Delineating Sexual and Social Motivation in the Female Rat Using Operant Responding

by

Kristin A. Kops

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Advisors: Dr. Jill Becker and Dr. Jennifer Cummings

Abstract

Our laboratory has recently developed an apparatus that utilizes an operant response paradigm to allow for quantification of sexual motivation. In order to fully understand sexual motivation, social components of interaction between animals must also be taken into account. The experiment presented here uses a within-subjects design to compare the social and sexual motivation of a group of female rats by comparing operant responding for a sexual versus a social partner (i.e., an intact versus a castrated male, respectively). The findings suggest that while the current measure of motivation (i.e., nose pokes per door opening) was not different between the castrated and intact males, the number of responses in the active hole and the number of door openings was significantly higher with the intact male thus suggesting higher motivation to obtain access to a sexual partner.

Keywords: operant response, social behavior, sexual behavior, hormone priming

Delineating Sexual and Social Motivation in the Female Rat Using Operant Responding

Research thus far concerning reproductive behavior in the rodent has focused largely on the ability to engage in copulation and the act of engaging in copulation itself. While some research has attempted to examine sexual motivation, it has been largely focused on the male, leaving a significant gap regarding the study of female sexual motivation. Recently, more emphasis has been placed on the importance of the female and her behavior surrounding sexual encounters. Of the studies that have attempted to measure females' motivation to engage in sex, considerable limitations exist suggesting the need for the creation of a new paradigm. Specifically, a paradigm that measures female sexual motivation in a quantitative manner is required. When observing sexual interactions, however, it is important to keep in mind that the social aspects of the encounter provide a social reward for both male and female rats. Therefore, when quantifying female sexual motivation, it is important to consider the possibility that motivation for social interaction may contribute to what is observed and quantified as sexual motivation. If social interaction plays a role in sexual interactions and motivation, it is imperative that the two forms of motivation are delineated for the purpose of investigating both forms of motivation separately.

New Quantitative Paradigm for Female Sexual Motivation

Constructing the appropriate paradigm to quantify female sexual motivation has not been easy. Previous studies examining female sexual motivation have used a multi-level apparatus and consequent level changing exhibited by the female as a measure of female sexual motivation (Afonso, Sison, Lovi, & Fleming, 2007; Pfaus, Smith, & Coopersmith, 1999). However, whether the number of level changes exhibited by the female prior to the introduction of the male equates to female sexual motivation is debatable. In addition, level changes could be caused by the desire for social interactions as opposed to motivation for sexual activity. Other researchers have used female proximity to a sexually active male as a measure of sexual motivation (Clark, Pfeifle, & Edwards, 1981; Cummings & Becker, 2012; Edwards & Pfeifle, 1983; McDonald & Meyerson, 1973; Meyerson, Lindstrom, Nordstrom, & Agmo, 1973; Williams, Goldman, McGinnis, Possidente, & Lumia, 1991). However, proximity to a sexually active male could also be a result of social interest in the male. As such, these paradigms do not differentiate between female sexual and social motivation.

Cummings and Becker (2012) published a study that utilized a two-chambered apparatus that quantified female sexual motivation through employment of an operant response paradigm (i.e., nose pokes). The chamber allowed for the female to demonstrate her motivation to gain access to the male through the amount of nose pokes she exhibited before obtaining access to the male (Cummings & Becker, 2012). Consequently, it is possible that the female would demonstrate motivation to gain access to other stimulus animals (i.e., a castrated male or another stimulus female) which could be used to evaluate the female's social motivation. The chamber also allows for female paced interaction (i.e., the female controls the rate of sexual encounter with the male), which, as described below, can have significant effects on motivation.

Female Paced Mating and Sexual Motivation

Females find sexual interactions rewarding when they are able to pace the sexual encounter (Jenkins & Becker, 2003b; Paredes & Vazquez, 1999). This is partially due to the rewarding nature of the sexual stimulation that they receive (Paredes & Vazquez, 1999). Female paced interaction has also been shown to cause dopamine (DA) release in the nucleus accumbens (NAcc) before sexual interaction which is important for reward in the brain (Jenkins & Becker, 2003a; Mermelstein & Becker, 1995). Therefore DA increases in the brain could be an

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important factor in the motivation to seek sexual interaction. Research has also shown that female paced sexual interactions are a key component to the onset of the progestational response and therefore the females' reproductive success (Coopersmith & Erskine, 1994; Yang & Clemens, 1997). Therefore, models utilizing female paced sexual interactions are imperative for the study of female sexual motivation because sexual stimulation, DA release, and the progestational response could all be components contributing to female sexual motivation.

In addition to factors influencing motivation, there is also evidence that conditioned place preference (CPP) takes place during sexual interactions. A CPP develops when a positive source of reinforcement or stimulation causes one environment to be more preferable than other environments not associated with that positive reinforcement or stimulation. This is especially true when the female is able to pace her interaction with the male and when she receives vanginocervical stimulation from the male (Jenkins & Becker, 2003b; Meerts & Clark, 2009).

Socially Rewarding Behavior

Rats receive a social reward when interacting with other rats. As they become more used to a social interactions, the rate and frequency at which they approach a social partner increases (Peartree et al., 2012). The idea of socially rewarding interactions has been looked at in detail, and results have indicated that even limited contact with another rat (i.e., through a mesh barrier) is rewarding enough for the establishment of a CPP (Calcagnetti & Schechter, 1992; Peartree et al., 2012).

An inherent component of sexual activity is the social interaction due to proximity of the animals. When in close proximity during a sexual interaction, social rewards are also present in addition to the sexual rewards. In rats, social interactions between the mother and her pups decrease fear and stress responses later on in adulthood (Ruthschilling et al. 2012). Trezza,

Campolongo, and Vanderschuren (2011) also found that rats that did not partake in social play during adolescence were more likely to have social and cognitive consequences when they reached adulthood. Clearly, social interaction is necessary for proper social and cognitive functioning as well as reasonable responses to environmental stimuli (Han, Li, Xue, Shao, & Wang, 2012; Trezza et al., 2011). As a result, social interaction is vital to fitness and survival of the species. Therefore, when looking at female sexual motivation, motivation for the social aspects of the encounter must also be considered.

Brain Regions Involved in Sexual and Social Behavior

Social play behavior in the rat is mediated in part by the NAcc (Han, Wang, Shao, & Li, 2011; Niesink & Ree, 1983; Ploeger, Willeman, & Cools, 1991). Lack of social play has been shown to cause increased expression of the D2 dopamine receptor in the NAcc (Han et al., 2012). This indicates that low levels of social play correlate with increased sensitivity to DA release in the brain. With high sensitivity to DA, there would likely be an abnormal response to activities that cause DA release in the brain. Therefore, healthy levels of social play are important for proper response to DA releasing activities. One behavior that releases DA in the brain is sexual activity (Moses, Loucks, Watson, Matuszewich, & Hull, 1995; Pleim, Matochik, Barfield, & Auerbach, 1990). Therefore, social play behavior is necessary for proper response to sexual behavior. Particularly for females, the NAcc mediates sexual receptivity, proceptivity, and pacing behavior (Jenkins & Becker, 2001; Rivas & Mir, 1990). Thus, it is also likely involved in mediating sexual motivation. It is important to note, however, that sexual behavior and social behavior, while mediated by the same part of the brain, are separate forms of behavior and should be treated as such (Vanderschuren, Niesink, & Van Ree, 1997). Consequently,

differentiating between sexual and social behavior and motivation is difficult but it must be done in order to fully understand them both.

Using an Operant Response Model to Differentiate Between Social and Sexual Motivation

For this experiment, an operant response model was utilized in order to quantify sexual and social motivation for the purposes of determining if a difference between sexual and social motivation exhibited by the female could be observed. This model has been used previously to test hormonal control of motivation in the female rat and has demonstrated that females showed increased motivation to gain access to a sexually active male when they were hormone primed (Cummings & Becker, 2011). In the current study, we will further examine the difference between female sexual and social motivation in hopes of differentiating between the two forms of motivated behavior by comparing the nose pokes per door opening exhibited for a sexually active male (i.e., an intact male) versus a sexually inactive male (i.e., a castrated male), as well as investigating the females' behavior during both types of testing sessions. In addition, we hope to determine if the current operant response paradigm used to test sexual motivation can be applied to differentiate between sexual and social motivation.

We hypothesized that the female's motivation to gain access to a sexually inactive male would be less than her motivation for a sexually active male because we believe that the sexual reward for an interaction will be greater than the social reward alone. In addition, sexual versus social interactions will be distinguishable since they are dependent on the state of the stimulus male (i.e., intact or castrated). To this end, we hypothesized the females would demonstrate significantly fewer nose pokes per door opening, showing decreased motivation to gain access to the castrated male as compared to the intact male. We also hypothesized that the behavior exhibited by the females would differ depending on the stimulus male.

Method

Subjects

For the experiment, eight 55-60 day old Long-Evans female rats were obtained from Charles River in Portage, MI. When the animals arrived at the laboratory, they were housed in same-sex pairs. Animals were allowed continuous access to rat chow and water. The animal housing rooms were put on a reverse light cycle of 14:10 with 14 hours of light and 10 hours of darkness (lights off at 10:00 am and on at 8:00 pm each day). Reversing the light cycle allowed for testing to be conducted during the animals' active period. The temperature of each room was between 20 and 22 °C for the entire experiment. Shortly after their arrival in the laboratory, females were ovariectomized. Ovariectomies were performed under Isoflurane anesthesia (5% given via inhalation) and ovaries were removed via a single, dorsal incision. Females were allowed two weeks to recover before beginning the experiment. All animal use protocols were approved by the University of Michigan Committee on Use and Care of Animals (UCUCA) and experiments were conducted in accordance with the National Institutes of Health (NIH) guidelines for laboratory animal care and use.

In addition to the experimental animals, ten 60-80 day old Long-Evans male rats were obtained from Charles River in Portage, MI for use at stimulus animals. Males were randomly assigned into two groups, intact and castrated. The males in the castrated group (n=4) were castrated using Isoflurane anesthesia (5% given via inhalation) and testicles were removed via two small incisions on the bottom of the scrotum. Males were allowed four weeks to recover prior to testing. No hormone was given to either group of males for the entirety of the experiment.

Apparatus

Training and test sessions occurred in an operant response apparatus that permitted for sexual interaction while allowing the female to control the rate of the interaction (described in detail in Cummings and Becker (2012)). The operant response apparatus that was used contained two chambers separated by a door. The two chambers included a chamber where the female is originally placed during the experiment and where she returns after interaction with the male (i.e., the operant compartment). This chamber is also where the female exhibits nose pokes (that is, the operant response) in order to gain access to the male. The operant chamber contains two nose poke holes on the wall along the back of the apparatus. The nose poke hole that is nearest the door acted as the active hole, and responses in this hole resulted in activation of the appropriate fixed ratio schedule. The other nose poke hole was an inactive hole, in which responses activated the corresponding light and were recorded but did not contribute to responses utilized for opening the door.

The stimulus males were tethered in the male chamber and remained there for the duration of the test. The tether was made of a very strong wire, which was attached to the back of a suede coat worn by the male as well as to the corner of the chamber. The suede coat that the male wore contained arm holes and wrapped around his upper body to Velcro across his back. This allowed the male the ability to move around his side of the chamber as per normal including the ability to perform usual sexual and social acts with the female while restraining him from entering the operant chamber. In order to accommodate for sexual activity, the male chamber is slightly larger than the operant chamber.

The female was allowed to move back and forth between the chambers when the door was open, and the opening of the door was dependent on different fixed ratio or fixed interval schedules. A Sony Mini DV HandyCam was connected to the computer and utilized by ANYmaze to track the female's movements and nose pokes so that the computer could control the activation of the light above each nose poke hole and the opening of the door at the appropriate times.

Procedure

Before each testing session, the females were hormone primed to induce sexual receptivity. Females were given 10 μ g β -estradiol benzoate (EB; subcutaneous injection) prepared in 0.1 ml of peanut oil, 48 hours before testing, and 500 μ g progesterone (P; subcutaneous injection), also prepared in 0.1 ml of peanut oil, 4-6 hours before testing.

Testing occurred once per week during the middle of the animal's dark period in a manner similar to that described in Cummings and Becker (2012). During the first three training sessions, the female was allowed to roam the apparatus with the door open and an intact male tethered in male chamber. During this phase of training, the female was free to engage in sexual activity and pace the rate of the interaction, allowing her the opportunity to get used to the chamber. After the first three sessions with the door open, the door between the chambers was closed and each female was trained to exhibit nose pokes in order to open the door, allowing her access to the male chamber and consequently the male. Training began on a fixed ratio (FR) 1 schedule, in which the door between the chambers opened upon each nose poke in the active hole. The first FR 1 test was experimenter controlled and the second FR 1 test was computer controlled. Following the FR 1 tests, females were moved to an FR 3 schedule for one test (i.e., the door opened after 3 active nose pokes).

Finally, the females were switched to a fixed interval 15 second (FI 15 s) test. In the FI 15 s tests, the first nose poke in the active hole began a 15 second timer and the first active nose

poke at the conclusion of the 15 seconds opened the door. The amount of nose poking exhibited in the 15 seconds was variable and was used as a measure of sexual motivation, as females who are more motivated to obtain the reward (i.e., interaction with the stimulus male) will work harder to open the door (Cummings and Becker, 2012). In this experiment, the nose poking exhibited in the 15 seconds was also used as a measure of social motivation when the female was poking to gain access to a castrated male, as the castrated males were not capable of engaging in sexual activity. The nose poke and door opening data from each group were also examined separately as number of nose pokes and number of door openings can be individually indicative of the female's motivation.

The female was tested on a FI 15 s schedule in a hormone primed condition with an intact male and a castrated male on separate occasions. The second time that the female was tested on a FI 15 s schedule, the data were recorded and analyzed for the purpose of the study. 30 minute tests were recorded but only 15 minutes of each test were analyzed for consistency with the Cummings and Becker (2012) study. Data from one of the eight females was eliminated due to the female's distraction with jumping out of the cage for the entirety of each of the final testing periods.

The data recorded by the ANY-maze program included latency to first nose poke, latency to first door opening, number of door openings, and number of nose pokes in the inactive and active holes. From these data, average number of nose pokes per door opening was calculated. The JWatcher Program (UCLA Office of Instructional Development) was used in order to determine the time spent in the operant chamber, time spent in the male chamber, and time spent in the doorway of the apparatus. The videos were scored by the same experimenter after all of the testing had been completed. The data were analyzed using a pairwise comparison that utilized a paired samples t-test to analyze within subjects data of the female when she was partnered with a castrated male versus an intact male.

Results

Figure 1 shows that females exhibited significantly more active nose pokes on average per session when tested with the intact male compared to the castrated male (p = 0.021). Thus, when a sexually active male was present the female worked more to gain access to the male. Figure 2 shows that the number of door openings was greater when an intact male was in the other chamber, compared to a castrated male (p = 0.021). Females exhibited more nose pokes and activated the door significantly more to reach the intact male, however, the number of nose pokes exhibited per door opening for the castrated and intact males was not significantly different between groups (data not shown).

Male condition did not affect the latency to first door opening or first active poke since there was not a significant difference between the groups (data not shown). When looking at time spent in various regions of the chamber, however, male condition was important in determining where the female spent the majority of her time. Figure 3 shows females spent significantly more time in the operant chamber when paired with an intact male than when paired with a castrated male (p < .001). This means that the female spent significantly more time away from the male when paired with the intact male compared to the castrated male. As shown in Figure 3, when paired with a castrated male females spent significantly more time in the doorway (p = .001) and in the male chamber (p = .001) than when tested with the intact male. Therefore, the female spent more time in locations that were in close proximity to the male when paired with the castrated male compared to the intact male.

Looking within groups, Figure 3 shows that when the female was tested with the castrated male, she spent significantly more time in the male's chamber compared to time spent

in the doorway (p = 0.010) and the operant chamber (p = 0.017), again indicating that the female would prefer to spend more time in close proximity to the castrated male rather than alone in the operant chamber. When the female was tested with the intact male, Figure 3 shows that she spent significantly more time in the operant chamber than the male side (p = .004), and significantly more time in the male side than in the doorway (p = .002). Therefore, when paired with the intact male, the female preferred to spend the most amount of time in the operant chamber rather than in close proximity to the male (either in the male chamber or in the doorway; in view but out of reach of the male).

Discussion

With the creation of a new paradigm to measure female sexual motivation by Cummings and Becker (2012), it is important to consider the likelihood that social motivation has a significant contribution to overall female sexual motivation and to understand the need to differentiate between the two. The current study found that a female who was hormone primed exhibited more active nose pokes for a sexually active male (i.e., the intact male) than for a sexually inactive male (i.e., the castrated male). In addition, the females also had a significantly higher number of door openings when paired with the intact male. The significantly greater number of door openings indicates that the female worked to gain access to the intact male more frequently than the castrated male during the 15 minute testing period. This also indicates that the female was pacing her interaction with the intact male as she would normally do during a sexual interaction, leaving the male after sexual contact and returning some time later. Indeed, in all cases when females were paired with the intact males, sexual activity did occur in contrast to the lack of copulation during sessions with castrated males.

The significantly decreased amount of time that the females spent on the male's side during testing with the intact male is further evidence that the females were pacing the

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interaction. The decreased time spent on the male's side can be explained as a result of the female leaving the male after each intromission and ejaculation during sexual encounters. Since the female had more frequent, shorter encounters with the sexually active male indicating that she was pacing properly, we can assume that amount of time spent near the male is not the only indicator that should be taken into account when measuring sexual motivation as has been found in other studies (Clark et al., 1981; Cummings & Becker, 2012; Edwards & Pfeifle, 1983; McDonald & Meyerson, 1973; Meyerson et al., 1973; Williams et al., 1991). However, hormone priming, as was used in the current study, does increase the female's appetitive behavior and preference for interactions with a male compared to a non-hormone primed state (de Jonge & van de Poll, 1986). In this case, it is possible that the hormone priming influenced the female to be near the castrated male for the opportunity to copulate even though he was sexually inactive.

It is possible that the increased amount of time the females spent in the male's side of the chamber while being tested with the castrated male was due to increased social interest in the castrated male or a social CPP. On the other hand, it could indicate that the females formed a CPP for the male's side of the chamber when they were engaging in sexual activity with the intact male during a separate test. Since females were tested in the same chamber for every round of testing, it is possible that they developed a CPP in the male's side of the chamber due to sexual interaction with the male in that chamber during testing (Jenkins & Becker, 2003b).

It is difficult to say if the condition placed preference came from sexual behavior or social behavior that took place in the chamber because the females were exposed to the castrated males two times prior to the final round of testing. Therefore, the CPP could have been a result of sexual or social interactions that took place in the male's side of the chamber before the final round of testing. Experimenters have observed that paced sexual encounters, interactions with castrated males, and olfactory memory may contribute to the development of a CPP in rodents (Coria-Avila, Ouimet, Pacheco, Manzo, & Pfaus, 2005; Jenkins & Becker, 2003b; Oldenberger, Everitt, & De Jonge, 1992). All of these variables could have contributed to a CPP in the male's side of the chamber. This CPP was less obvious for the sexually active males because the females were actively engaged in copulation and, as such, were pacing the sexual encounters. In order to eliminate the possibility of a CPP, females could be tested without another animal in the male's chamber. Another option would be testing with a variety of chambers or wiping down the apparatus and changing the bedding after each testing session to eliminate olfactory influences on formation of a CPP.

Latency to first door opening was not variable and could also be a consequence of a CPP. This finding was expected since the female did not know which male she was poking for at the beginning of the test. However, the amount of nose pokes during the first 15 second interval could have acted to skew the nose poke per door opening motivation data since the female could have been highly motivated at the beginning of the test to see which male, castrated or intact, would be in the male's chamber. In addition, the amount of nose pokes per door opening may have seemingly blunted the female's motivation to gain access to the male since she never knew which male would be in the male's chamber during testing. To eliminate the possibility of this problem in the future, testing for sexual motivation and social motivation could be grouped together rather than interspersed so that the female would know what stimulus animal she is poking for at the beginning of the test and thus her motivation throughout the test would be indicative of sexual or social motivation, specifically.

Aside from the paradigm, it is possible that the amount of training sessions that were conducted before the final testing session affected the outcome. Because of the rigorous testing

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schedule, it is possible that the females learned that they only needed to poke at the end of the 15 seconds to get the door open, instead of continuously poking to gain access to the male. In order to address this hypothesis, we subsequently examined the data for the first round of FI 15 s tests. This did not yield significantly different results for nose pokes per door opening between the intact and castrated male as was seen in the second test. Therefore, either the females did not realize that they were on a 15 s interval or they had learned this prior to our examination.

Finally, the males that were used as castrated males to observe social motivation were not castrated until after engaging in sexual encounters during adulthood. Remaining hormones or previous sexual experiences in the castrated males could have influenced the females to exhibit the same amount of motivation to gain access to the castrated males as they would for the intact males. If the males had been castrated from birth, or at least prior to sexual experiences, the tests may have yielded different results. Alternatively, using other animals as social stimulus animals (i.e., another female) may eliminate this problem.

While the current paradigm for evaluation of sexual motivation did not differentiate between sexual and social motivation with respect to number of nose pokes per door opening, it did show that sexual and social motivation could be distinguished by the total number of operant responses in the active nose poke hole and the number of door openings. For example, when paired with a sexually active male, females worked to open the door more frequently and also display more active nose pokes per session than when paired with the sexually inactive male. In order to further examine the differences between sexual and social motivation, modifications to the current testing paradigm could be employed to gain an even better understanding of how to differentiate between sexual and social motivation.

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Author Note

Kristin A. Kops, Department of Psychology, University of Michigan, Ann Arbor.

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My address for correspondence is 4216 Locust Lane, Jackson, MI, 49201. I can also be reached by email at kristinalexis248@gmail.com.

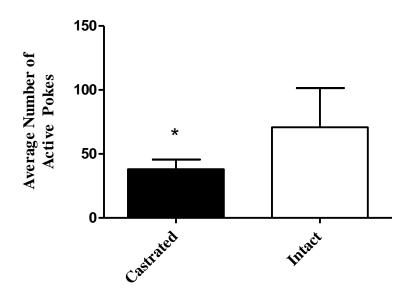


Figure 1. This graph is a representation of the average amount of active nose pokes exhibited by the females for each testing session. The female poked significantly more to gain access to the intact male (indicated by the *, p = 0.021).

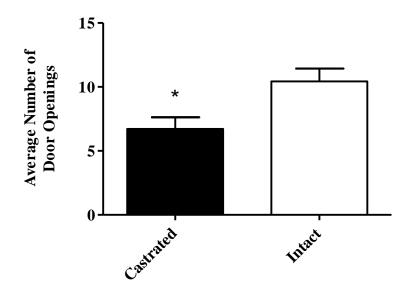


Figure 2. This graph represents the average number of door openings per testing session with intact and castrated males. Females opened the door significantly more when tested with the intact male than when tested with the castrated male (indicated by the *, p = 0.021).

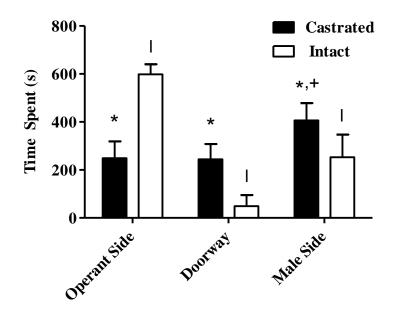


Figure 3. This graph is a representation of the amount of time that the female spent in each chamber of the apparatus during the 15 minute testing session. When paired with the intact male, the female spent significantly more time in the operant side of the apparatus than when paired with the castrated male (indicated by the *, p < 0.001). The female also spent significantly less time in the doorway (indicated by the *, p = 0.001) and on the male side (indicated by the *, p = 0.001) when paired with the castrated male compared to the intact male. As far as amount of time spent in each area within a session, during testing with the castrated male, females spent significantly more time in the male's chamber that in the doorway or the operant chamber (indicated by the +, p = 0.010, 0.017). However, during testing with the intact male, females spent significantly more time in the operant chamber than in the male's chamber (indicated by the 1, p = .004) and significantly more time in the male's side than in the doorway (indicated by the 1, p = .002) indicating that the time spent in each location was significantly different than the time spent in either of the other locations.