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The effects of sexual experience and estrus on male-seeking motivated behavior in the female rat

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Abstract

Ovariectomized (OVX) female rats were trained to traverse a straight alley and return to a goal box where they had previously encountered a male rat, a female rat or an empty goal box. The time required to run the alley was used as an index of the subjects' motivation to re-engage the goal box target. Subjects were tested in both estrus and non-estrus, first sexually naïve and then again after sexual experience. Female rats ran most quickly for a male target, most slowly for an empty goal box, and at intermediate speeds for a female target. Sexual experience tended to slow run times for all but male targets. Estrus enhanced approach behavior for males and an empty goal box, but tended to slow the approach toward females, both before and after sexual experience. This latter finding was further investigated in a second experiment in which sexually naïve OVX females were tested during estrus and non-estrus in a locomotor activity apparatus, a runway with an empty goal box, and an open field. Estrus produced no changes in spontaneous locomotion either in the activity box or the open field, but decreased run times in the alley and increased the number of center-square entries in the open-field. Thus, estrus produces increases in sexual motivation that selectively enhance exploratory, presumably male-seeking behavior, but not simple spontaneous locomotion.

Keywords

sexual motivation; runway; female rats; sexual experience; copulation; estrus; progesterone; estrogen

A great deal is known about the sexual behavior of the female rat. For instance, in his seminal work on estrous females, Beach [1] outlined and illustrated a distinction between appetitive and consummatory behaviors, or proceptivity and receptivity, respectively. Receptivity is most closely understood as those behaviors "... which are necessary and sufficient for fertile copulation with a potent male" [1]. Receptive behaviors are those that facilitate the act of copulation, female rats, for example, exhibit displays of lordosis characterized by a crouching, sway-backed posture, with the tail flicked to the side to facilitate the male mounting and intromitting. It is well known that sexual receptivity in the female rat is dependent on the presence of estrogen [e.g., see 2,3,4].

Proceptivity, on the other hand, represents an antecedent condition to the copulatory act. Here the female exhibits solicitation activity that is intended to attract and stimulate the male [1]. In rats, such proceptive behaviors include hopping and darting, ear wiggles, and other orient-

runaway behaviors such as those observed in studies of paced mating [4–6]. These behaviors have been shown to be dependent on the action of progesterone [e.g., 7,8]. Thus, a female rat needs both estrogen and progesterone to display the full complement of sexually motivated behavior. While the brain circuitry involved in producing lordosis is thoroughly characterized [e.g., 9], much less is understood about proceptivity and female sexual motivation in general. Therefore, a valid, reliable model of female rodent sexual motivation would be of great utility for studying the behavioral and neurobiological basis of sexual motivation.

In previous work we assessed the motivation of male rats to traverse a straight-alley and enter a goal box where several seconds earlier they had been exposed to one of a variety of target stimuli placed on the opposite side of a Plexiglas partition. Although researchers have long used the runway as a means of measuring the male rat's motivation to seek and encounter a female target [e.g., 10,11–13], a unique aspect of our runway procedure is that the subjects' motivation, as measured by running or approach behavior, is assessed independent of actual consummatory behavior. In our apparatus the male subject does not copulate with the female target upon entering the goal box as she is behind a Plexiglas partition [14–17]. Sexually naïve male rats exhibited faster run times (heightened motivation) when returning to a goal box containing a receptive/proceptive female than one containing either a non-receptive female, a male or no target stimulus [17]. Thus, naïve males were found to be inherently motivated by female precopulatory cues. In the current study we extended this model to the investigation of female sexual motivation.

While some studies have used a runway to assess the behavior of female rats approaching a goal-box containing a male [18–21], these studies have typically been interested in sexual reinforcement or the consequences of copulation and not motivation per se (i.e., the antecedent state that induces the female to seek a male prior to copulation). Our current procedure was devised to assess female sexual motivation independent of sexual reinforcement by examining approach behavior to a male target rat located behind a perforated Plexiglas partition, and in an apparatus in which copulation has never occurred. One notable exception in this regard is the work of Eliasson and Meyerson [19] who employed a runway choice apparatus in which the female subjects ran down an alley and entered either of two goal-boxes: one containing a male and the other a female target. In their study, as in the current experiment, the female subjects were prevented from physically accessing the target animals through the use of a wire mesh obstruction. Eliasson and Meyerson [19] reported that females increased their preference for male targets during estrus and that this effect declined when the female subjects became pregnant. These authors did not, however, directly describe or address the impact of sexual experience on the subjects' preferences. Additionally, they concluded that “latency” to reach the targets (what we call “run time”) did not reliably change over trials and between hormonal conditions – a result that is not particularly surprising since the subjects were faced with the task of approaching *both* targets on every trial and the impact of hormonal state (presence or absence of estrus) was only dictated by the final choice at the end-point of the alley. In contrast to this, we have reported that in a simple non-choice straight-arm runway, male rats return more quickly to a goal box containing a female target, than they do to one containing a male target or a no target at all [14–17]. It was therefore of interest to extend this approach to the study of female rats provided the opportunity to approach male targets. We therefore set out to: a) first replicate with our own methods some well-documented findings in the literature -- e.g., does the induction of estrus enhance male-seeking behavior (i.e., sexual motivation) in female rats [e.g. 19,22,23]; b) extend this investigation to assess the impact of sexual experience on the motivation to seek males; and c) to assess the impact of estrus on exploratory and locomotor behaviors as a means of evaluating the influence of the females' internal hormonal state on motivated versus spontaneous activity. Together, data from these studies were intended to help illuminate the complex interplay between hormonal state and experience in the production of sexual motivation in the female rat.

Methods

Subjects

Fifty-two female Sprague-Dawley rats approximately 3–4 months old were obtained from Charles River Laboratories (Georgia, VT) and housed individually in plastic tubs lined with CareFresh bedding (Newco, Rancho Cucamonga, CA). The animals lived in a temperature-controlled (22°C) vivarium environment maintained on a reverse light/dark schedule (lights off 0600) and provided *ad libitum* access to food and water. After arrival, each animal was handled daily for 5–10 min over a one-week period prior to testing. All testing took place between 0900 and 1400 h (during the rats' dark cycle.) All females were ovariectomized (OVX) by the supplier. OVX females were used here since sexual receptivity and proceptivity can be induced by hormone treatments (i.e., induction of a behavioral estrus) and copulation can be permitted without experiencing pregnancies in the test subjects. An additional 14 male Sprague-Dawley rats of about the same age served as studs and goal box targets, and 6 additional OVX female rats served as goal box targets and as initial copulatory partners for the males, in order to provide sexual experience for the males prior to their being used as studs for the female subjects.

Apparatus

The Operant Runway—Subjects were tested in a runway consisting of a wooden start box (20 cm L × 25 cm W × 36 cm H) with a removable start door that opened onto an alley (164 cm L × 15 cm W × 36 cm H.) At the opposite end of the alley was a cylindrical Plexiglas goal box (46.5 cm diameter, 41 cm H.) The goal box was divided in half by a Plexiglas divider (6.5 cm wide, 41 cm H) perforated with sixteen small holes 1.2 cm in diameter. This permitted the experimenter to place a target stimulus (a male or female rat) on one side of the goal box and the subject on the other side, allowing visual, auditory and olfactory cues to pass, but not physical contact. A goal door was located at the entry threshold to the goal box and, when closed, restricted the subject to the goal box. The floor of the entire apparatus consisted of small steel rods that ran perpendicular to the walls of the runway and were spaced less than 1 cm apart (see Figure 1).

Sexual Experience Chamber—Sexual experience took place in a small Plexiglas octagonal chamber (18 cm/side, approximately 45 cm in diameter, 60.5 cm H.) Sani-Chips (P.J. Murphy Forest Products, Montville, NJ) covered the floor and were changed between sessions. All runway testing and mating sessions were conducted under red light (40 W) conditions.

Locomotor Activity Boxes—As described below, some subjects were tested for general spontaneous locomotor behavior during both estrus and non-estrus. This was accomplished using a bank of 12 identical activity monitor cages (Hamilton-Kinder Scientific, San Diego, CA) each measuring 46 cm L × 24 cm W × 21 cm H and fitted with an 8 × 4 grid of infra-red photo-emitters and detectors to track movements in real time. Each chamber sat on a metal tray covered in Sani-Chips which were changed between sessions. Data were collected in the form of “inches traveled per unit time” and analyzed on a PC running custom software.

Open-Field Apparatus—Some rats were tested in an open field that consisted of large square (130 cm sides, with 41 cm H walls) constructed of laminated particleboard. The enclosure was located in a separate room and placed directly on the laminate-tile floor that was marked to identify 16 equal-sized squares – 4 in the center and 12 along the walls of the apparatus. Testing involved observation and recording of the squares entered by animals that were individually placed into the apparatus (as described in the procedures section for Experiment II below).

Procedure

Experiment I: Runway

Phase I: Sexual motivation in sexually naïve female rats: Each of 36 female subjects was permitted to investigate the runway apparatus for 10 minutes a day on two separate days prior to the beginning of runway trials in order to familiarize them with the testing environment. The subjects were then randomly assigned to one of three groups (n=12/group), each corresponding to a different goal box target condition. On a given trial, each subject was placed on one side of the goal box for 2 min with the door closed. On the opposite side of the perforated Plexiglas divider was a male target, a female target or an empty space (no target). Each subject was always exposed to the same target condition on every trial. After 2 min, the subject was picked up and placed in the start box where, 10 sec later, the start and goal doors were lifted and the trial began. The subject's motivation to return to the goal box was assessed by measuring the time required to traverse the alley and enter the goal area (run time.) After the subject entered the goal box, the goal door closed behind her, and the subject remained confined to her side of goal box for approximately 1 minute after which time she was removed and returned to her home cage.

Each female subject was trained in the runway twice a week – once in non-estrus and once in estrus – and each training session consisted of two trials, separated by approximately one hour. In this work, “non-estrous” refers to an OVX female not given any hormonal treatments, while “estrous” refers to an OVX female given subcutaneous (SC) injections of estrogen and progesterone according to the following schedule: estradiol benzoate (25 µg/ml/kg dissolved in sesame oil, SC) was administered at the same time of day on two consecutive days. On the third day, each rat received an injection of progesterone (600 µg in 0.1 ml propylene glycol, SC) followed 4–6 hours later by the first runway trial. Non-estrous trials were always conducted at least 3 days after an estrous trial. After two weeks of runway training, a single additional week of estrus and non-estrus runway trials was conducted and constituted the “pre-sex” test data.

Phase II: Sexual experience: Following the week of “pre-sex testing” all female subjects received sexual experience. After estrus induction (as described above), each animal was paired with an experienced novel male stud and allowed to copulate for 30 min in the sexual experience chamber. Note that the female subjects were not presented with a male that had previously served as a goal box target to ensure that subsequent performance in the runway was not affected by prior experience with a specific target. Sexual experience was given 3 times for each subject over a two week period, with each session introducing a novel male.

Phase III: Sexual motivation in sexually experienced female rats: To examine the effects of sexual experience on the subjects' motivation to seek males, the female rats were tested again in the runway for one additional week precisely as described in Phase I of the study. Thus, each subject was tested once in estrus and once in non-estrus (two trials for each hormone condition,) for the same type of target that had been experienced in the goal box previously (albeit using different specific target animals).

Experiment II: Effects of Estrous on Spontaneous and Exploratory Behavior—

This second Experiment was devised to more closely explore the nature of the behavioral activating effects of estrus (i.e., motivational arousal) in situations where no obvious goals/targets were available. The intent was to collect data that would be of use in interpreting the runway behavior of animals in Experiment I. To accomplish this, a new group of 16 OVX female rats served as subjects in this experiment; half were assigned to an estrous group and the remainder to a non-estrous group (corresponding to the hormonal state under which testing took place.) These rats were tested in three well-established procedures that provided

information on the effects of hormonal manipulations on general locomotor and exploratory behaviors. All animals were sexually naïve.

Phase I: Locomotor activity testing: The rats were each assigned to one of the 12 identical locomotor activity chambers and provided 60 min of acclimation to their assigned chamber prior to the start of data collection. The following day, the estrous group was administered EB (10 µg in 0.1 ml sesame oil, SC) on two consecutive days and then P (600 µg in 0.1 ml propylene glycol, SC) on the third day followed 4–6 hours post-injection by placement into the locomotor activity apparatus. The total distance traveled inside the chamber was recorded by computer for each animal during 5 min intervals over a 60 min test session. The data from this procedure were used to assess whether or not estrous and non-estrous females differed in their level of general locomotion/activity.

Phase II: Runway testing: Four days after the locomotor testing, each subject was introduced and allowed to explore the runway apparatus for 10 min. The next day, a subset of animals again underwent estrus induction as described above and three days later, 4–6 hrs after the final progesterone injection, all subjects were tested in the runway. As in Experiment I, each animal was placed in the empty goal box (no target was provided on the opposite side of the Plexiglas divider) for 2 min and then placed in the start box for 10 secs, after which the start and goal doors were opened and the trial began. In this experiment, the time required to return to the goal box was recorded for each animal on only a single trial. This served as a replication of one of the conditions in Experiment I, albeit with animals for whom the runway was a relatively novel environment (they had only been placed in the runway on one previous occasion, during habituation). The intent here was to assess whether estrus and non-estrus animals behaved differently in the runway – in the absence of any associations with male targets.

Phase III: Open field: The final test procedure involved placing each subject in the center of the open field apparatus for 5 min. Half the animals were tested during estrus and half during non-estrus. The dependent measures consisted of the number of center and outer squares entered for each animal during each 5 min test. An animal was deemed to be within a square when all four of its paws were located within that square. This simple test provided information regarding the effects of estrus compared to non-estrus on the general locomotor activity (number of squares crossed) and exploratory behavior (center square entries) of the subjects.

Results

Experiment I

The mean (+ SEM) run times of each group of subjects under each treatment condition are shown in Figure 2. Runway performance is depicted as a function of the presence or absence of estrus and the nature of the goal box target (male, female or empty). The left panel (A) of the figure depicts run times averaged over the week just prior to copulation, when the subjects were still sexually naïve, while the right panel (B) depicts performance occurring one week after the animals had experienced copulation (three 30 min sessions with a male stud). Three animals were removed from the study prior to sexual experience because their run times did not stabilize and varied from the group mean by more than two standard deviations. Thus, sample sizes for the three groups were 12, 10 and 11 for the Empty goal box, Female Target and Male Target conditions respectively. Since the same subjects were used in both phases of the experiment (sexually naïve and sexually experienced), a three-way mixed-design ANOVA (Experience $\times$ Hormone $\times$ Target) was computed on the data depicted across both panels of Figure 2. The analysis revealed a main effect of goal-box target, $F(1, 30) = 3.8, p < .05$, stemming from the fact that when averaged across hormones and sexual experience, female subjects ran fastest for male targets, slowest for an empty goal box, and at intermediate speeds for female

targets. Indeed, Fisher's post-hoc Least Significant Difference (LSD) tests confirmed that animals returned to the goal box more quickly for a male target compared to an empty goal box ($p=.012$), while female targets generated somewhat faster run times than an empty goal box but not significantly so ($p>.05$). There was also a significant interaction between hormone and target, $F(2, 30) = 4.5$, $p<.05$, indicating that the speed with which the subjects returned to the goal box for a specific target differed as a function of whether or not they were in estrus. No three-way interaction (hormone $\times$ target $\times$ experience) was found. An examination of the two panels of Figure 2 clearly shows that estrus reduced run times for both the male target and the empty goal box conditions while increasing run times for female targets. Finally, the ANOVA yielded a main effect of sexual experience, $F(1, 30) = 6.6$, $p<.05$, where on average the rats surprisingly ran more slowly after sexual experience than they did when they were sexually naïve. However, upon closer examination of the Figure, it appears that when sexually experienced animals were tested during estrus, their run times slowed differentially across the targets compared to pre-sex performance (comparing the dark bars of each target group in Figure 2 before and after sexual experience). More specifically, sexual experience appeared to slow the run times of female subjects approaching either an empty goal box (by an average of approximately 8 sec) or approaching a female target (by approximately 14 sec) while having virtually no impact on the approach toward male targets (where run times slowed by less than 1 sec).

Experiment II

Locomotor Testing—The mean locomotor activity (distance traveled in inches, $\pm$ SEM) of the estrous and non-estrous groups is depicted in Figure 3. A two-factor (Group $\times$ Time) analysis of variance computed on the data plotted in the Figure confirmed a statistically reliable reduction in activity over time – a common finding where within-session activity slows over the course of testing as the animals acclimate to the test box (main effect of time: $F(11, 154) = 27.6$, $p<.001$). There was, however, no main effect of group, $F(1, 14) = 1.3$, $p>.05$, nor a Group $\times$ Time interaction, $F(11, 154) = 0.5$, $p>.05$). Thus both groups exhibited highly comparable reductions in locomotion over the course of the test session. The inset in Figure 3 represents the mean ($\pm$ SEM) total activity per group (total distance traveled during the one-hour testing session). As we had an *a priori* prediction that the activity of the estrous group would be greater than that of the non-estrous group, we used a one-tailed, independent samples *t* test, which confirmed that there was no difference in the behavior of the two groups, $t(14) = 1.2$, $p>.05$. Therefore, estrus did not alter the spontaneous locomotion of the rats relative to that of non-estrus controls.

Runway Testing—The mean ($\pm$ SEM) run times of the estrous and non-estrous groups on a single test trial in the runway are shown in Figure 4. Based on the performance of animals in the comparable conditions of Experiment I, it was expected that the induction of estrus would enhance the runway performance of animals in the current test. Indeed, a one-tailed independent samples *t*-test computed on the data depicted in the Figure yielded a modest group difference in run times, $t(14) = 1.7$, $p=.056$. While this tendency was both present and statistically reliable in Experiment I, the current results demonstrate that the effect of estrus to induce faster run times in the empty alley is present even with minimal training in the runway.

Open Field Testing—The mean ($\pm$ SEM) number of squares crossed (general locomotion) and the mean number of center squares entered (exploration) during a single 5 min test are depicted for the estrous and non-estrous groups in Figures 5A and 5B respectively. Although there was no significant group difference in the total number of squares entered, $t(14) = -0.1$, $p>.05$, estrous females entered the center squares of the open field more frequently than did non-estrus females, $t(14) = -1.91$, $p<.05$ (independent samples, one-tailed).

Discussion

While the female rat's role as a target of male sexual activity is well-characterized, less is understood about the female's active role in the initiation of copulation. The current study employed a model of sexual motivation to assess the incentive value of a male rat target (relative to a female rat target or an empty goal box) for female subjects in both behavioral estrus and non-estrus. Prior to sexual experience, estrous female subjects took the most time to return to an empty goal box and the least amount of time returning to a goal box containing a sexually experienced male. Such results are consistent with reports demonstrating that: sexually naïve estrous females will choose a male over a female [19,22], OVX females given estradiol benzoate alone will also choose a male [22], and that partner preference in hormone-primed females exists prior to sexual experience [23]. In the current study we also found such effects to be hormone-dependent. That is, when runway trials were conducted in the same animals during non-estrous conditions, the female subjects ran faster but equivalently for both male and female targets as compared to the empty goal box. Thus, these results suggest that while female sexual motivation in rodents is largely under the control of their internal hormonal state [24–28] male and female targets also have value as social reinforcers for non-estrous females.

Sexual experience for female rats produced complex behavioral results that varied as a function of the animals' hormonal condition. While the overall impact of sexual experience was to slow runway behavior (i.e., when averaged across all conditions, animals exhibited slower run times after sex compared to their pre-sex responding) this effect was primarily attributable to the empty goal box and female target conditions (see Figure 2.) This was particularly obvious during estrous trials when subjects running for empty or female goal box targets were much slower post-sex compared to pre-sex, while their performance for male targets was virtually unchanged. This slowing of run times is unlikely to be a simple effect of repeated testing since, if it were, one would expect to see slower running for all targets – which was not the case. In summary then, it appears that prior to sexual experience, non-estrous female rats are motivated to approach both male and female targets, while the same rats tested during estrus run fastest for male targets (Figure 2, Panel A.) This suggests that internal hormonal state produces an unlearned motivation to seek males. Once the animals have experienced copulation, they use their internal hormonal state as a discriminative stimulus and thereby slow their runway behavior for an empty goal box and female targets, but not for male targets (Figure 2, Panel B). Finally, both before and after sexual experience, estrus produces faster run times for female rats approaching an empty goal box (see below) or one containing a male target, but slows running for female targets. If estrus indeed produces an internal motivational state of arousal related to an unlearned “male seeking” behavior, then one would expect to see the observed increase in running for male targets and slowing for female targets, as we have reported. Our results suggest that the sexual incentive value of a male is unlearned and unchanged by sexual experience.

Virtually all theories of motivation have in common the presumption that the initiation of overt responding requires some form of energy to fuel or drive the organism's behavior [e.g., 29, 30–32]. Thus, a common and primary component of hunger, thirst, sexual arousal, and drug craving, is thought to be an internal activational state that is necessary for the initiation of goal-seeking behavior. The notion that estrus represents an unlearned, internal activational state is supported by reports that estrus produces increases in spontaneous activity [as cited in 33], running wheel behavior [34,35], maze exploration [36] and that estrogen itself can increase general locomotor activity [37] and facilitate stimulant-induced locomotion [38,39]. In the context of the current study, it was therefore presumed that estrus would produce a non-specific increase in general activity that would translate into faster running times in the alley regardless of target. Indeed, in their work using a runway-choice apparatus (in which females ran down an alley and then chose between two goal-boxes, one containing a male and the other a female

target), Eliasson and Meyerson [19] concluded that the observed increases in running observed during estrus were merely a “reflection of changes in spontaneous activity”. However, the results of Experiment I are not consistent with such a conclusion. As described above, estrous females we observed to run more quickly when the goal box was empty or when it contained a male target, but more *slowly* when it contained a female target (compared to run times of the same animals during non-estrous conditions). Experiment II was therefore devised precisely to investigate the underlying behavioral mechanisms responsible for this finding.

Experiment II involved a set of simple, well-documented behavioral tests designed to examine and further dissociate the possible effects of estrus on locomotor activity from its effects on motivation. The results of Experiment II suggest that the arousal that accompanies the induction of estrus does not simply enhance basal levels of activity, as suggested by others [e.g., 19,33, 37], but rather selectively enhances behaviors having functional utility for the subjects. If behavioral estrus was in fact producing a motivational state that induced or facilitated male-seeking behavior, then surely such behaviors ought to be most pronounced in those environments most conducive to exploration, and less obvious in small, confined spaces in which no male is obviously present. Indeed, when females were placed into the small, home-cage sized locomotor activity boxes, spontaneous locomotor activity was found to be virtually identical in estrous and non-estrous animals (Figure 3). This suggests that general ambulation was equivalent in both the estrous and non-estrous animals. Motivation, on the other hand, should induce animals to exhibit exploratory behaviors in environments conducive to such behaviors and indeed we observed that behavioral estrus produced more center square entries (Figure 5) and modestly faster ($p=0.056$) runway responses even for an empty goal box (Figure 4). This interpretation of our results is in fact consistent with demonstrations that estrus is related to decreases in the anxiety associated with exploring novel environments, and overall increases in novelty seeking behaviors [e.g., 40,41–43]. Thus the enhanced run times exhibited by estrous females in the empty target condition can be accounted for by the motivational state of the animal and not some non-specific general arousing consequence of estrus.

In summary, then, our findings first confirm that the incentive value of males appears to be unlearned; that is, sexually naïve females will traverse an alley as fast as sexually experienced females to reach a male target. Second, that the behavioral impact of sexual experience is to reduce the incentive value of social targets (a female rat) during behavioral estrus such that experienced females no longer prefer female targets to an empty goal box during estrus. Finally, that these increases in behavioral output seen in estrous animals are not likely a result of general arousal as previously suggested [e.g., 19,33,37] but rather due to the presence of a motivational state that appears as a function of estrus itself.

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Figure 1.

A schematic representation of the runway apparatus. Note that the circular goal box is partitioned by a perforated Plexiglas wall that permits subjects who are placed on one side to see, hear and smell, but not come in direct contact with, target stimuli placed on the opposite side. Subjects are exposed to the target stimulus, then lifted and placed in the start box. The doors to the start box and goal box then open and the time required for the animal to return to the goal box (run time) provides an index of the subject's motivation to seek the target stimulus.

Figure 2.

Mean (+ SEM) run times of three groups of female rats returning to a goal box containing one of three different target stimuli: an empty goal box, a female rat, or a male rat. Each animal was tested under both estrus (dark bars) and non-estrus (open bars). Panel A depicts the run times of sexually naïve animals and Panel B represents the run times of the same animals a week after having experienced sexual behavior. A 3-factor ANOVA on the combined data (see Results for more details) confirmed a significant main effect of target ($p < .05$) (when averaged across all trials, females ran fastest for males and slowest for an empty goal box), a main effect of experience ($p < .05$) (overall animals were slower in the runway after sexual experience than before it), and a hormone $\times$ target interaction ($p < .05$) indicating that estrus produced different effects depending upon the goal box target (e.g., faster running for male but not female targets).

Figure 3.

Mean ($\pm$ SEM) locomotor activity (measured as distance traveled in inches) assessed every 5 min during a 60 min test session for two groups of female rats. One group was tested during estrus and the other during non-estrus. The inset represents the overall mean total activity ($\pm$ SEM) summed over the entire 60 min test. There was no statistically reliable difference in locomotor activity between the two groups.

Figure 4.

Mean (+ SEM) run times in the alley for two groups of female rats returning to an empty goal box. These data were collected during a single test trial with half the animals in estrus and half non-estrus. There was a statistically modest ($p=0.056$) increase in run times in the estrous relative to the non-estrus group.

Figure 5.

Mean (+ SEM) open-field behavior of two groups of female rats (one in estrus and the other non-estrus) during a single 5 min test. Panel A depicts the mean total number of squares entered (a measure of general locomotor activity) and panel B depicts the mean number of center squares entered (a measure of exploratory behavior). While there were no difference in total square entries, the estrous group exhibited more center square entries (less thigmotaxis or “wall-hugging” behavior) than the non-estrus group (Panel B, $p < .05$).