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Reduced proceptivity and sex-motivated behaviors in the female rat after repeated copulation in paced and non-paced mating: Effect of changing the male

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HIGHLIGHTS

- Proceptivity and receptivity were studied along continuous paced and non-paced mating.
- Sexual motivation decreased after repeated mating suggesting sexual satiety.
- In pacing an unknown male re-stimulated sexual motivation suggesting a *Coolidge effect*.
- Lordosis was kept maximal along the 3 h of constant mating.

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ABSTRACT

The mating inhibition after repeated copulation (sexual satiety) and its re-commencement after changing the sexually active partner (*Coolidge effect*) are well recognized phenomena in males, but their occurrence in females is little explored. These two phenomena were compared in conditions when the female regulates copulation timing (pacing) and under non-paced mating. Female rats selected in proestrus copulated incessantly for 3 h with two different partners (for 90 min each), both of them sexually active and unknown for the female. During the entire test we recorded the hop/dart and ear wiggling frequencies and the lordosis quotient. In the pacing test we also registered the percentage of exits and the return latencies after mounts, intromissions and ejaculation within each copulatory series, the mean time the female spent in the neutral chamber and the number of crossings. In the non-paced mating situation there was a reduction in ear wiggling and hop/darting frequencies after 3 h of constant copulation. In the paced mating condition, also by the end of the test, the female spent more time in the neutral compartment and showed fewer crossings to the male's zone. Only when the female regulated mating, the change of the male provoked an increased hop/darting frequency accompanied by a reduced percentage of exits from the male's chamber after an intromission and in the time in the neutral compartment. These changes were not associated with alterations in receptivity, which was maximal along the test. Data are discussed by comparing the mating conditions and the sex differences in the effect of repeated copulation and partner replacement.

1. Introduction

Males of many mammalian species, including humans, show sexual satiety that is defined as the long term inhibition of mating behavior produced after some ejaculations with a given female [1,2]. Sexually satiated males do not stop copulating due to physical exhaustion because their spontaneous ambulatory behavior is normal [3]. Most data indicate that the inhibition of copulation, characteristic of sexual satiety, results from a reduced sexual motivation [4]. Thus, shortly after the male ceases mating with a given female, if it is changed for another sexually-receptive one, the male restarts mating [1,5]. This phenomenon named the *Coolidge effect*, is generalized to males of various species ranging from bugs to mammals, and denotes the importance of a motivational component underlying sexual satiety [2]. This conclusion receives further support from the observation that as males approach sexual satiety the motivational aspects of the mating pattern, as the length of the postejaculatory interval, drastically increase [3,6,7]. In the female, there is a short period of reduced responsivity after the male has intromitted or ejaculated into the female [8,9]. In general, it is assumed that female rats stop mating due to the end of the sexually receptive phase, when the endocrine profile is no longer optimal [10–12]. In addition, vaginal stimulation as a result of repeated

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intromissions and ejaculations decreases receptivity and increases male's rejections by the female rat [13]. Furthermore, although controversial ([14] vs. 15–17) intensive mounting, even without intromissions, may also decrease lordosis behavior.

In female rodents, receptivity or lordosis refers to the dorsiflexion reflex posture with the consequent pelvic elevation that allows the penis entrance into the vagina [18–20]. Usually, the occurrence of this reflex is preceded by proceptivity which comprises a series of species-typical behaviors that have the aim of arousing and soliciting the male to mate. In the rat they include ear wiggling (rapid alternating movements of the head that provokes vibrations of the ears), hop (a short leap with the female landing on all four paws followed by the assumption of a crouching posture) and dart (a run of several steps abruptly terminated by the assumption of a crouching posture) [21]. Beach defined proceptive behaviors as those which involved the "female initiative" to initiate a sexual interaction [22]; implicit in this definition is the recognition that solicitation behaviors reflect the appetitive aspect of sexual behavior. Thus, behaviors such as hopping, darting and ear wiggling have been used as an index of feminine sexual motivation [9,19,23].

Few studies have analyzed sexual satiety and the *Coolidge effect* in females. Lisk and Baron [24] showed that in the female hamster there is a lordosis inhibition after continuous mating with the same male. Such inhibition was considered a reflection of sexual satiety and was reversed when a new sexual partner was presented, demonstrating the occurrence of the female *Coolidge effect*, although the lordosis duration with the second partner was shorter than that displayed with the first one. This study, as others in rats and hamsters [13,14,25,26], analyzed the effect of continuous mating on the lordosis reflex, even though, as in males, the inhibitory actions of repeated copulation and the *Coolidge effect* most likely would reduce the motivational components of the female sexual response.

The observation of rat sexual behavior under semi-natural conditions has revealed that most sexual encounters are initiated by the female. Additionally, if the female can regulate sexual stimulation – as in pacing – the rate of copulation is slower, because the intervals between intromissions and after ejaculation are longer than those in the non paced-mating condition [27]. In view of these observations, some researchers have decided to study the rat sexual response under laboratory mating arenas that are divided by a wall with a small opening, through which the female, but not the male, can easily pass from one chamber to the other [27–29]. Under such circumstances an interesting interaction occurs: after an intromission or an ejaculation the female rapidly leaves the male compartment through the hole, but returns some minutes later [30]. In this way the female determines the timing of copulation. This procedure is known as paced mating or pacing [23,27,28,31]. It has been demonstrated that copulation under this condition is rewarding for the female [28,29,32], while it is aversive when the male regulates its timing, as under most laboratory conditions where the couple is simply placed in single chambered observation cages (non-paced mating) [32]. In the pacing test, in addition, the return latencies to the male's cage after a mount, an intromission or an ejaculation denote the female's motivation to continue copulating, while the percentage of exits after each male sexual behavioral parameter is related with the sensory stimulation the female has received [23,28,31,33]. According to previous reports [27,30,31,34] the contact-return latency and percentage of exits from the male rat compartment have been found to correlate positively with the type of sexual stimulation received. Thus, the shortest contact return latency to the male rat occurs after a mount, an intermediate interval occurs after an intromission, and the longest interval occurs after an ejaculation. Similarly, the female rat is more likely to leave the male rat compartment after an intromission than after a mount, and the greatest likelihood of an exit occurs after an ejaculation. Finally, seeking proximity or avoiding the sexually active male (measured as the mean time in the male or neutral chamber, respectively) reflects the motivation or refusal of the female to interact with the male [35–37].

The objectives of the present study were to analyze if in the female rat there were changes in receptive and proceptive behaviors along 3 h of continuous copulation, comparing the time-course variations between the non-paced and pacing conditions. It was also determined, in both conditions, if changing the male partner would alter the levels of female sexual activity. We hypothesize that after repeated copulation there would be a reduction in proceptive behaviors — particularly in the copulation condition that is aversive for the female (non-paced mating), and that the male's change would re-stimulate the display of proceptivity and other sex motivation-related behaviors. Female rats were selected in proestrus since it has been demonstrated that in this phase, sexual behavior is optimally presented in non-paced [20] and paced-mating [33] conditions. Moreover, proestrus females were used because Zipse et al. [33] demonstrated that in pacing, ovariectomized females treated with estradiol plus progesterone showed higher return latencies after a mount or an intromission than naturally cycling females in proestrus.

2. Materials and methods

2.1. Animals

Young adult sexually experienced male (300–450 g) and sexually naïve female (200–270 g) Wistar rats were used in this study. All the animals were kept in general laboratory conditions and were housed in groups of 6 per cage within a temperature controlled room under reversed 12:12-h light–dark cycle, starting the light phase at 22:00 h. Food and water were available ad libitum. All procedures were done in accordance with the guidelines of the Laws and Codes of México (Seventh Title of the Regulations of the General Law of Health Regarding Health Research) [38] and also followed the guidelines of the NIH for the use of animals. All the procedures were approved by the Institutional Animal Care and Use Committee.

2.2. Apparatus

Sexual behavior under the paced mating condition was observed in a transparent acrylic arena (61 cm long × 30.5 wide × 45 cm high) divided into two equally sized compartments, which had two 4.0 cm holes in each bottom corner. Through these holes the female, but not the male, may freely moved from one compartment to another. This design was similar to those used elsewhere [27,30,32].

Non-paced mating behavior was observed in a transparent, cylindrical acrylic arena (52 cm diameter × 45 cm high).

2.3. Behavioral mating test

All experimental procedures were done in females in early proestrus, which was identified by the presence of round large cells in the vaginal cytology [39], during the first 4 h of the dark part of the cycle. Two groups of females in proestrus were exposed to continuous copulation under either non-paced mating ($n = 9$) or pacing ($n = 11$). In the non-paced mating condition the female was left in the cylinder for 5 min before the male introduction. In the pacing test, each female was placed for 5 min into the left compartment of the cage, thereafter an experienced vigorous male was placed into the right compartment. For both conditions ad libitum mating was allowed for 90 min with a first male. This period was chosen because previous reports showed that this is the minimum time a male copulates continuously before attaining sexual satiety [2]. After 90 min of constant mating the male was replaced with another sexually active male and ad libitum copulation was permitted for another 90 min, after which the test was ended. Thus, in both conditions a female copulated continuously for 3 h with two different partners, both of them sexually active and unknown for the female. All tests were videotaped for further analyses.