ELSEVIER

Physiology & Behavior 87 (2006) 857–862

PHYSIOLOGY & BEHAVIOR

Sensory mediation of female–male mounting in the rat: I. Role of olfactory cues

Veronica M. Afonso, Amélie Woehrling, James G. Pfaus *

Center for Studies in Behavioral Neurobiology, Department of Psychology, Concordia University, 7141 Sherbrooke St. W., Montréal, QC, Canada H4B 1R6

Received 18 August 2005; received in revised form 14 December 2005; accepted 3 January 2006

Abstract

Previous research has shown that olfactory cues mediate the mounting of female rats by male or other female rats. The present study examined whether olfactory cues might mediate the mounting of castrated, sexually inactive male rats by sexually receptive female rats (female–male mounting, or FMM). The effects of olfactory impairment, created by either olfactory bulbectomy (OBx) or olfactory occlusion (OOc), on FMM were investigated. Ovariectomized, hormone-primed female rats were given either OBx (OBx+) or sham (OBx−) surgeries. OBx+ females did not engage in any FMM after surgery, whereas sham-operated females continued to mount at baseline levels. This effect was replicated using OOc, a reversible form of olfactory impairment that involves the cannulation of the nasal cavity with a flexible tube. Females were either given the OOc surgery (OOc+), the OOc surgery with the tube removed immediately after placement (OOc−), or sham surgery in which the animal was only anesthetisized. OOc+ females, like OBx+ females, did not display FMM, whereas both control groups continued to mount at baseline levels. The effect of prior experience with FMM was also examined. Females were given either 0 or 5 encounters with castrated males prior to OBx+, OOc+, or OOc− surgeries. OBx+ and OOc+ females did not mount, regardless of prior mounting experience. These data indicate that the olfactory sense is a prime mediator of FMM, and that prior mounting experience does not offset the disruption of FMM caused by the elimination of olfactory cues.

Keywords: Olfaction; Sexual experience; Olfactory impairment; Female rat

1. Introduction

Female rats mount sexually receptive females at high rates following treatment with androgens [14,50]. Although such behavior appears "masculinized" [34,39,50], female–female mounting (FFM) occurs in naturally cycling rats throughout the phases of their estrous cycle, suggesting that mounting behavior serves social functions in females, including the maintenance of social status [4,7,21]. In contrast, gonadally intact, sexually receptive females of a variety of species will mount sexually sluggish or inactive males [6], and we have recently reported that OVX female rats given estrogen replacement will mount castrated, sexually inactive male rats [1]. This female–male mounting (FMM) was displayed spontaneously and at higher rates if the females were sexually naive relative to females with prior heterosexual experience with sexually active or inactive males. Thus, FMM occurs naturally in rats as a "super solicitational" behavior to activate mounting in sexually sluggish males [1,6].

In addition to hormones and heterosexual experiences, olfactory cues are known to modify mounting behavior in males [13,40,48]. Indeed, the effect of olfactory impairment depends on the sexual experience of the male. In sexually inexperienced male rats, olfactory bulbectomy (OBx) prevents the occurrence of sexual behavior [32]. In sexually experienced male rats, several researchers found that lesions of the nasal epithelium produced by infusions of zinc sulfate increased the latencies to intromit following the introduction of a stimulus female, and decreased the number of mounts and intromissions overall compared to control males [5,12,27]. Although other researchers [33] reported no disruption of sexual behavior in sexually experienced male rats following OBx, the initiation of sexual behavior was severely and consistently impaired in sexually inexperienced males with OBx or zinc sulfate treatment [5,8,12,17,33,37].

* Corresponding author. Fax: +1 514 848 2817.
E-mail address: Jim.Pfaus@concordia.ca (J.G. Pfaus).

0031-9384/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.physbeh.2006.01.009

Similar to males, olfactory cues appear to be important for mounting behavior in females. Increased FFM has been observed in females given exposure to urine from estrous females [9]. Although the effects of OBx on FMM are unknown, some researchers report OBx decreases the ability of female rats to display FFM [10,35], whereas others report no effect [14]. Interestingly, the level of prior heterosexual experience does not play a role in these discrepant findings, whereas FFM experience does [14]. OBx females with prior experience mounting receptive females display more FFM compared to inexperienced OBx females. Manipulations of olfaction have produced conflicting reports on traditional female sexual behavior. For example, OBx in female rats facilitates the induction of lordosis [18,36,38] and certain proceptive behaviors such as ear wiggling [35,37,51]. In contrast, we found that olfactory impairment (produced by either OBx or olfactory occlusion, OOc) suppressed other proceptive behaviors such as solicitations and hops and darts [52]. Thus, it is unclear how olfactory deficits may affect FMM in sexually naïve versus experienced females.

The present experiments were undertaken to determine whether male olfactory cues are important for the initiation of FMM. Experiments 1 and 2 investigated the effects of OBx and OOc on FMM. Experiment 3 investigated whether experience with FMM compensates for the induction of an olfactory deficit.

2. Materials and methods

2.1. Animals and hormone treatment

Sexually naive female Long–Evans rats, weighing 200 and 250 g, were obtained from Charles River Canada, Inc., St. Constant, QC. They were housed in groups of five in hanging cages in a colony room maintained on a reversed 12/12 h light/dark cycle (lights off at 08:00 h) at approximately 21 °C. Food and water were continuously available. Females were ovariectomized (OVX) bilaterally through lumbar incisions following injections of ketamine hydrochloride (50 mg/ml) and xylazine hydrochloride (4 mg/ml) anesthetic, mixed in a ratio of 4:3 respectively and injected i.p. in a constant volume of 1 ml/kg of body weight. All females were maintained for the duration of the experiment on hormone replacement by subcutaneous injections of estradiol benzoate (EB; 10 μg in 0.1 ml of sesame oil) 48 h, and progesterone (P; 500 μg in 0.1 ml of sesame oil) 4 h prior to behavioral testing.

Fifteen Long–Evans males, from the same breeder were anesthetized with the same ketamine/xylazine mixture and castrated through a midline incision of the scrotum, after which they received 3 months of no sexual experience for consummatory sexual behaviors to decrease to zero [1]. These males served as the stimuli for FMM behavior.

2.2. Olfactory bulbectomy

Females given bulbectomy surgeries (OBx+) were anesthetized and an incision to the skin covering the skull was made. A hole was drilled through the overlying bone to expose the olfactory bulbs. A surgical hook was inserted to sever the neural connections between the cerebral hemispheres and main and accessory olfactory bulbs. Bulb tissue was removed by aspiration through a glass pipette. Gelfoam was packed lightly in the space left after the bulbs were removed, and the initial incision was closed with wound clips. The procedure for the OBx sham (OBx−) operation involved drilling the bone and uncovering the bulbs without disturbing them. After all testing procedures were performed, the OBx females were perfused with saline and 4% paraformaldehyde. The brain was extracted from each female and the percentage of olfactory bulb removed was evaluated. Animals with less than 85% of their olfactory bulb ablated or any neocortex damage were not included for statistical analysis (see Fig. 1).

2.3. Olfactory occlusion

The olfactory occlusion (OOc+) procedure consisted of inserting a 23.65 mm long platinum-cured silicone tubing (i.d. 0.025 mm, o.d. 0.647; Harvard Apparatus, NP 72–1044) into the nasal cavity through the nostril [52]. The tube was covered with a thin layer of lidocane gel and was guided through the nasal cavity into the opening of the throat with wire in the middle of the tube. The wire then was carefully pulled out, leaving the tube securely in the cavity. This procedure was repeated for both nasal passages. The females were given 6 days of recovery. The sham occlusion (OOc−) procedure was identical, except that the tube was taken out immediately after placement. Finally, the sham operated females were only anesthetized.

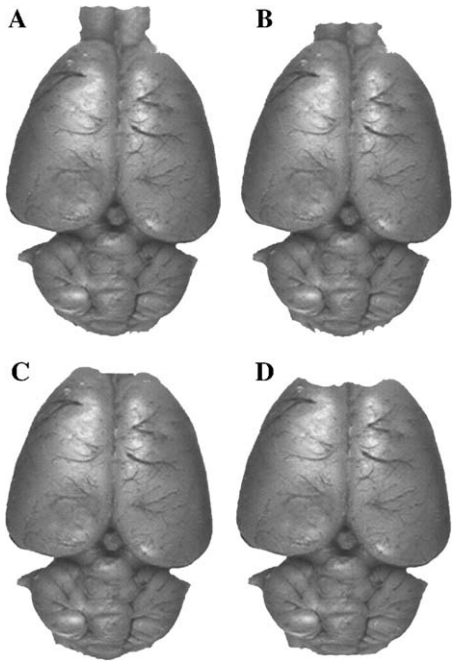

Fig. 1. Pictorial representation of: (A) 50%, (B) 85%, and (C) 100% ablation of the olfactory bulb; and (D) neocortex damage. Pictures B and C represent acceptable olfactory damage in the present experiments.