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Paced mating behavior is affected by clitoral-vaginocervical lidocaine application in combination with sexual experience

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HIGHLIGHTS

- Sexual experience affects the display of paced mating behavior
- Clitoral-vaginocervical lidocaine shortens contact-return latency to ejaculation
- Rats that acquired sexual experience when untreated are not affected by lidocaine

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ABSTRACT

The present study tested the effects of lidocaine anesthetic ointment applied to the vaginocervical (Experiment 1) or clitoral-vaginocervical (Experiment 2) areas on the display of paced mating behavior over the course of five weekly tests in ovariectomized, hormone-primed, Long-Evans rats. Experiment 3 tested whether rats that acquired sexual experience without ointment application would exhibit altered paced mating behavior on a fifth test under clitoral-vaginocervical lidocaine or vehicle application. Although rats in Experiment 1 and Experiment 2 exhibited shorter contact–return latencies after intromission and reduced likelihood of leaving the male compartment following mounts and intromissions after gaining sexual experience, only rats that received clitoral-vaginocervical lidocaine exhibited altered paced mating behavior relative to vehicle. Specifically, clitoral-vaginocervical lidocaine resulted in shorter contact–return latency to ejaculation and greater percentage of time with the male. Paced mating behavior of sexually experienced rats in Experiment 3 was not disrupted when tested after clitoral-vaginocervical lidocaine treatment. Together, these studies suggest that the sensory input during repeated mating encounters affects the pattern of paced mating behavior that develops with sexual experience.

1. Introduction

Tactile stimulation received during a mating encounter influences the female rat's behavioral responses to male mounting. Flank and perineal stimulation occurs when a male rat mounts a sexually receptive female rat, inducing the lordosis posture, the dorsoflexion of the spine and deflection of the tail to the side to facilitate penile intromission [1–4]. Lordosis is initially intensified by vaginocervical stimulation (VCS), but lordosis responsiveness decreases with repeated VCS received during the course of the mating bout, as does the display of proceptive behaviors, such as hop/darts and ear wiggling [4–7]. Genitosensory input also affects the display of paced mating behavior, which is the pattern of approach and withdrawal from a sexually vigorous male exhibited by female rats when tested in an enclosure that enables them to control proximity to the male [8]. The receipt of more intense sexual stimulations (mount < intromission < ejaculation) leads to longer contact–return latencies and increases the likelihood of withdrawal [9]. Somatosensory input during mating influences a number of aspects of female rat sexual behavior.

Pelvic thrusting of the male rat during mating stimulates densely innervated perivaginal surfaces, including the perineum, clitoris, vagina, and cervix [1,10–12]. Researchers have identified the nerves activated by stimulation of specific parts of the reproductive tract and explored the contribution of sensory input relayed by these nerves in the display of paced mating behavior. The pelvic nerve, which innervates the vaginal canal, distal end of the cervix, and midline perineal skin between the vaginal opening and anus [13–16], transmits genitosensory information critical for the display of paced mating behavior. Transection of the pelvic nerve leads to shorter contact–return latencies after intromissions [17,18] impaired ability to discriminate between mounts and intromissions [19], and more time spent with the male [17,20]. In contrast, paced mating behavior is not disrupted by transection of the pudendal nerve,

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which innervates the clitoris and perineum [15,16,19,21,22] or the hypogastric nerve, which innervates the proximal end of the cervix and uterine horns [16,17,19]. Despite data illuminating the role of the genitosensory nerves in the display of paced mating behavior, current understanding of the influence of specific genital regions on the approach and withdrawal behavior observed during mating is limited.

The application of the topical anesthetic lidocaine to reduce genital sensation has had mixed success in identifying the contributions of certain genital areas to the display of paced mating behavior. Some studies report altered paced mating behavior in lidocaine-treated female rats compared to controls [23,24], whereas others do not [20,25,26]. Two features – repeated testing with lidocaine treatment and clitoral application of lidocaine – appear to be shared aspects of studies reporting significant lidocaine effects on mating behavior. Rats that received six total tests, alternating between lidocaine and control treatment, showed shorter contact–return latencies to mounts, intromissions, and ejaculations in lidocaine tests compared to control tests [24]. Bermant and Westbrook [24] swabbed lidocaine paste in and around the vagina, so whether treatment was deliberately applied to the clitoris is unclear, but probable. Rats that received precise injections of lidocaine into the clitoral sheath under anesthesia, without targeting other genital regions, spent less time with the male and showed a trend toward longer contact–return latencies after ejaculation on the fifth, but not the first, mating test [23]. In contrast, studies report no behavioral differences in rats that experienced only one sexual interaction following lidocaine application to the vaginocervical, but not the clitoral, region [20,25,26]. Together, the evidence indicates that repeated mating encounters and sensory information from the clitoris may be key components to detecting lidocaine effects on paced mating behavior.

A number of studies support the idea that sexual experiences, i.e., repeated mating, particularly early copulatory experiences, shape the sexual behaviors and responses expressed in subsequent mating interactions, which are fairly stable once established [27–32]. For example, rats can develop conditioned preferences for a place or partner associated with previous mating experience [27,30,31,33], the androgen receptor modulator LGD-3303 enhances preference for a male in sexually experienced but not naïve female rats [34], and hamsters with sexual experience make pelvic adjustments that aid the male in achieving intromission during a mount [35]. Female rats with multiple paced mating experiences return to the male more quickly after intromission on later tests compared to earlier tests [36]. In addition, contact–return to ejaculation lengthens and the percent of time spent with the male increases when a female rat continues to have access to the male during his post-ejaculatory period [36,37]. Male rat sexual behavior is difficult to disrupt in sexually experienced rats even if the penis is anesthetized with lidocaine [27,38]. Thus, it appears that sexual experience, and the specifics of that experience, influence behavior displayed during subsequent mating encounters.

Although studies on female sexual response have predominantly focused on vaginal blood flow in humans [39] and vaginocervical stimulation in rats [40], there is a growing recognition of the importance of the clitoris for female sexual function and behavior in both humans and rats [41–43]. Stroking the external clitoris at 5 s intervals with a lubricated paintbrush is rewarding to sexually naïve female rats [44,45], as is the orgasm that results from clitoral stimulation in humans [43,46,47]. Clitoral stimulation given to rats at 5 s intervals induces a distinct pattern of Fos expression in the medial preoptic area [45], leads to fewer solicitation behaviors directed toward the male, and increases the rate of pregnancy [48]. However, sexual experience interferes with the development of a conditioned place preference for clitoral stimulation, highlighting that familiarity with all aspects of mating influences whether particular genital stimulation is rewarding or not [49].

Given the indications from the literature that sexual experience and clitoral stimulation affect female rat mating behavior, we tested whether paced mating behavior would be altered in rats that received sexual experience with lidocaine applied to the vagina and cervix (Experiment 1) or clitoris, vagina, and cervix (Experiment 2). Finally, we tested whether simply being sexually experienced would be sufficient to induce changes in paced mating when treated with clitoral-vaginocervical lidocaine (Experiment 3). Only repeated mating under clitoral-vaginocervical lidocaine treatment altered the display of paced mating behavior.

2. Materials and methods

2.1. Subjects

Sexually naïve adult female Long-Evans rats weighing approximately 200 g, were obtained from Harlan (Indianapolis, IN). Rats were pair-housed in a light- (12:12, lights off at 1100 h) and temperature-controlled vivarium. Water and food were available ad libitum. Female rats were ovariectomized under ketamine/xylazine anesthesia (50 mg/kg, Butler Schein, Indianapolis, IN) 7–10 days before testing began. Sexually experienced male Long-Evans rats, 3–6 months of age, were used as stimulus animals. Experimental rats received subcutaneous injections of 10 μg estradiol benzoate (Sigma, St. Louis, MO) 48 h, and 1 mg progesterone (Sigma) 4 h prior to testing. Hormones were dissolved in reagent grade sesame oil vehicle (Sigma). Application of vehicle (petroleum jelly, Vaseline, Unilever) or lidocaine ointment (5%, Butler Schein) occurred as described below. Behavioral testing occurred under dim red illumination. The Institutional Animal Care Use Committee at Carleton College approved the use of rats in these studies, and all procedures were conducted in accordance with NIH guidelines.

2.2. Paced mating behavior

Rats were exposed to the chambers for two separate 15 min periods the week prior to testing. Tests of paced mating behavior were conducted as previously described [36] in clear Plexiglas chambers ($75 \times 37.5 \times 31.7$ high) with wood shavings covering the floor. Each chamber was divided into two equally sized compartments by a clear Plexiglas divider (36.5×31.7 cm) containing 5 cm holes in each bottom corner. The holes in the clear divider permitted the female rats to approach and withdraw from the male rat that was trained to not cross the divider. A solid, opaque divider was placed next to the clear divider to separate the rats prior to the start of the test.

After rats acclimated to the chamber for 5 min, the experimenter began the test by raising the opaque divider, permitting the female rat access to the male rat. After an ejaculation, male rats enter a post-ejaculatory recovery period when mating ceases; neither rat was removed from the chamber during this time. The test ended after 30 min. If a female rat received a mating stimulation and exited the male compartment during the 30-min test period, the experimenter waited to record the contact–return latency even if the test extended past 30 min. Experimental female rats mated with different males each week to prevent development of a conditioned partner preference [50].

Experimenters recorded the type and timing of entries/exits, mounts, intromissions and ejaculations along with sexual receptivity (lordosis quotient (LQ) defined as the number of lordosis responses of 2 or 3 divided by the number of stimulations multiplied by 100) [51]. The following measures were calculated for analysis: (1) contact–return latency, defined as the length of time between receipt of a sexual stimulation (i.e., mount, intromission or ejaculation) and the female rat's return to the male compartment; (2) percentage of exits, defined as the rate of withdrawal from the male compartment following each type of sexual stimulation; (3) interintromission interval, the mean time between intromissions, not including post-ejaculatory intervals; and (4) the percentage of test time spent in the male compartment.