Paper 2

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

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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.

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

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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 Ågmo, 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 ± 1 °C) and humidity (55 ± 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 & Ågmo, 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

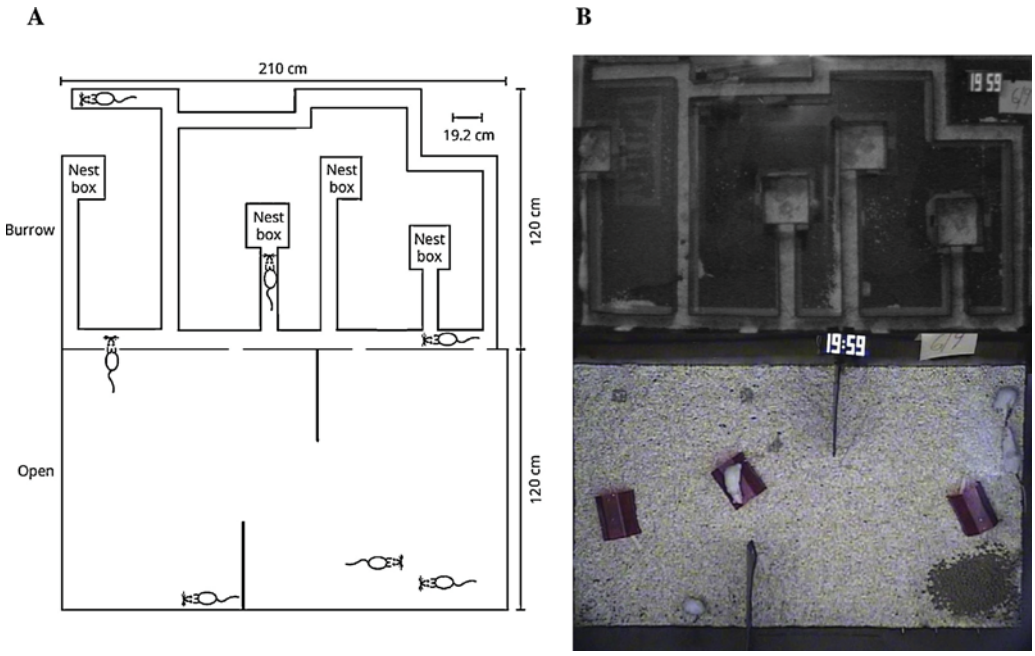

Fig. 1. Schematic diagram (A) and photograph (B) of the seminatural environment used in this study. For further details, see text.

Table 1
Description of registered behaviors (Chu and Ågmo, 2014a,b).

Male and female behavior	Data collected as	Behavior description
Sniffing	Duration and number	The rat places its snout close to any body part, except the anogenital region, of another rat while its whiskers move briskly.
Anogenital sniffing	Duration and number	The rat sniffs, occasionally grooms and licks, another rats' anogenital region.
Pursuit	Duration and number	The rat runs closely behind another rat.
Nose-off	Duration and number	Facing another rat either standing on 4 legs or while rearing; it includes boxing and teeth showing.
Flee	Number	The rat runs away from another rat after an agonistic interaction.
Male copulatory behavior		
Mount	Number	The rat stands on its hindlegs and places its forepaws on another rat's rump from behind and displays pelvic thrusting.
Female behavior		
Paracopulatory behavior	Duration and number	Approach to a male followed by runaway, often associated with hops, darts, ear wiggling.
Lordosis	Number	Female stands immobile with the back arched downward and the rump pushed upward while the tail is deflected to the side.
Rejection	Number	The rat kicks, bites or turns around against its suitor.

(8 × 8 cm) between the burrow and the open area. A light-blocking wall of extruded polyethylene foam was used to divide the room in which the environment was installed into two parts, thereby providing the possibility to vary the light intensity in the open area while maintaining the burrow in complete darkness. Video cameras were centered above the open area and the burrow, respectively.

2.3. Procedure

Before a group of animals was introduced into the seminatural environment, the floor was covered with aspen wood shavings. A few wood sticks and plastic shelter huts were provided in the open area, and nest building material was put in the nest boxes. About 3 kg of pellets were provided in a corner of the open area, and 4 water bottles were also freely available in that corner. The subjects were marked in two ways: different areas of the back were shaved and the tail was marked with different numbers of black stripes, making it easy to identify each individual subject. Both marks were clearly visible during the entire observation period. The 12:12 h light/dark cycle was preserved in the open area. During the dark phase, the intensity of the light reflected from the floor covering was about 1 lx. It was about 180 lx during the light phase. The burrow was maintained in total darkness for the rats but illuminated with infrared light for the video camera. The video recorders were activated when introducing the animals at 13:00 on day 0. Recording was then continuous for a period of 8 days. Additional procedural details can be found in Chu and Ågmo, 2014a,b.

2.4. Design

Five groups were used. Each group consisted of 4 females and 3 males. All subjects were intact and sexually naïve. Subjects in the same group came from different cages to ensure that they were unknown to each other at the beginning of observation. In the period of 8 days, each female would enter into estrus at least once. This supposition was based on the fact that most females have an estrus cycle of 4 or 5 days (Long and Evans, 1922; Nequin et al., 1979).

2.5. Behavioral observations

From the video record, we registered the behaviors defined in Table 1 during four specific periods. First we determined the moment at which a female displayed her first lordosis. This was considered as the beginning of behavioral estrus. Then we determined the moment at which a lordosis was not followed by another one within 60 min in that same female. This was considered the end of behavioral estrus. The time elapsed from the first to the last lordosis was the duration of behavioral estrus. This definition of estrus duration has been employed in our earlier studies in the seminatural environment (Chu and Ågmo, 2014a,b). It varied from 4.05 to 10.87 h, with a mean ± SEM of 7.41 ± 0.49 h. For each female, we divided the period of behavioral estrus in 20 equal intervals, meaning that each interval corresponded to 5% of estrus duration. Observations of sociosexual behaviors during the preestrus interval started at a time corresponding to 5% of the estrus length before the first lordosis. Observation was ended at 5% of estrus length following this lordosis (first estrous interval). At the end of estrus, we observed the second estrous interval, corresponding to the time from 5% of estrus length before the last lordosis until that lordosis. The postestrus interval lasted from the final lordosis until 5% of the estrus length after it (see Fig. 2 for illustration). For example, if a female had a behavioral estrus lasting for 400 min, 5% of this duration is 20 min. Thus, the preestrus interval started 20 min before the first lordosis, and the first estrus interval went from the first lordosis until 20 min after it. The last estrus interval started 20 min before the final lordosis, and the postestrus interval ended 20 min after it.

The reason for basing observation length on units of 5% of estrus duration rather than a prefixed time was that we needed to know the behavior in the initial and final parts of behavioral estrus. Since the duration of estrus varied considerably between females, a fixed time would have represented highly different proportions of estrus. After the fact, we know that this was not of any importance, because the behavioral changes occurred very close to the exact moment of transition.

2.6. Data preparation and statistics

Before analysis, the number of occurrences and/or the total duration of behaviors during an interval were divided by the actual length of the interval. Thus, behaviors were either expressed as the number of occurrences per minute or as duration (s) per minute of observation. In addition to compare the four intervals defined above, we needed to detect rapid changes in behavior around the transitions from non-receptivity to receptivity and the opposite. Therefore we divided the 8 min periods preceding and following the first and last lordosis into one minute segments. Careful examination of the data suggested that an 8 min period was sufficiently long for detecting relevant changes in behavior. At the same time, repeated measures analysis of 8 one min intervals is perfectly feasible. Only behaviors showing changes between estrus intervals were subjected to this analysis.

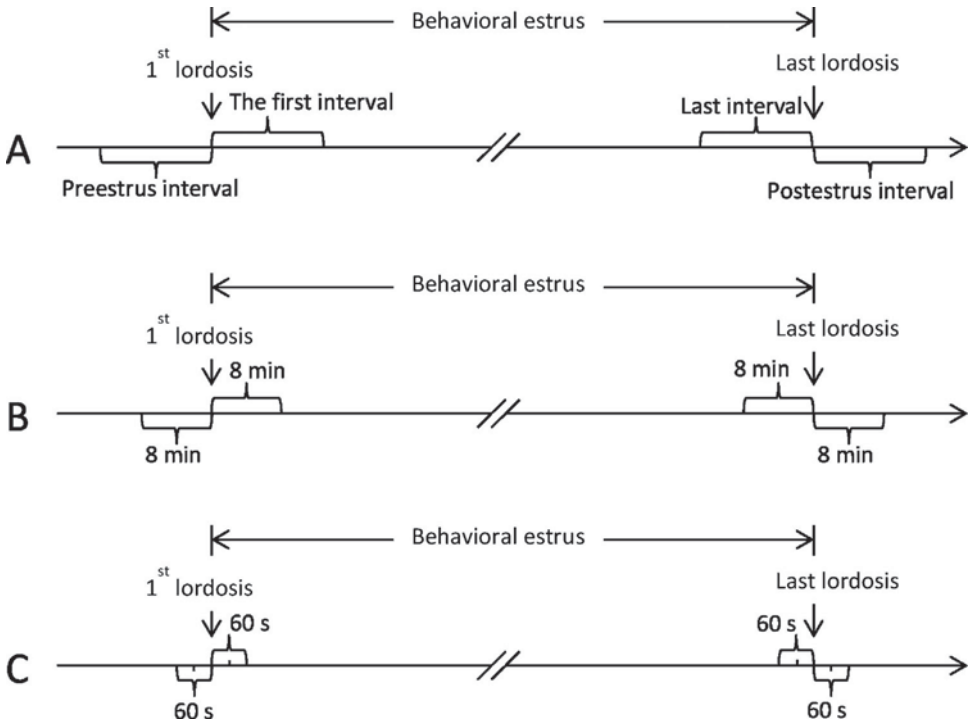

Fig. 2. Illustration of the interval, period and segment around the first and last lordosis employed in the analyses. Comparisons were conducted between (A) preestrus interval, the first estrus interval, last estrus interval, and postestrus interval, each of intervals was as long as 5% of estrus duration; (B) the 8 min period before and after the first and last lordosis, respectively; (C) the 60 s segment before and after the first and last lordosis, respectively.

As it turned out, most of the transition-associated changes occurred in the one min segment immediately preceding or following the first and last lordosis. Therefore, we divided these minutes in 30 s segments for further analysis. The 4 segments were −60 s to −30 s, −29 to 0 s (0 was the moment of lordosis), 0–29 s, and 30–60 s.

The Shapiro–Wilk test showed that most data deviated from a normal distribution and the Mauchly's test revealed that some variables violated the assumption of sphericity, thereby making parametric repeated measures ANOVA inappropriate (Girden, 1992). Therefore, we employed nonparametric tests for determining statistical significance. Dependent data were analyzed with Friedman's ANOVA. After a significant result, post hoc tests were corrected for multiple comparisons according to Conover (1999). The Mann–Whitney *U* test was used for analyzing independent data. All probabilities given in text, tables and figures are two-tailed.

3. Results

3.1. General

Three of the 20 females did not enter into behavioral estrus during the 8 days of observation. These females belonged to two different groups. Among those displaying estrus, 7 females' had partly overlapping periods with 1 or 2 other females. The duration of the preestrus and postestrus intervals was 22 ± 1 min with a range of 12–33 min.

3.2. Male behavior towards estrous and nonestrous females when both were available

There was almost no mounting of females neither before the beginning of estrus nor after the end of estrus (see Table 2). In fact, only 1 female was mounted once by each of two males during the interval preceding estrus. Interestingly, 3 females had their preestrus interval overlapping with another female's estrus. While the estrous females received a mean ± SEM of 0.15 ± 0.07 mounts/min from the 9 males in the 3 groups where such an overlap was found, the preestrous females did not receive any mount at all. The difference in male mounting between the estrous and nonestrous females is significant ($U = 0$, $p = 0.04$). Similarly, the postestrus interval in 4 females overlapped with other females' estrus. The postestrous females received only 0.01 ± 0.01 mounts/min from the 9 males distributed in 3 groups whereas the female or females remaining in estrus received 0.19 ± 0.09 mounts/min. Again, the difference in the number of mounts received was significant ($U = 2$, $p = 0.047$). The fact that the males almost exclusively mounted the estrous females during intervals in which both estrous and non-estrous females were simultaneously available shows not only that the males could distinguish estrous females from females not in behavioral estrus but also that only females in estrus incited the males to mount.

3.3. Changes in behavior between preestrus, estrus and postestrus

Female pursuit of the males was an extremely rare behavior. The longest mean duration, 0.08 ± 0.03 s/min, was in the preestrus interval and the shortest, 0.003 ± 0.003 s/min, was in the postestrus interval. The frequency of female fleeing from the males and the duration of female anogenital sniffing of the males were also extremely low. Actually very few females displayed these behaviors at all. Similarly, the number and/or duration of male nonaffiliative behaviors (fleeing from, nose off, fighting) towards the females were very low. None of these behaviors could, therefore, be subjected to any meaningful analysis and data are not shown.

The duration and frequency of paracopulatory behaviors varied between intervals. It was low before the beginning and after the end of behavioral estrus and high during the interval following the first lordosis as well as during the interval preceding the last.

Table 2
Changes in behavior in transitions between preestrus, estrus and postestrus.

Transition non-receptive–receptive			Transition receptive–non-receptive		
Behaviors in duration (s/m)	Nonreceptive	Receptive	Receptive	Nonreceptive	Friedman ANOVA
Paracopulatory behavior	2.09 ± 0.49*a	7.87 ± 1.11	9.21 ± 2.33	1.29 ± 0.63*b	χ^2 (3) = 26.96, p < 0.001
Male pursuit of females	1.88 ± 0.47*a	5.84 ± 0.93	4.88 ± 1.36	0.53 ± 0.18*b	χ^2 (3) = 31,73, p < 0.001
Female nose - off males	0.64 ± 0.34	1.28 ± 0.60	1.25 ± 0.59	1.13 ± 0.56	χ^2 (3) = 5.65, p = 0.13
Female sniffing males	2.38 ± 0.52	3.13 ± 0.38	1.33 ± 0.27	1.41 ± 0.73	χ^2 (3) = 12.80, p = 0.005
Male sniffing of females	3.02 ± 0.60	4.15 ± 0.94	3.65 ± 1.22	2.30 ± 0.96	χ^2 (3) = 6.39, p = 0.09
Male anogenital sniffing of females	0.80 ± 0.23	1.11 ± 0.37	2.89 ± 1.00	0.72 ± 0.40*b	χ^2 (3) = 9.52, p = 0.02
Behaviors in frequency (times/m)					
Mounts received	0.01 ± 0.01*a	0.26 ± 0.06	0.48 ± 0.23	0.00 ± 0.00*b	χ^2 (3) = 36.26, p < 0.001
Paracopulatory behavior	0.32 ± 0.07*a	0.98 ± 0.12	0.67 ± 0.11	0.11 ± 0.03*b	χ^2 (3) = 36.18, p < 0.001
Male pursuit of females	0.53 ± 0.13*a	1.06 ± 0.17	0.81 ± 0.23	0.12 ± 0.03*b	χ^2 (3) = 31.17, p < 0.001
Rejection	0.22 ± 0.08	0.26 ± 0.07	0.12 ± 0.05	0.06 ± 0.04	χ^2 (3) = 1.20, p = 0.75
Female nose - off males	0.16 ± 0.07	0.23 ± 0.05	0.19 ± 0.07	0.14 ± 0.06	χ^2 (3) = 5.85, p = 0.12
Female sniffing males	0.53 ± 0.10	0.77 ± 0.06	0.30 ± 0.05	0.17 ± 0.04	χ^2 (3) = 25.54, p < 0.001
Male sniffing of females	0.72 ± 0.12	0.93 ± 0.14	0.49 ± 0.10	0.27 ± 0.08	χ^2 (3) = 21.39, p < 0.001
Male anogenital sniffing of females	0.14 ± 0.04	0.21 ± 0.05	0.26 ± 0.08	0.10 ± 0.05	χ^2 (3) = 9.13, p = 0.03

*a Different from the receptive state in transition nonreceptive–receptive.
*b Different from the receptive state in transition receptive–nonreceptive (corrected for multiple comparisons test, ps < 0.05).

Male anogenital sniffing of the female did not differ between the interval preceding estrus and the interval following the first lordosis, but there was a significant decline from the interval preceding the end of estrus to the postestrus interval. The duration and frequency of male pursuit of the females varied between intervals. It increased from the interval preceding estrus to the interval following its beginning, and it was much reduced from the last interval of estrus to the postestrus interval. Whereas there was no difference between the first and last intervals of the estrus period, it turned out that the amount of pursuit was lower after the end of estrus than before its beginning (Table 2).

There was no difference between intervals with regard to rejection of the males or nose-off. Female sniffing of the males did not change during the transition periods. However, the females sniffed the males more around the beginning of estrus than around the end. To the contrary, male sniffing of the females did not vary between intervals.

In the males, the only behaviors varying according to the females' estrous state were mounting and pursuit. Male anogenital sniffing appears to be unrelated to the beginning of the females' behavioral estrus, but declined sharply in the postestrus interval. In the females, only paracopulatory behaviors were associated

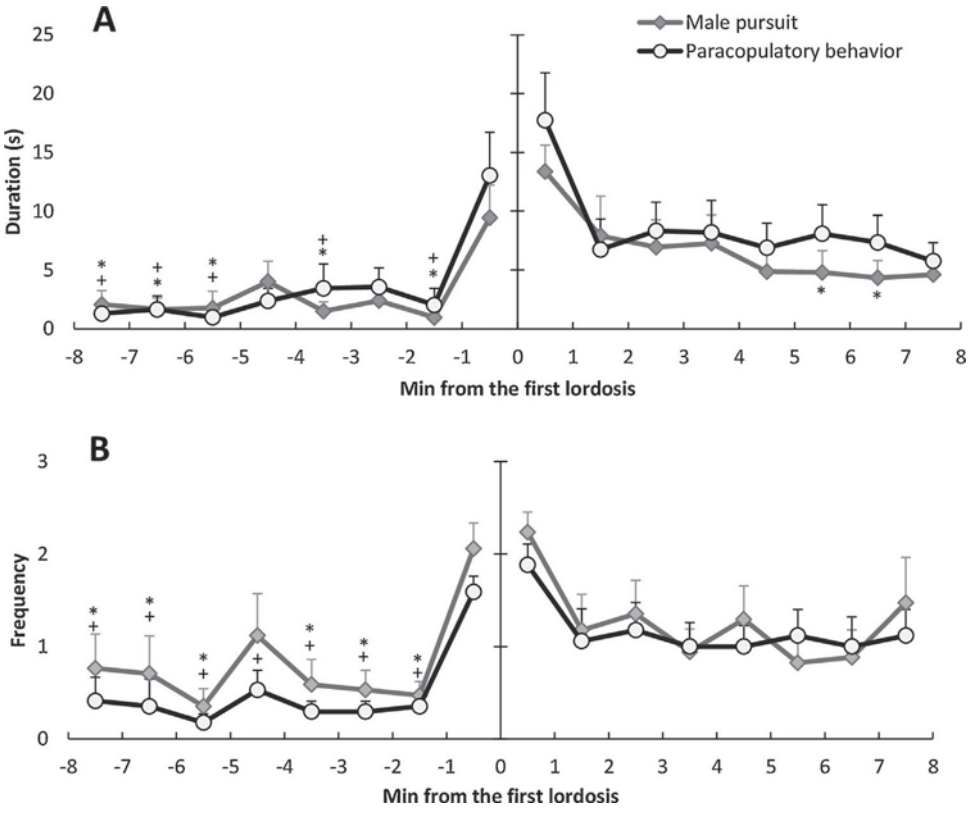

Fig. 3. Paracopulatory behavior and male pursuit of the female during the 8 min period preceding and following the first lordosis of behavioral estrus. A: duration; B: frequency. Data are mean + SEM. *different from the minute before or after lordosis in male pursuit, + different from the minute before lordosis in paracopulatory behavior, corrected for multiple comparison, p < 0.05.

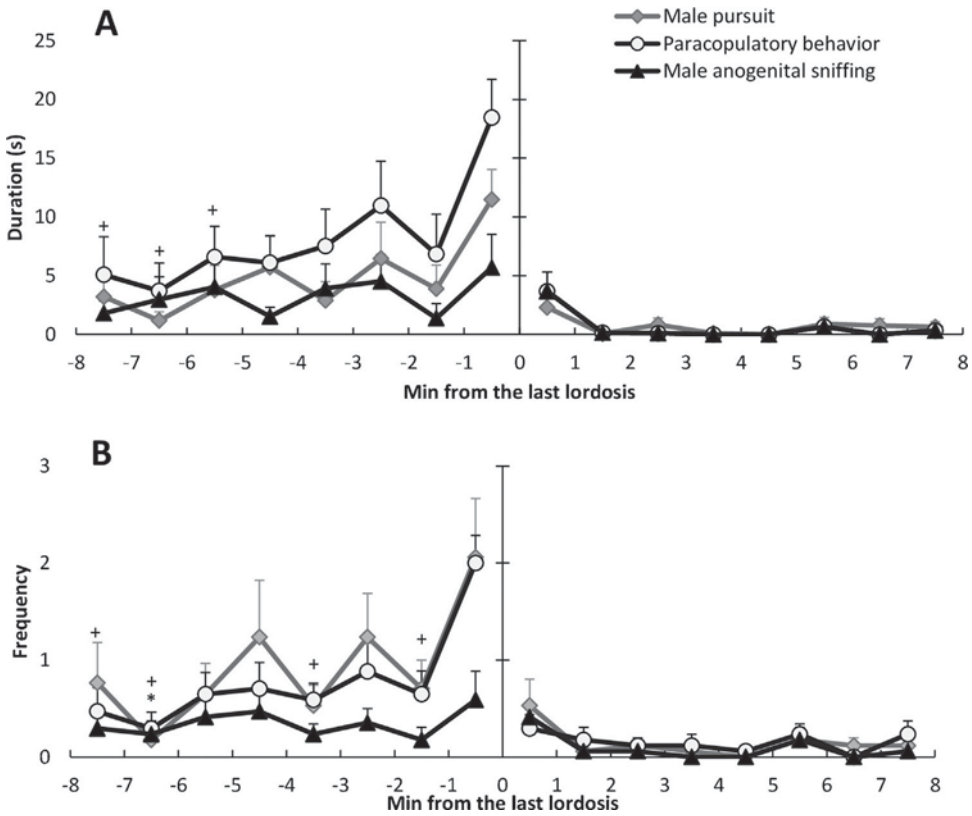

Fig. 4. Paracopulatory behavior and male pursuit of the female during the 8 min period preceding and following the last lordosis displayed during behavioral estrus. A: duration; B: frequency. Data are mean + SEM. *different from the last minute before the lordosis in male pursuit, + different from the last minute period in paracopulatory behavior, corrected for multiple comparison, $p < 0.05$.

with changes between receptivity and non-receptivity. Only the behaviors that varied between intervals were subjected to further analysis.

3.4. Changes in behavior during the 8 min periods before and after lordosis

The number of lordoses displayed during the first 8 min period of estrus was not different from the number displayed during the last 8 min period (4.29 ± 0.70 and 5.71 ± 1.83, respectively, $z = 0.26$, $p = 0.795$). The analysis of the display of paracopulatory behaviors during the 8 min preceding the first display of lordosis (and almost always the first male mount) shows that these behaviors remained at a low level until the last minute, when there was a sharp increase in both duration and frequency. Friedman's ANOVA revealed a significant difference between minutes (duration, χ^2 (7) = 40.00, $p < 0.001$; frequency, χ^2 (7) = 50.96, $p < 0.001$). Post hoc comparisons showed that there was no systematic change between –8 min and–1 min (0 being the moment of the first lordosis), whereas both the duration and frequency of paracopulatory behaviors were longer/higher during the minute preceding lordosis than during all other minutes ($p < 0.05$ when corrected for multiple comparisons). When analyzing the 8 min period following the first lordosis it was found that the duration of paracopulatory behavior declined (χ^2 (7) = 15.37, $p = 0.030$). However, post hoc comparisons between the 8 periods did not yield any significant difference. Likewise, the frequency of these behaviors remained stable during the 8 min following the first lordosis (χ^2 (7) = 11.88, $p = 0.110$). Data are illustrated in Fig. 3A and B. The analysis of paracopulatory behavior preceding the last lordosis of behavioral estrus revealed a difference between periods (duration, χ^2 (7) = 28.51, $p < 0.001$; frequency, χ^2 (7) = 32.32, $p < 0.001$). Particularly, there was an increase in the frequency of this behavior during the minute preceding the lordosis, according to post hoc tests. The 8 min period following the last lordosis showed a completely different pattern. There was no difference between the one min periods according to Friedman's ANOVA (duration, (χ^2 (7) = 8.41, $p = 0.30$; frequency, χ^2 (7) = 8.18, $p = 0.32$) (Fig. 4).

Male anogenital sniffing of the female was not analyzed around the first lordosis since there was no change in this behavior. Similarly, there was no change during the 8 min preceding the last lordosis ($ps > 0.90$). To the contrary, there was a decline after the lordosis (duration, χ^2 (7) = 24.63, $p = 0.001$; frequency, χ^2 (7) = 22.92, $p = 0.002$). However, multiple comparisons of the 8 one min periods did not reveal any significant effect when the appropriate correction was used. Data are shown in Fig. 4. The absence of any increase preceding the lordosis suggests that anogenital sniffing is not associated with that behavior in the way pursuit or paracopulatory behavior are. The decline to almost zero shortly after the lordosis might suggest that the female had completely lost her capacity to attract the males.

When pursuit was analyzed minute by minute during the 8 min preceding the first lordosis it became apparent that the duration as well as the frequency of this behavior dramatically increased during the last minute (Fig. 3). There was a significant difference between minutes (duration, χ^2 (7) = 35.34, $p < 0.001$; frequency, χ^2 (7) = 37.41, $p < 0.001$). The amount of pursuit between –1 min and the first lordosis was larger than that in most other intervals ($p < 0.05$, corrected for multiple comparisons). Analysis of the entire 8 min period following the first lordosis showed an effect of time (duration, χ^2 (7) = 19.52, $p = 0.007$; frequency, χ^2 (7) = 17.68, $p = 0.010$; Fig. 3). There was a moderate reduction in pursuit. The last lordosis, like the first, was preceded by an increase in pursuit. There was a difference between the 8 one min periods (duration, χ^2

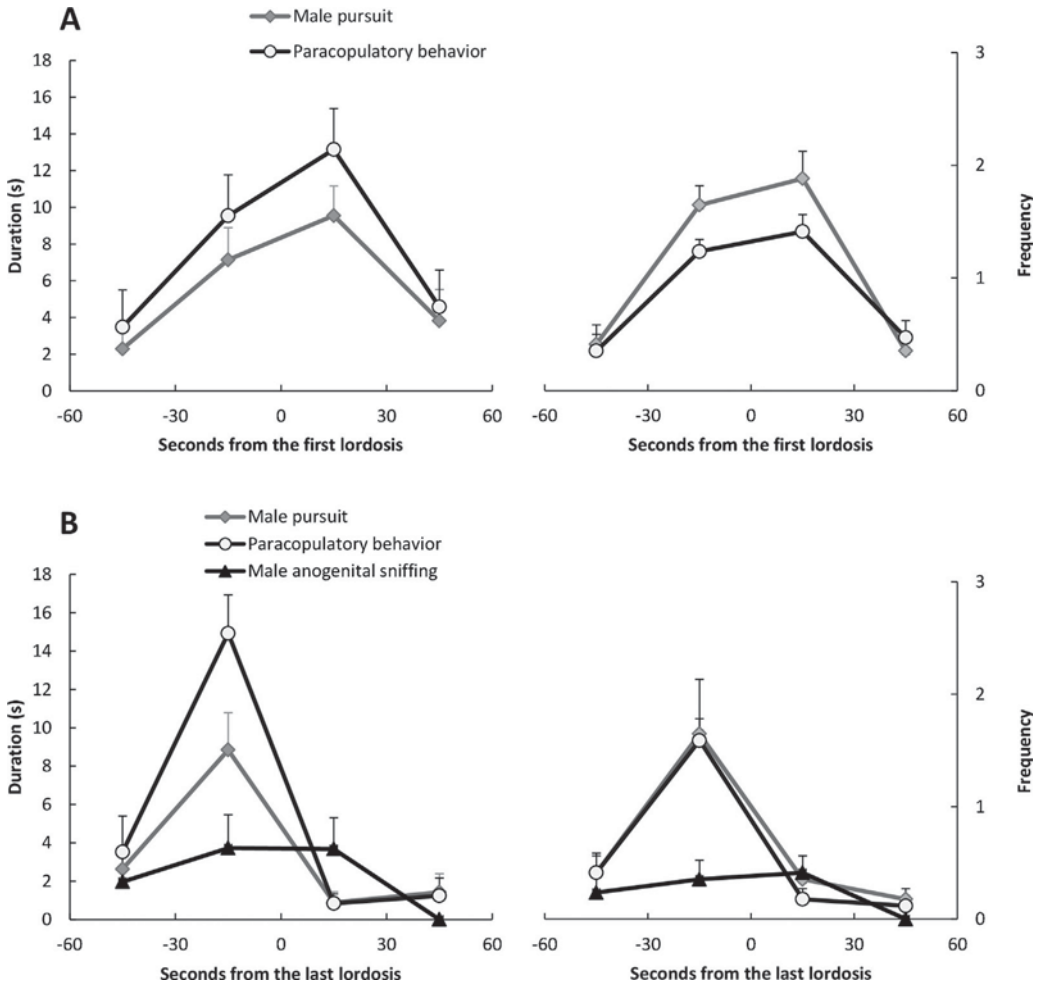

Fig. 5. Duration and frequency of paracopulatory behavior and male pursuit of the female during the minute preceding and following the first (A) and the last (B) lordosis of behavioral estrus, respectively. These minutes were divided in 30 s segments. For the last lordosis, male anogenital sniffing is also shown. Data are mean + SEM.

(7) = 21.14, $p = 0.004$; frequency, χ^2 (7) = 27.59, $p < 0.001$). After the last lordosis there was an immediate decline, and pursuit remained at a stable, low level throughout the 8 min. There was no difference between the one min periods (duration, χ^2 (7) = 8.05, $p = 0.330$; frequency, χ^2 (7) = 9.16, $p = 0.240$; Fig. 4).

3.5. Changes in behavior during the 60 s segments preceding and following the first and last lordosis of behavioral estrus

The four 30 s segments around the first lordosis differed with regard to paracopulatory behavior (duration, χ^2 (3) = 29.22, $p < 0.001$; frequency, χ^2 (3) = 27.59, $p < 0.001$). There was a sharp and significant rise in paracopulatory behavior in the 30 s segment immediately preceding lordosis (Fig. 5). Interestingly, the high level of paracopulatory behavior persisted during the 30 s segment following the first lordosis. The reason is that 13 of those lordoses (76%) were a response to a male mount. Since males normally mount in bouts, most males performed additional mounts, and the females displayed additional lordoses, within seconds of the first. Because of these supplementary mounts, paracopulatory behavior remained at a high level. However, there was a decrease from the 0–29 s period to the 30–60 s period according to post hoc comparisons (Fig. 5).

The analysis of the 30 s segments around the last lordosis revealed significant differences (duration, χ^2 (3) = 37.18, $p < 0.001$; frequency, χ^2 (3) = 32.19, $p < 0.001$). Post hoc comparisons established that an increase in paracopulatory behavior occurred during the last 30 s before it (Fig. 5). The events following the last lordosis turned out to be distinct from those occurring after the first. There was sharp decline in paracopulatory behavior already during the 30 s segment following the lordosis and there was no difference between 0–29 s and 30–60 s (ps > 0.27; Fig. 5). Since only 4 (23%) of the last lordoses were associated with male ejaculation and only 2 (12%) with male mission this immediate decline cannot be attributed to male inactivity following these behaviors. In fact, when we compared the 11 females whose last lordosis was provoked by male mounting (9 females) or sniffing (2 females) with the 6 females having received an ejaculation (4 females) or an intromission (2 females) with the Mann–Whitney test, we failed to find any significant difference at any time segment (*p*s > 0.05). These data are illustrated in Fig. 6.

Male anogenital sniffing of the female varied around the last lordosis with regard to duration (χ^2 (3) = 9.16, $p = 0.027$) but not with regard to frequency (χ^2 (3) = 7.79, $p = 0.051$). When corrected for multiple comparisons, there was no significant difference between the four 30 s segments.

As was the case for paracopulatory behaviors in the females, the amount of male pursuit changed around the first lordosis (duration, χ^2 (3) = 25.63, $p < 0.001$; frequency, χ^2 (3) = 29.52, $p < 0.001$). There was an increase in the 30 s segment prior to that lordosis. Pursuit remained at a high level during the 30 s segment following the first lordosis. As was the case for paracopulatory behavior, this can easily be explained by the fact that many of the males performed additional mounts during this segment. However, pursuit

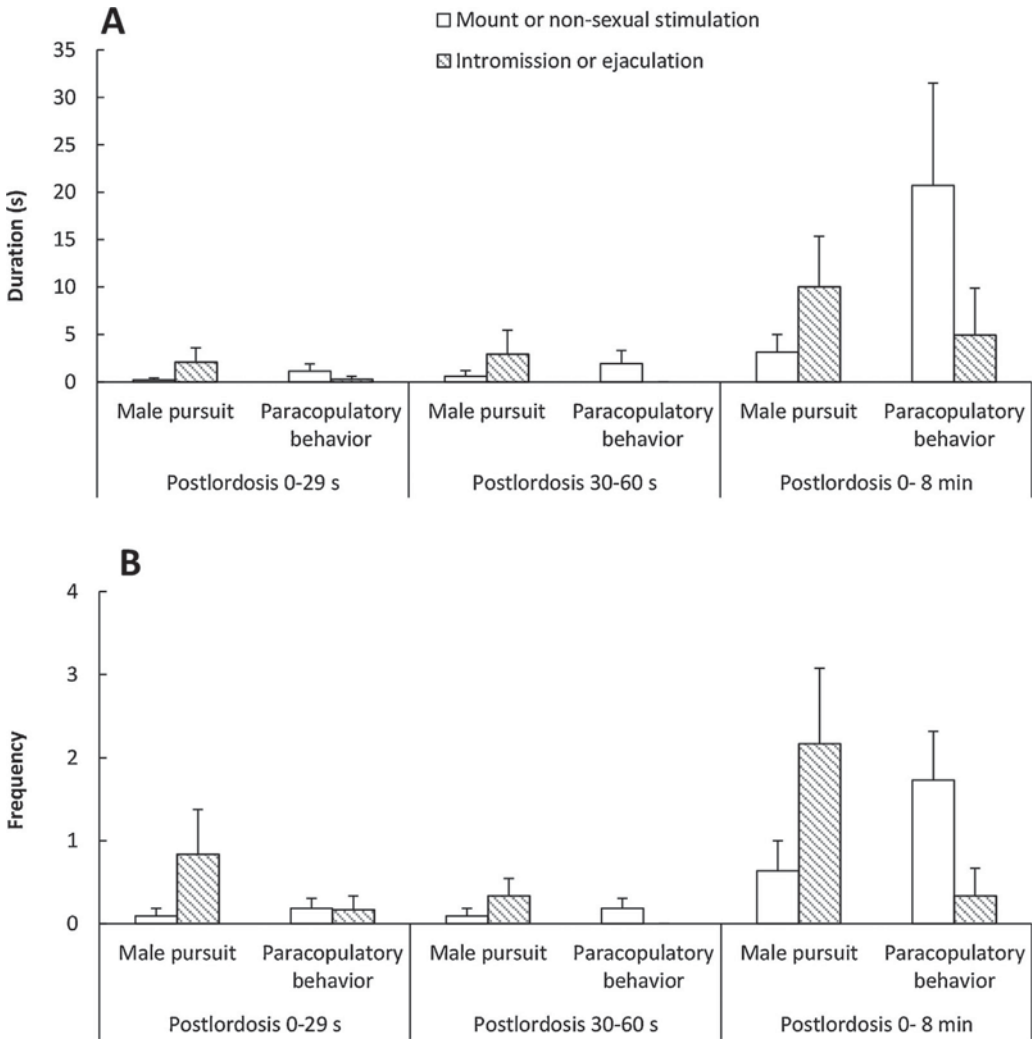

Fig. 6. Paracopulatory behavior and pursuit in females either displaying their last lordosis of behavioral estrus in response to a mount or to non-sexual stimulation ($N = 11$) or females displaying lordosis in response to a male intromission or ejaculation ($N = 6$). There was no group difference neither during the 60 s segment following lordosis nor during the 8 min period following it. Data are mean + SEM.

declined significantly in the segment between 30 and 60 s after the first lordosis. With regard to changes around the last lordosis, they were also significant (duration, χ^2 (3) = 27.44, $p < 0.001$; frequency, χ^2 (3) = 24.46, $p < 0.001$, Fig. 5B). There was a large increase during the 30 s segment preceding the last lordosis. After it there was an immediate decline in pursuit, and no difference was found between 0–29 s and 30–60 s.

3.5.1. Relationships between paracopulatory behavior and male pursuit

In order to get a clearer picture of the transition from non-receptivity to receptivity we determined the male and female behavior immediately preceding the first lordosis. In all females the last act performed before that lordosis was paracopulatory behavior. In all males, the corresponding act was pursuit of the female. In 11 of the females, the display of paracopulatory behavior preceded male pursuit. In the 6 remaining females, male pursuit preceded paracopulatory behavior. A chi square test shows that there was no difference between female paracopulatory behavior leading to male pursuit and male pursuit leading to female paracopulatory behavior ($\chi^2(1) = 1.47$, $p = 0.225$). The last lordosis was also always preceded by female paracopulatory behavior and by male pursuit of the female.

4. Discussion

4.1. Changes in behavior associated with the beginning of behavioral estrus

The female behavior pattern defining the beginning of estrus is the display of lordosis. The main stimulus leading to the presentation of this behavior is tactile stimulation provided by the mounting male (Kow and Pfaff, 1976). Data reported here show that the males only exceptionally mounted the females before the mount was able to activate a lordosis response. This suggests that the females only had the capacity to stimulate the males to mount when they would respond with lordosis. This, in turn, must mean that the females emitted some stimulus or stimuli specific for the state of sexual receptivity. It is well known that sexually receptive female rats produce olfactory stimuli attractive to males. The production of these stimuli is hormone-dependent, since odors from ovariectomized females are far less attractive than odors from intact, estrous females or from ovariectomized females treated with estradiol (e.g., Carr et al., 1965; Lucas et al., 1982). Whether there is a sudden change in female odor associated with the initiation of male mounting or not is presently unknown. However, it appears a quite unlikely event. Although the mechanisms underlying the hormone-induced changes in odor remain obscure, there are many reasons to

believe that they, like most other steroid effects, are gradual rather than sudden. Furthermore, male rats have never been observed to display mounting in response to female odors. They do respond with erection (Sachs, 1997), release of gonadotropins (Graham and Desjardins, 1980 Kamel et al., 1977) as well as of some transmitters (e.g., (Mas et al., 1995), and approach to the odor source (Ågmo, 2003). Nonetheless, the tactile stimulation of the perineal region required for activating a mount (Contreras and Ågmo, 1993) cannot be provided by any odor.

In addition to odor, sexually receptive females emit high frequency vocalizations. The hormone-dependence of these vocalizations has been firmly established (Floody, 1981 Matochik et al., 1992), but a vocalizing female is no more attractive to a male than a silent female (Snoeren and Ågmo, 2013). Moreover, when males have simultaneous access to several females their choice of copulation partner is independent of female vocalizations (Snoeren et al., 2014). Consequently, there is not much reason to believe that female vocalizations provoked the males to initiate mounting. Instead of searching for additional specific stimuli emitted by the sexually receptive female we tried to find the sudden presence of a behavior pattern that might incite the male to mount and/or the sudden absence of behaviors that might impede the male to mount.

The duration or frequency of the prosocial behavior of sniffing and the antisocial behaviors of rejection and nose-off did not change between intervals, i.e., they were at the same level before the beginning of estrus, during the first and last intervals of the estrus period, and after the end of estrus. Thus, these behaviors do not seem to be associated with the appearance and disappearance of sexual receptivity. In contrast, the duration of male anogenital sniffing of the female got much reduced from the last interval of estrus to the postestrus interval. This reduction might be related to the disappearance of pursuit of the females and mounting. Against such a proposal it could be argued that there was no increase in anogenital sniffing associated with the beginning of estrus. Moreover, we have earlier reported that there is no relationship between the intensity of female or male sexual behavior and social or antisocial behaviors (Chu and Ågmo, 2014a). It appears doubtful that the reduction in anogenital sniffing is of any major importance for the cessation of sexual activity.

One of the remarkable results found in the seminatural environment was that the duration of paracopulatory behaviors suddenly increased from close to zero shortly before the first lordosis to a rather high level immediately before it. Thereafter, the females maintained a high level of paracopulatory behavior throughout the entire behavioral estrus (Chu and Ågmo, 2014a). Ever since the publication of Beach's (1976) seminal paper is has been generally accepted that these behaviors are powerful stimuli for activating male mounting (Erskine, 1989). Indeed, in males without sexual experience, in castrated males maintained on low testosterone replacement, and in males with otherwise impaired copulatory behavior, female paracopulatory behaviors are essential for the initiation of mounting (Hlinak and Madlafousek, 1977; Hlinak et al., 1987; Madlafousek and Hlinak, 1983; Madlafousek et al., 1976).

With regard to the male, it is known that pursuit of the female almost always precedes mounting (Ågmo, 1999). In the present study, male pursuit of the female showed a pattern most similar to that of paracopulatory behaviors, that is a sharp increase immediately before the first lordosis and a sharp and lasting decline after the last. The temporal coincidence between the increase in paracopulatory behaviors and pursuit and the beginning of behavioral estrus together with the coincidence in decline at the end of estrus may suggest a causal relationship. The exact nature of that relationship is, however, not completely clear. Considering that the males could already be engaged in copulatory activities with other females, it is likely that the female entering estrus simply communicated that she also was ready to copulate. Obviously, this would also hold for situations in which no other female was available. The way the female apparently communicated her readiness was either by displaying paracopulatory behavior, thereby inciting the male to pursue and eventually mount her, or by responding to the male's pursuit with paracopulatory behavior, which was ended by the male when he performed a mount. It might be remembered that the first lordosis was always preceded by paracopulatory behavior on the part of the female and by pursuit on the part of the male.

An intriguing question here is why the occasional displays of paracopulatory behavior and pursuit during several minutes preceding the first lordosis did not lead to male mounting and female lordosis. The duration of each episode of paracopulatory behaviors and pursuit did not increase shortly before the first lordosis, whereas the frequency of these episodes did. In view of this, we propose that isolated displays of pursuit or of paracopulatory behavior do not lead to sexual interaction. Several of these displays in rapid succession are needed for stimulating the subjects to engage in copulatory behavior. It is most likely that each display of pursuit or of paracopulatory behavior contributes to enhance both general arousal and sexual motivation in ways outlined in some detail elsewhere (Ågmo, 1999; Ågmo, 2011). This enhancement declines spontaneously with time. Consequently, in order for these behaviors to increase arousal/motivation to the point required for activating copulatory behavior they must occur with a relatively high frequency. This is exactly what happens in the 30 s period preceding the first lordosis.

The central nervous events leading to the dramatic increase in paracopulatory behavior and male pursuit in a time span of 30 s are entirely unknown. Since an extensive discussion of the many possible explanations is far beyond the scope of the present paper we will only mention some hypothetical mechanisms. The most straightforward would probably be enhanced release of some transmitter. It is known that female rats release dopamine in the nucleus accumbens and striatum when exposed to sexually relevant stimuli (Jenkins and Becker, 2003; Pfaus et al., 1995), and although the precopulatory release is smaller than that produced by copulation it might contribute to the initiation of behavior. However, in the preoptic area dopamine is not released in response to an inaccessible male, although dopamine concentrations are much increased during copulation (Matuszewich et al., 2000). Likewise, oxytocin is released in the paraventricular nucleus during copulation (Nyuyki et al., 2011), but whether this peptide could participate in the initiation of copulation is entirely unknown. Noradrenaline may also be involved, because estrogens and progesterone have been shown to modify noradrenergic function in the ventromedial nucleus and preoptic area (Etgen et al., 2001), and release of this transmitter increases during copulation (Vathy and Etgen, 1989). However, vaginocervical stimulation is necessary for release (Etgen and Morales, 2002), making it unlikely that noradrenaline participates in the initiation of female copulatory behavior. There is also a number of peptide transmitters in addition to oxytocin that are involved in the control of copulatory behavior in female rats (reviewed in Argiolas and Melis, 2013), but there are no data as to whether any of them might participate in the transition from non-receptivity to receptivity. A different possibility is that a transitory increase in estrogen availability stimulates fast-acting membrane receptors. The activation of these receptors may have behavioral effects within seconds (reviewed in Mani et al., 2012). Since estrogen release from the ovaries show considerable fluctuations (Nequin et al., 1979; Södersten and Eneroth, 1981), a sudden increase in extracellular estrogen concentration is feasible. It is also possible that estrogens and/or progesterone are produced and released locally from neurons (Cornil et al., 2006). Further studies

are needed before any of these speculations can be discarded or confirmed.

4.2. Changes in behavior associated with the end of behavioral estrus

Many hypotheses concerning the cause for the end of estrus have been launched. Among those is the suggestion that intromissive stimulation contributes to the end of sexual receptivity (e.g., Erskine, 1985). Since the duration of estrus is reduced by exposing also ovariectomized rats to a copulating male (e.g., Lodder and Zeilmaker, 1976) or to experimenter-provided vaginocervical stimulation (e.g., Bennett et al., 2002) it was concluded that diminished availability of ovarian hormones cannot be related to the termination of behavioral estrus. There is little reason to believe that genital stimulation would accelerate the catabolism of ovarian hormones. Instead it has been suggested that sexual stimulation leads to modified release of transmitters, for example vasopressin (Södersten et al., 1983) or glutamate (Georgescu et al., 2012), and this modified release would bring behavioral estrus to an end. It may also be noted that intense genital stimulation sometimes fail to reduce the duration of estrus, and if it does, the reduction may be explained as a purely peripheral effect (van der Schoot et al., 1993). The mechanisms behind the end of behavioral estrus in females not receiving any genital stimulation have received little attention, but since all females in the present study did receive such stimulation it is of no concern here.

Both intense stimulation from a male and artificial vaginocervical stimulation not only causes a reduced estrus duration but also a considerable enhancement of female rejections of the copulating male (Blaustein et al., 2009; Coopersmith et al., 1996; Pfaus et al., 2000). In the seminatural environment there was no increase in rejections as estrus termination approached. Indeed, rejections remained at a low level throughout the period of estrus (Chu and Ågmo, 2014a). This fact is probably a consequence of the lower rate of sexual interactions in the seminatural environment, even in situations where only one receptive female was available to the three males. It is also important to observe that there was no reduction in paracopulatory behaviors in the period preceding estrus termination. Indeed, in every female the last lordosis was preceded by paracopulatory behavior. Furthermore, the males continued to pursue the females with undiminished intensity, showing that they remained attractive, and male pursuit always anteceded the last lordosis. Immediately after the last lordosis there was a drastic reduction of paracopulatory behaviors and of male pursuit. A similar, short-lived reduction was seen after every lordosis. After the last, however, this reduction became permanent. We suggest that the postestrus level of paracopulatory behaviors and of male pursuit was too low to stimulate the animals to engage in further copulatory acts. Thus, behavioral estrus came to an end when the female suddenly ceased to display paracopulatory behavior and/or the male ceased to pursue her. Male fatigue can be excluded, because whenever other females remained in estrus, the males continued to copulate with them. Likewise, changes in the number of rejections can be of no importance since there were no such changes.

The neurochemical changes associated the end of behavioral estrus are obscure. Even though increased release of glutamate might explain reduced estrus duration as observed in pair tests, it cannot account for the end of estrus in the seminatural environment. A prominent effect of glutamatergic agents is to stimulate rejections and reduce paracopulatory behaviors (Georgescu and Pfaus, 2006a; Georgescu and Pfaus, 2006b), something not observed in the present study. Likewise, another transmitter proposed to be involved in estrus termination, vasopressin, also reduces paracopulatory behavior and stimulates rejection (Pedersen and Boccia, 2006). Whether any of the other transmitters that occasionally have been reported to reduce female rat sexual behavior is involved in estrus termination or not is completely unknown.

5. Conclusion

The transition from a state of non-receptivity to receptivity as well as the inverse has been thought to be gradual. This notion was based on data from discrete pair-tests (see Introduction). In the present experiment, in which groups of rats were observed continuously during the estrus cycle, an entirely different picture emerged. The females did not show a gradual change in sexual behavior, but suddenly entered and left a state of receptivity at the beginning and end of behavioral estrus, respectively. We have earlier pointed out that prolonged observation of groups of rats in an environment sharing some characteristics with the natural environment is essential for the external validity of any description of behavior (Chu and Ågmo, 2014a). Therefore, we propose that female rats normally show abrupt changes in sexual behavior during the estrus cycle, and that the gradual change described earlier is an artifact of the observation procedure. We also suggest that the increase in female rejections and reductions in paracopulatory behavior prior to the end of estrus in pair-tests is another artifact, caused by a frequency of sexual interactions far above that we have observed in the seminatural environment. Nevertheless, it is possible that a different group composition could lead to results more in line with data from pair tests.

The initiation and termination of copulatory behavior were strictly associated with rapid modifications of the amount of female paracopulatory behavior and male pursuit of the female. When these modifications occur at the beginning of behavioral estrus, the female is already fully receptive, meaning that she displays lordosis in response to every mount. Since she did so until the very last lordosis, we propose that she was fully receptive also when behavioral estrus ended. This assertion is strongly supported by the fact that the amount of estrogens needed for activating lordosis is lower than that needed for the paracopulatory behaviors. The end of behavioral estrus is, therefore, not related to reduced receptivity but to reduced paracopulatory behavior and/or reduced male pursuit. Since that behavior may either incite the male to pursue and mount the female, or be a response to male pursuit also leading to a mount, its absence will effectively terminate mounting, and, in consequence, lordosis.

We have here offered a behavioral explanation for the beginning and end of behavioral estrus. The neurochemical events subjacent to these behavioral changes are unknown. Future research needs to employ procedures for studying transmitter release with a time resolution at the subminute level.

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