous females exhibited no significant preferences for either subordinate or dominant male odors. We recently confirmed such a preference for dominant versus subordinate male odors in female laboratory (*C57Bl/6j*) mice (Veyrac and Bakker, 2008). We also found that this preference depended on the hormonal status and prior sexual experience of the female. Thus sexually naïve, female mice ovariectomized in adulthood needed to be treated with both estradiol and progesterone to show a significant preference for dominant over subordinate male odors, whereas sexually experienced females showed this preference when treated with estradiol alone (Veyrac and Bakker, 2008). This odor preference was based on volatile odors alone, since female subjects could not make any direct nasal contact with the odor sources. Thus, the dominance status of males is a criterion used by female mice for mate selection. However, at present it is still unknown which olfactory system detects the odors that result in a preference for a dominant male. Therefore, in the present study we asked whether dominant versus subordinate male urinary odors differentially activate the main and accessory olfactory systems in female mice, using the expression of the immediate early-gene, *c-fos*, as a marker of neuronal activation. Female subjects were first provided with mating experience with different males since a more pronounced preference for a dominant over a subordinate male was previously observed in females following sexual experience (Veyrac and Bakker, 2008).

2. Results

2.1. *Accessory olfactory bulb*

Exposure to either dominant or subordinate male urine induced Fos expression in both the granular (Fig. 2A, C) and mitral cell layers of the AOB (Fig. 2B, D). Kruskal–Wallis tests showed a significant effect of urine exposure on the induction of Fos in the anterior and posterior parts of the AOB (granular anterior part $p=0.0272$; mitral anterior part $p=0.0294$; granular posterior part $p=0.0164$; mitral posterior part $p=0.0312$). Subsequent Mann–Whitney comparisons showed no significant effects of type of urine on the number of Fos positive cells ($p>0.05$ dominant versus subordinate urine for all the AOB regions analyzed).

2.2. *Accessory olfactory pathway*

Exposure to dominant male urine induced a greater Fos expression in several brain regions of the accessory olfactory pathway, including the posteroventral part of the medial amygdala (MePV), the anterior medial part of the BNST, the medial part of the preoptic nucleus (MPN) and the ventrolateral part of the VMH, than exposure to subordinate male urine or water (Fig. 3B, C, D and E; Kruskal–Wallis tests: MePV $p=0.0064$; BNST $p=0.049$; MPN $p=0.0273$; VMH-VL $p=0.0243$). Thus, a greater Fos response was induced by dominant male urine compared to subordinate male urine in the MePV (Mann–Whitney test $p=0.0275$), BNST (Mann–Whitney test $p=0.0339$), MPN (Mann–Whitney test $p=0.0273$) and VMH-VL (Mann–Whitney test $p=0.0493$). By contrast, no significant differences in Fos expression were observed in the posterodorsal part of the medial amygdala of females exposed to either dominant or subordinate male urine (Kruskal–Wallis tests $p=0.0185$ and Mann–Whitney comparison dominant versus subordinate urine $p=0.4624$). Likewise, no significant activation was observed after exposure to dominant male urine in the medial amygdala (MeA), the posterior part of the BNST or the dorsomedial part of the VMH (Table 1).

2.3. *Main olfactory bulb*

Similar patterns of glomerular activation in the MOB were observed between females exposed to dominant male urine vs. subordinate male urine (Fig. 4A). As shown previously (Martel and Baum, 2007), the regions with the greatest number of urine odor-activated glomeruli (in red) included the rostral–lateral as well as the caudal–medial portions of the MOB. Point-by-point Mann Whitney *U*-tests (bottom panels Fig. 4B) showed significant differences (red-yellow colors) between plots for clean vs. dominant male urine, and for water vs. subordinate male urine, but no significant differences between plots for dominant vs. subordinate male urine.

2.4. *Main olfactory pathway*

Exposure to either dominant or subordinate male urine induced Fos expression only in the posterior ACo which is part of the olfactory amygdala (Table 1; Fig. 5A; Kruskal–Wallis test $p=0.0375$;) and the piriform cortex (Fig. 5B Kruskal–Wallis test $p=0.0064$). However, Mann–Whitney tests showed that subordinate male urine induced a greater Fos expression in the piriform cortex than exposure to dominant urine (Fig. 5B; subordinate versus dominant urine $p=0.0143$). Interestingly this effect was observed both in the anterior and posterior parts of the piriform cortex (Fig. 5C anterior part: Kruskal–Wallis test $p=0.0201$, Mann–Whitney test subordinate versus

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