



Previous sexual experience alters the display of paced mating behavior in female rats



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ABSTRACT

The present study tested whether the display of paced mating behavior in female rats over four weekly tests is affected by sexual experience and whether test parameters, i.e., ending the test based on time or number of stimulations received, influence behavioral changes. In Experiment 1A rats with nonpaced sexual experience returned to the male more quickly overall compared to sexually naïve rats in a 30-min test of paced mating behavior. In Experiment 1B, rats received four weekly 30-min tests with one, different, male rat partner each week. Over the four tests, rats returned to the male significantly more quickly after intromissions, but significantly more slowly after ejaculations. Experiment 2A tested whether sexual experience would influence paced mating behavior in tests with a 15-intromission end criterion and the male replaced after ejaculation. Rats tested weekly under 15-intromission test conditions returned to the male significantly more quickly after intromissions, but no behavioral change was observed after ejaculations. When those same rats were given a 30-min test of paced mating behavior (Experiment 2B), they returned to the male significantly more slowly after ejaculations. Collectively, these data show that sexual experience influences the display of paced mating behavior in female rats and that the test parameters interact with sexual experience to influence the nature of the changes. Sexual experience may facilitate behaviors that promote reproductive success in female rats.

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Introduction

During a mating interaction, male and female rats engage in a complex sequence of events involving highly stereotyped, sex-specific behaviors (Agmo, 1999; Pfaff and Agmo, 2002). In the wild, and when tested in laboratory conditions that enable the female to escape from the male rat, female rats regulate the temporal pattern of the mating encounter through a series of approach and withdrawal behaviors from the male rat, termed paced mating behavior (Bermant, 1961; Erskine, 1989; McClintock and Adler, 1978; Peirce and Nuttall, 1961). In contrast, in standard, nonpaced laboratory conditions the male rat largely controls the timing of the mating interaction because the tests occur in small, undivided enclosures (Agmo et al., 2004). Behaviors exhibited by the female rat, including the latency to return to the male after a sexual stimulation (contact-return latency) and the likelihood of withdrawal from the male compartment after a sexual stimulation (percentage of exits), are proportional to the intensity of the preceding mating stimulation (mount < intromission < ejaculation) (Erskine, 1989). Paced, relative to nonpaced, mating leads to longer intervals between intromissions and durations of intromissions, enhances

dopamine release and Fos expression in several mating-relevant nuclei, more effectively induces pregnancy/pseudopregnancy and increases litter size (Blaustein and Erskine, 2002; Coopersmith and Erskine, 1994; Coopersmith et al., 1996; Erskine, 1989; Erskine and Hanrahan, 1997; Erskine et al., 1989, 2004; Kornberg and Erskine, 1994; Mermelstein and Becker, 1995). Thus, the pattern of sexual stimulations received during paced mating triggers a different neuroendocrine response in female rats than nonpaced mating behavior and increases the likelihood of reproductive success.

Sexual experience, operationally defined as the receipt of vaginocervical stimulation (VCS), clearly affects subsequent paced mating behavior within the same mating interaction; inter-intromission intervals and contact-return latencies to intromission and ejaculation progressively lengthen while fewer solicitation and more rejection behaviors are exhibited as the female rat receives more VCS (Agmo et al., 2004; Blaustein and Erskine, 2002; Coopersmith et al., 1996; Yang and Clemens, 1996, 1997, 1998). However, percentage of exits and levels of receptivity do not vary over the course of a mating interaction involving multiple ejaculatory series (Agmo et al., 2004; Coopersmith et al., 1996; Yang and Clemens, 1996). Thus, sexual experience has short-term effects on some, but not all, measures of paced mating behavior within a single mating interaction.

The role of previous sexual experience on paced mating behavior displayed during subsequent mating interactions is less well understood. Several studies report that paced mating behavior is spontaneously and

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consistently displayed, whether rats are sexually naïve or have paced or nonpaced mating experience (Erskine, 1985; Erskine, 1989; Krieger et al., 1976; Yang and Clemens, 1997). Nonetheless, sexual experience in general has been shown to influence female rat preference for a male or female sexual partner (Woodson et al., 2002; de Jonge et al., 1987; c.f. Clark et al., 2004), discrimination between sexual and nonsexual partners (Nofrey and Ettenberg, 2008), display of female–male mounting behavior (Afonso and Pfaus, 2006), neurogenesis in the olfactory bulb (Arzate et al., 2012) and Fos expression in MeAD, mPOA and NAcc core (Hosokawa and Chiba, 2007). Moreover, female rats with sexual experience do not show a conditioned place preference for clitoral stimulation whereas sexually naïve rats do (Parada et al., 2013). Sexual experience in female hamsters affects postural adjustments that improve male intromission rate during mounting, and enhance dopamine release, dendritic spine densities, Fos, and delta-FosB expression in the nucleus accumbens (for review, see Meisel and Mullins, 2006). Recently, our laboratory observed that in weekly 30-min tests of paced mating behavior female rats with sexual experience returned to the male rat more slowly after receiving ejaculations (Meerts et al., 2012) over repeated tests. These reports indicate that some facets of female rodent mating behavior and underlying neural circuitry are modulated by sexual experience. Here, we tested whether the display of paced mating behavior is also affected by sexual experience.

Although laboratory tests of paced mating behavior all enable the female rat to control sexual interaction with the male rat, the specific parameters of the tests differ between studies. In particular, female rats may mate with one (Coria-Avila et al., 2006, 2008; Guarraci and Benson, 2005; Meerts and Clark, 2007; Parada et al., 2013) or several males (Coopersmith et al., 1996; Guarraci et al., 2004; Meerts and Clark, 2007) during the course of a test. The criterion for ending tests also varies; some tests conclude after a period of time (Coria-Avila et al., 2006, 2008; Holder and Mong, 2010; Parada et al., 2013) whereas others conclude based on the number or type of sexual stimulations received (Erskine, 1985; Frye et al., 2007; Guarraci and Benson, 2005; Guarraci et al., 2004; Meerts and Clark, 2007). Little is known about the variations in the display of paced mating behavior under these different test parameters.

The present series of experiments was designed to answer two main questions: 1) does the nature of sexual experience (nonpaced or paced) affect the display of paced mating behavior and 2) do test parameters differently affect changes in paced mating behavior due to sexual experience? Experiment 1 demonstrates that in 30-min tests of paced mating behavior with a different male partner each week, rats with nonpaced mating experience return to the male more quickly overall after receiving sexual stimulation compared to sexually naïve rats (Experiment 1A) whereas rats with paced mating experience return more quickly after intromissions but more slowly after ejaculations (Experiment 1B). Because the altered display of paced mating behavior in rats with sexual experience differed from previous reports (Erskine, 1985; Erskine, 1989; Krieger et al., 1976; Yang and Clemens, 1997) we hypothesized that the changes might be due to different test parameters. Tests of paced mating behavior can be ended after a period of time, as in Experiment 1, or based on a receipt of a set number of mating stimulations (Erskine, 1985; Guarraci et al., 2004; Meerts and Clark, 2007). Therefore, Experiment 2 tested whether sexual experience in weekly 15-intromission paced mating tests with multiple male rats affects the display of paced mating behavior. Female rats showed changes in contact-return latency to intromission, but not to ejaculation (Experiment 2A) across the four 15-intromission tests but when those same rats received an additional 30-min test with a single male they exhibited significantly longer contact-return latency to ejaculation (Experiment 2B). These results bolster the idea that sexual experience alters the display of mating behavior in female rats and that test parameters are a factor in the display of paced mating behavior.

Material and methods

Subjects

Thirty-six sexually naïve female Long–Evans rats weighing approximately 200 g were obtained from Harlan Laboratories (Indianapolis, IN). Rats were pair-housed in clear polycarbonate cages in a light–(12:12-h light/dark cycle, lights off at 1100) and temperature-controlled vivarium. Commercial rat food pellets and water were freely available. Rats were ovariectomized under ketamine/xylazine anesthesia (50 mg/kg; Henry Schein, Indianapolis, IN) 7–10 days before the start of behavioral testing. All female rats received 10 µg estradiol benzoate (EB, Sigma, St. Louis, MO) 48 h and 1 mg progesterone (P, Sigma) 4 h, prior to test day. Hormones were administered sc in a sesame oil vehicle. Sexually experienced male Long–Evans rats, aged approximately seven months, served as stimulus rats. All testing was performed during the dark period of the light cycle under dim red lighting. The Institutional Animal Care and Use Committee at Carleton College approved the use of rats in these studies and all procedures were conducted in accordance with NIH guidelines.

Nonpaced mating behavior

Nonpaced mating occurred in undivided clear Plexiglas chambers (39.4 × 22.9 × 31.1 cm high) with pine shavings covering the floor. Female rats acclimated to a chamber for 5 min, and then the test began when a sexually vigorous male was introduced to the chamber. The test concluded once the female received a total of 10 intromissions. All rats received at least one ejaculation during the test. When a male rat ejaculated before achieving 10 intromissions, the rat was removed, and then a new male was introduced.

Paced mating behavior

Tests of paced mating occurred in clear Plexiglas arenas partitioned by a pair of removable dividers (36.5 × 31.7 cm) into three compartments (each 37.5 wide × 37.5 long × 32 cm high) with pine shavings covering the floor. One divider was opaque and solid, and the other divider was clear with a five-cm hole in each bottom corner. Rats were exposed to the arena for 15 min on two separate occasions the week before testing began. During the exposure, experimental female rats were permitted to freely pass through the clear divider to explore both empty chambers of the arena. At different times, the male rats were trained to stay in one compartment by administering a gentle tap on the nose if they tried to pass through the divider to access a female rat lure that was able to enter and exit the male compartment.

Paced mating tests followed the procedure outlined previously (Guarraci et al., 2004). Each rat was confined to one compartment during a 5-min acclimation period immediately before the start of each test. The test began when the timer was started and the opaque divider was removed, leaving only the clear divider separating the compartments, which allowed the female rat to control visits to the male rat compartment. The criterion for ending tests was either a time limit (30-min tests, with a single male and variable number of stimulations) or a set number of intromissions (15-intromission tests, with the male replaced following ejaculation). During a test, rats mated in two of the three compartments at a given time while an opaque divider prevented access to the third compartment. For 30-min paced mating tests only two compartments were used because the female rat mated with one male during the test. After an ejaculation, mating stopped until the male recovered and resumed mounting, but the female had access to the male compartment throughout the test. For 15-intromission tests, one male rat was acclimated in each outer compartment while the female acclimated in the center. The female rat mated with one male at a time. When a female rat received an ejaculation before the 15th intromission, the experimenter waited for the female

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