



Sociosexual behaviors during the transition from non-receptivity to receptivity in rats housed in a seminatural environment



Xi Chu*, Anders Ågmo

Department of Psychology, University of Tromsø, Norway

ARTICLE INFO

Article history:

Received 20 October 2014

Received in revised form 4 December 2014

Accepted 5 January 2015

Available online 6 January 2015

Keywords:

Seminatural environment

Sociosexual behavior

Behavioral estrus

Transition

Rat

ABSTRACT

Female behavioral estrus is defined as the period between the first lordosis displayed during the estrus cycle to the lordosis that is not followed by another within 60 min. In a seminatural environment, an estrous female consistently displays lordosis in response to every male mount from the start of behavioral estrus until the end of it. This means that the female suddenly changes from a state of complete non-receptivity to full receptivity and then abruptly changes back to non-receptivity. It is unlikely that these abrupt changes are caused by sudden changes in serum concentration of ovarian steroids. Here, we present the results of a detailed study of sociosexual behaviors during the transition from non-receptivity to receptivity and vice versa. The frequency of male mounting was close to zero before and after estrus. It remained at a constant, high level throughout estrus. Female paracopulatory behavior and male pursuit of the female increased drastically from a very low level before estrus to a high level during estrus. They returned to low levels immediately after estrus. None of the many other behavior patterns registered changed during the transitions. It appears that the sudden increase in male pursuit and female paracopulatory behavior can explain the beginning of behavioral estrus, and their equally sudden disappearance causes it to end. The neurochemical mechanisms behind these almost instantaneous behavioral changes are unknown.

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1. Introduction

In a strict sense, sexual behavior in female rats consists of assuming a lordosis posture in response to a male's mount. This posture is characterized by a concave flexion of the back, extension of the neck, elevation of the hindquarters and rump and deflection of the tail to one side. A female displaying this behavior in response to male mounting is frequently described as sexually receptive. In addition to lordosis, a receptive female may display some other stereotyped motor patterns. These include running, darting, hopping, and ear wiggling (Beach, 1976; Erskine, 1989). They are often grouped together under the labels proceptive behavior or solicitation. However, since the function of these behaviors is somewhat unclear, it has been suggested that a more appropriate label would be paracopulatory behaviors (Blaustein and Erskine, 2002; Blaustein et al., 2009).

Ovarian steroids are necessary for the display of female rat sexual behaviors. Ovariectomized females never display lordosis

or paracopulatory behavior, and estrogen treatment can restore these behaviors to the level seen in intact females (e.g., Boling and Blandau, 1939; Meyerson, 1964; Zipse et al., 2000). Progesterone, given several hours after estradiol, enhances the response to estradiol (e.g., Beach, 1942), and is believed to be particularly important for the stimulation of paracopulatory behaviors (Fadem et al., 1979; Frye et al., 1998). The female rat's response to estrogen treatment is dose dependent. At low doses, the female displays lordosis in response to only some mounts, and she may also repeatedly reject the mounting male. With increasing estrogen dose, the proportion of mounts activating lordosis also increases and the frequency of rejections gets reduced (e.g., Spiteri and Ågmo, 2006). Eventually the female will display lordosis to every mount. In intact females, the onset of sexual receptivity is gradual, in the sense that only a fraction of the male's mounts activates lordosis (e.g., Madlafousek and Hlinak, 1978). This is also the case at the end of the period of sexual receptivity. Only for a few hours in the middle of this period the female responds with lordosis to all male mounts (e.g., Hardy, 1972). When manual stimulation is used to activate lordosis, it appears that the stimulation needs to be more intense at the beginning and the end of the period of sexual receptivity than in the middle of this period (Blandau et al., 1941). The observations concerning the gradual appearance and disappearance of the lordosis

* Corresponding author at: Department of Psychology, University of Tromsø, Huginbakken 32, 9037 Tromsø, Norway. Tel.: +47 77 64 92 13; fax: +47 77 64 52 91.

E-mail addresses: xi.chu@uit.no (X. Chu), andersa@psyk.uit.no (A. Ågmo).

response coincide with data on changes in serum concentrations of the ovarian hormones, particularly progesterone (Södersten and Eneroth, 1981). There is a gradual increase in serum concentration of progesterone, which precedes the appearance of sexual behavior with a few hours. Interestingly, the end of receptivity seems to be unrelated to reduced serum concentration of ovarian hormones (Södersten and Eneroth, 1982).

The gradual increase in the propensity to respond with lordosis either to a male's mounts or to the experimenter's fingers has been established in experiments in which the females were subjected to short tests at regular intervals varying from 30 min to 6 h. When males were used for activating lordosis, they were preselected for intense copulatory behavior, and a male failing to mount was immediately replaced with a more vigorous one. When manual stimulation was employed, the experimenter assured that it was appropriately applied, regardless of whether the female offered resistance or not. These testing procedures are quite different from what occurs in the rat's natural context in which males and females share the same habitat, sometimes even the same burrow (Calhoun, 1962). It appears that the males rarely try to mate with non-receptive females, whereas a number of males pursue and copulate with any sexually receptive female (Robitaille and Bouvet, 1976). Likewise, when females are non-receptive, they resist the rare mounting attempts from males, thereby avoiding the receipt of the tactile stimulation needed for activation of lordosis. The forced sexual interaction occurring in the short tests mentioned above seems to be of little ecological relevance, and might not offer an appropriate description of the female's sexual dealings with males during the estrus cycle.

We observed groups of intact, cycling females housed together with males in a seminatural environment for several days. These females did not show a gradual increase in responsiveness to the males' mounts. As soon as the female entered behavioral estrus (defined as the period between the first lordosis displayed and the lordosis that was not followed by another one within 60 min) she responded with lordosis to every mount until the end of estrus (Chu and Ágmo, 2014a). Thus, instead of a gradual increase in lordosis responses at the beginning of estrus and a gradual decline at the end of estrus, the females in the seminatural environment suddenly changed from complete non-receptivity to full receptivity,

and then from full receptivity to non-receptivity. This observation suggests that the gradual changes in serum concentration of ovarian hormones are not associated with any gradual changes in sexual responsiveness at the beginning and end of behavioral estrus in a seminatural environment. Instead it seems that a non-receptive female is not attractive to males, and she displays no lordosis simply because she is not mounted before being fully receptive. In support of this notion there are data suggesting that female attractivity requires more ovarian hormones than the activation of receptivity (Albert et al., 1991). Consequently, as soon as a female is able to attract a male, she is ready for performing lordosis in response to all his mounts. This, somehow, would mean that the duration of behavioral estrus in a seminatural environment is determined by the males' responses to the female as much as or more than the female's responses to the male.

The purpose of the present study was to analyze changes in female and male sociosexual behaviors around the transition from non-receptivity to receptivity and vice versa. Even though such an analysis does not directly enhance our understanding of the neurobiological mechanisms behind these changes, it would make it possible to determine the relative importance of male and female behavior.

2. Method

2.1. Subjects

Male (300 g upon arrival) and female (250 g upon arrival) Wistar rats were obtained from Charles River WIGA (Sulzfeld, Germany). Animals were housed in same sex pairs in Macrolon® IV cages in a room with controlled temperature ($21 \pm 1^\circ\text{C}$) and humidity ($55 \pm 10\%$) and a 12:12 h light/dark cycle (lights on 0800). Commercial rat pellets and tap water were provided ad libitum.

2.2. Apparatus

The seminatural environment used in this study has been described in detail elsewhere (Chu & Ágmo, 2014a,b). Briefly, it measured 2.8×2.4 m and consisted of a complex burrow system and an open area (see Fig. 1). There were four small openings

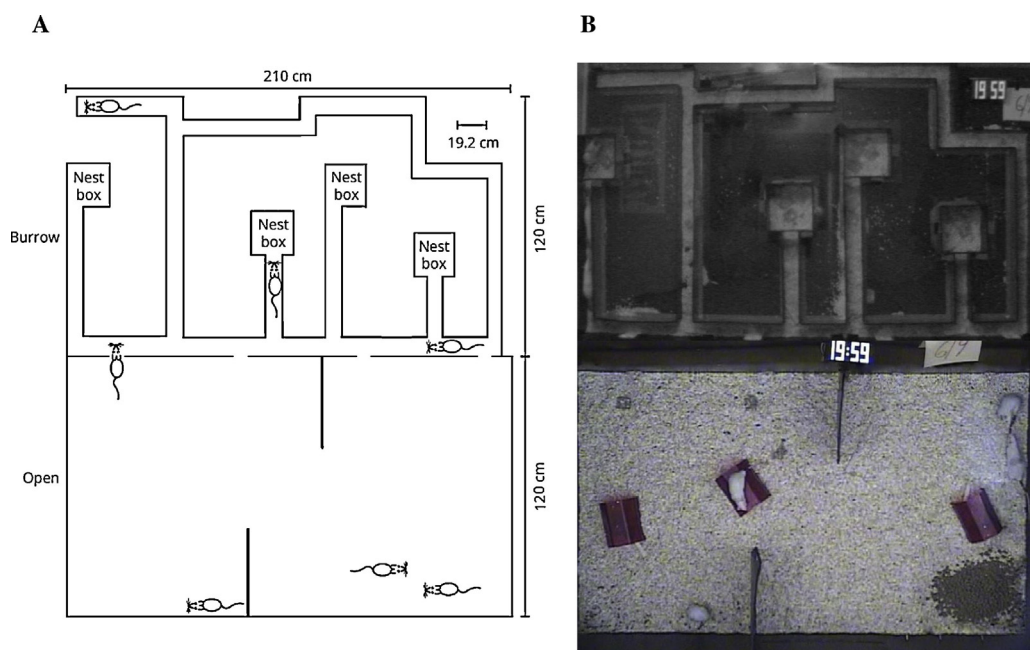


Fig. 1. Schematic diagram (A) and photograph (B) of the seminatural environment used in this study. For further details, see text.

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