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Conditioned Sexual Arousal in a Nonhuman Primate

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Abstract

Conditioning of sexual arousal has been demonstrated in several species from fish to humans, but has not been demonstrated in nonhuman primates. Controversy exists over whether nonhuman primates produce pheromones that arouse sexual behavior. Although common marmosets copulate throughout the ovarian cycle and during pregnancy, males exhibit behavioral signs of arousal, demonstrate increased neural activation of anterior hypothalamus and medial preoptic area and have an increase in serum testosterone after exposure to odors of novel ovulating females suggestive of a sexually arousing pheromone. Males also have increased androgens prior to their mate's ovulation. However, males presented with odors of ovulating females demonstrate activation of many other brain areas associated with motivation, memory and decision making. In this study we demonstrate that male marmosets can be conditioned to a novel, arbitrary odor (lemon) with observation of erections, and increased exploration of the location where they previously experienced a receptive female, and increased scratching in postconditioning test without a female present. This conditioned response was demonstrated up to a week after the end of conditioning trials, a much longer lasting effect of conditioning than reported in studies of other species. These results further suggest that odors of ovulating females are not pheromones, strictly speaking, and that marmoset males may learn specific characteristics of odors of females providing a possible basis for mate identification.

Keywords

Sexual conditioning; sexual arousal; pheromones; common marmosets; pair-bonding

Introduction

One of the puzzles of research on sexual conditioning is why evolutionary processes should allow organisms to respond to unnatural cues for sexual arousal. However, a few studies have demonstrated that sexual conditioning actually increases reproductive success and fitness. In fish, blue gouramis (*Trichogaster trichopterus*), Hollis and colleagues (Hollis *et al*, 1989, 1997) found that Pavlovian conditioned signaling in advance of the presentation of a mate inhibited territorial aggression and increased courtship and appeasement behavior. As a result conditioned males spawned sooner with females, clasped females more often and produced more surviving young than males that did not have mate arrival signaled. Domjan

et al. (1998) demonstrated that male quail conditioned to expect a female after presentation of orange colored feathers produced greater volumes of ejaculate and greater numbers of spermatozoa than control quail, also suggesting an adaptive advantage to sexual conditioning.

Conditioned sexual arousal or conditioned sexual inhibition has also been of considerable research interest for possible therapeutic reasons to either increase or decrease sexual arousal or provide models for how sexual responses might be redirected to other targets. Much of the basic work has been carried out with nonhuman animals. For example, Crowley *et al.* (1973) used a tone paired with mild electric shock to stimulate copulation in sexually unresponsive male rats so that they would pace sexual behavior to the tone stimulus alone. Zamble and colleagues (1985, 1986) placed male rats in distinctive containers adjacent to receptive females and found decreased latencies to ejaculation. They also showed that 6–9 conditioning trials were needed and that rats became conditioned to background stimuli as well. Kippin *et al.* (1998) paired a presumably neutral almond odor (but see below) with access to sexually receptive female rats and found a learned ejaculatory preference for that female with the conditioned odor. Domjan *et al.* (1988) found that Japanese quail (*Coturnix japonica*) demonstrated both conditioned approach behavior and conditioned copulation behavior to the head and neck of a female adorned with orange feathers. Johnston *et al.* (1978) paired aversion inducing lithium chloride with exposure to female vaginal secretions in male hamsters (*Mesocricetus auratus*) and found increased latency to sniff secretions and to mount a female after aversion training. In a study on female hamsters Meisel and Joppa (1994) found a conditioned place preference for the compartment in which they had engaged in sexual activity with a male. McDonnell *et al.* (1985) developed a model of sexual dysfunction in stallions (*Equus caballus*) using erection-contingent aversive training and could reverse these effects with Diazepam. These are illustrations of the type of sexual conditioning research, to facilitate or to deter sexual behaviors, done with nonhuman animals. For further reviews see Pfaus *et al.* (2001 (2004) and Akins (2004).

Similar studies have been done with humans with a few examples reviewed here. Letourneau and O'Donohue (1997) failed to find evidence of conditioned sexual arousal in women when an amber light was paired with erotic videotapes. Lalumière and Quinsey (1998) studied men using pictures of scantily clad women paired with an erotic videotape of sexual intercourse and found a modest, 10%, increase in genital arousal to the target stimulus presented alone after conditioning. Hoffmann *et al.* (2004) presented men and women with pictures of the abdomens of the opposite sex versus pictures of a gun using both subliminal and supraliminal exposure times. Both sexes demonstrated greater genital arousal to the subliminal pictures of abdomens than to guns, but oddly women showed greater conditioned arousal to supraliminal presentation of pictures of guns rather than to pictures of abdomens. Both *et al.* (2004) measured genital and subjective responses to neutral versus sexual films and asked participants to track sexual desires, fantasies and actual sexual activities for the day following exposure. Both men and women exhibited genital arousal and reported subjective feelings of arousal and lust after viewing the sexual film and these participants also had higher rates of sexual thoughts, fantasies and activities in the day following the study. What is noteworthy about these studies on humans is the failure to find strong conditioning to neutral stimuli and the broad use of erotic stimuli both as conditioned and unconditioned stimuli. These studies differ notably from the appetitive conditioning studies on animals that have used neutral physical environments, arbitrary visual stimuli, tones or odors as conditioning stimuli.

Although a wide range of taxa from fish to birds to rodents to stallions to humans have exhibited some form of sexual conditioning, we have not located any prior studies of sexual conditioning with nonhuman primates. An examination of sexual conditioning in nonhuman

primates is of value not only for greater taxonomic completeness, but also to provide empirical data on a controversy concerning mechanisms of sexual arousal in nonhuman primates.

In a landmark paper in *Nature* Michael and Keverne (1968) argued for the role of pheromones (odors that release innate behavioral responses in recipients) in communicating sexual status and inducing sexual arousal in nonhuman primates. Their research suggested the presence of a chemosensory signal from aliphatic acids in vaginal secretions in rhesus macaques varied across the ovulatory cycle and that promoted sexual arousal in males. Goldfoot (1982) rejected the notion of a vaginal pheromone in macaques finding that the aliphatic acids peaked in concentration during the luteal phase, and, contradictory to a pheromone hypothesis, males in his studies appeared to have individually preferred mates, would mate with ovariectomized females, and were attracted to the non-pheromone novel odor of green peppers. Goldfoot (1982) suggested that vaginal aliphatic acids did not serve as a sexual arousal and females, not males, regulated copulatory behavior. He further suggested that males learned various sensory features of preferred females although he did not demonstrate any conditioned sexual behavior.

The Callitrichid primates, marmosets and tamarins, are cooperatively breeding monkeys from the New World where males and females form pair-bonds and copulate throughout the ovarian cycle and even in pregnancy. For a long time it was thought that ovulation was concealed, but Ziegler *et al.* (1993) demonstrated that male cotton-top tamarins (*Saguinus oedipus*) were sexually aroused showing increased erections and increased mounts to their mates when presented with odors of a novel, ovulating female. Subsequently, Smith and Abbott (1998) demonstrated that male common marmosets (*Callithrix jacchus*) discriminated between odors of peri-ovulatory and anovulatory female marmosets. Additionally, cotton-top tamarin males demonstrate anticipatory hormonal responses to postpartum ovulatory signals of their own mate (Ziegler *et al.* 2004). Using functional magnetic resonance imaging (fMRI) methods, Ferris *et al.* (2001) showed that the odors of novel peri-ovulatory females produced significant increases in neural activation in the medial preoptic area (MPOA) and the anterior hypothalamus (AH), areas in which lesions led to diminished sexual behavior (Lloyd & Dixon, 1988).

Despite the fact that common marmosets are socially monogamous, studies in captivity (Anzenberger, 1985, Evans, 1983) found that males out of sight of their mates would demonstrate courtship behavior to novel females, and in the wild Digby (1999) and Lazaro-Perea (2001) found frequent sexual behavior between marmosets of different groups involving all but the breeding female in each group. Thus, despite social monogamy, male marmosets appear ready to mate with novel females, especially at ovulation. These findings were supported in part by Ziegler *et al.* (2005) which found that single and pair-housed male marmosets demonstrated behavioral interest and arousal in the odors of novel peri-ovulatory females as evidenced by increased rates of sniffing and erections and a significant elevation of serum testosterone levels relative to vehicle control odors. These findings suggest that perhaps in contrast to Goldfoot's (1982) findings in rhesus monkeys, in marmosets there may be a direct stimulatory effect of female peri-ovulatory scents and male sexual arousal.

However, there are some contradictory results that suggest caution in this interpretation. In Ziegler *et al.* (2005) an additional group of males who were fathers at the time of testing did not respond behaviorally and showed a minimal hormonal response to the odors of novel, peri-ovulatory females. Hence something about being a father affected the response to the odor. Furthermore, additional analyses of neural responses to peri-ovulatory odors during fMRI (Ferris *et al.* 2004) showed that many brain areas in addition to the MPOA and AH were activated. These included increased positive Blood Oxygen Level Dependent (BOLD)

signal to peri-ovulatory odors in striatum, hippocampus, septum, periacqueductal gray and cerebellum and increased negative BOLD signal to anovulatory odors in temporal cortex, cingulate cortex, putamen, hippocampus, substantia nigra, MPOA and cerebellum. Many of these areas are involved in sensory evaluation, decision making and/or motivation. The fact that fathers are less responsive to peri-ovulatory odors from novel females and that multiple brain areas beyond those involved in sexual arousal suggest that the scents of peri-ovulatory females are not acting as a true pheromone or that a true neuroendocrine response only occurs when males are presented with a socially relevant odor, *i.e.* one's mate with family males and a novel female with non-pair bonded males.

If marmosets that are not fathers can be conditioned to be sexually aroused by a novel, arbitrary odor, then it is likely that males do not respond automatically to female odors but in fact are able to identify specific olfactory features associated with mating. If conditioning to an arbitrary odor is successful, it might explain why fathers are non-responsive and why brain areas involved in evaluation and motivation are activated by female odors in addition to areas directly involved in sexual arousal.

In the current study we attempted to condition males to anticipate copulation with a sexually-receptive peri-ovulatory female using lemon extract as a conditioned stimulus unrelated to endogenous unconditioned cues of sexual arousal. We selected the lemon extract conditioned stimulus because (1) our subjects had no prior experience with this scent and (2) lemon (limonene) showed a low level of basal BOLD activation compared with other odors, especially almond (benzaldehyde) which produced spontaneous activation in many cortical and subcortical regions (Ferris et al., in review).

Materials and Methods

Subjects and Housing

We tested four adult male marmosets ranging in age from 3.5 to 6 years. Two of the males were brothers housed together with no prior sexual experience or exposure to an ovulating female other than their mother. The other two males were housed with female partners whose ovulatory cycles were controlled using 0.75 to 1.0 µg Estrumate, a prostaglandin F2α analogue (cloprostenol sodium). The two brothers and one of the other males were subjects in our previous studies of functional magnetic resonance imaging of responses to female odors (Ferris *et al.*, 2001, 2004).

We used 14 novel peri-ovulatory females (none of them familiar to subject males) to facilitate copulatory activity with the subject males. The ovarian cycles of all these females monitored by examination of serum progesterone levels (Saltzman *et al.* 1994) were controlled with Estrumate given during the luteal phase of the cycle. The subsequent peri-ovulatory period occurred within 8–11 days after this treatment. The females were divided into four cohorts timed to reach the peri-ovulatory state within 1–2 days of each other. We collected serum samples from each female three times each week and assayed for progesterone to confirm that each female was in the peri-ovulatory phase at the desired time.

All animals were housed as pairs in cages that were 0.6 × 0.91 × 1.83 m (W X L X H). Pairs were housed in colony rooms where they could see, hear and smell other marmosets. Animals were fed at midday and no afternoon testing was done until at least 1.5 hours following the midday feed. Additional colony and husbandry conditions have been described by Saltzman *et al.* (1994).

Design

Behavioral testing consisted of 5 phases (Fig. 1): Two habituation phases, preconditioning test phase, conditioning phase, and a post-conditioning test phase. During all phases the cage-mate was removed from the cage and curtains were installed over the cages of other animals in the room to prevent test males from seeing other marmosets to reduce territorial displays and maximize attention on conditioning trials. The first habituation was carried out over three successive days and involved mate removal, placement of curtains and adding the empty stimulus box to the cage. The second habituation involved mate removal, placement of curtains and stimulus box and the addition of an observer and was carried out over four successive days.

In the pre-conditioning test phase each male received six 20 min trials after exposure to lemon scent saturated wooden discs and six 20 min trials after exposure to control wooden discs (no scent) in a randomized counter-balanced design. The stimulus box was empty with no female present during observations.

During the conditioning phase each male received twelve trials (up to 15 min) with lemon scent pre-exposure followed by access to a peri-ovulatory female released from the stimulus box. A lemon conditioning trial was ended immediately upon male copulation to ejaculation (before post-copulatory grooming or aggression could occur) or 15 min, whichever occurred first. Lemon trials were counterbalanced with control trials with ten 15 min no-lemon odor, where a peri-ovulatory female was always in the stimulus box but was not released. Conditioning trials were equally balanced between morning and afternoon session and all were completed over 9 consecutive days.

The post-conditioning testing began 5 days after the end of conditioning trials and was similar to the preconditioning test with six 20 min trials after exposure to lemon odor and six 20 min control trials. As in the pre-conditioning test phase there was no female present in the stimulus box during the post-conditioning test phase. Counter-balanced pre-conditioning and post-conditioning test trials with each stimulus were carried out over a 4 day period either immediately before the conditioning phase or starting 5 days after.

Procedure

Each morning during all phases the cage-mate was removed and not returned until the day's trials were completed. Prior to any of the behavioral trials each male was removed from its home cage and transported in a clean stainless steel box to a separate room where the nest box air holes were aligned next to a strip containing four wooden discs. On lemon scent trials each disc contained 100 μ l of lemon extract and on control trials unscented wooden discs were presented. Males remained next to the discs for four min and then the male was manually removed from the box and returned to the home cage while either a lemon scented disc or an unscented disc (depending on condition) was held under the his nose.

For conditioning trials the stimulus box had been placed in the male's cage during scent exposure and always contained a peri-ovulatory female. The stimulus box door was secured with a clip containing a wooden disc, either lemon scented or unscented. Three minutes after the male was returned the clip was removed and placed into a sealed Zip-loc bag to contain the scent. On control trials we immediately replaced the clip with another clip with no disc and the peri-ovulatory female remained in the nest box. On lemon trials the door remained open and females immediately left the nest box. We recorded behavioral data on the male for 15 min after the stimulus box clip was changed, or until an ejaculation occurred (lemon trials only). Data were collected continuously using a time-tagged laptop computer program by an experienced observer. At the end of each conditioning trial or ejaculation, the female and stimulus box were immediately removed and the male's own nest box returned with the

door open. Fresh, clean stimulus boxes were used on each trial. At the end of the day's testing, the curtains were removed and the male's cage-mate returned.

Males received at least one lemon and one control conditioning trial per day and on each conditioning trial the male was presented with a novel female. No male and female were paired more than once. A female was used in a lemon conditioning trial only once per day. For each male a female served in a control trial prior to being in a lemon conditioning trial so that a male would never encounter on a control trial a female that had previously copulated on that day.

For the pre-conditioning and post-conditioning test trials, no females were present in the stimulus box. The stimulus box had been placed in the home cage and after 3 min the clip with the lemon scented or control wooden disc was replaced with another clip and we recorded behavioral data for 20 min.

Behavioral Data Collection and Analyses

During all test phases, an experienced observer coded time-tagged actor: behavior data into a laptop computer using customized software. All animals were habituated to the observer's presence. For the pre-conditioning and post-conditioning test trials (no female was present), we recorded the frequency of stimulus box-directed behaviors of looking, sniffing, or touching the box that were summed into a single measure of box-directed behavior. We also recorded locomotor activity based on quadrant crossing frequency within the cage, scratching frequency as a measure of anxiety (Cilia & Piper, 1997; Barros *et al.*, 2000) and on an ad lib basis (depending in visibility of genitalia) whether or not an erection was observed. During lemon conditioning trials we gathered data on these measures as well as sexual behavior, including copulation to ejaculation. Data were analyzed using planned comparison two-tailed correlated samples t-tests with alpha set at 0.05. No data set was used in more than one comparison.

Results

All males and females copulated to ejaculation on every lemon conditioning trial. There was no difference between control and lemon odors in acts directed to the nest box during the pre-conditioning test phase (Mean $\pm$ SEM lemon 2.03 ± 0.48 , control 1.95 ± 0.50 , $t(3) = 0.151$, *ns*) but a significant difference between lemon and control conditions in the post-conditioning test phase (lemon 17.5 ± 3.4 , control 1.75 ± 0.85 , $t(3) = 4.70$, $p = 0.018$, Figure 2). In contrast to the box-directed behavior there was no difference in locomotion between the lemon and no lemon trials in either pre-conditioning (lemon 28.5 ± 5.83 , control 29.1 ± 7.43 , $t(3) = 0.130$, *ns*) or post-conditioning phases (lemon 23.1 ± 4.97 , control 28.9 ± 9.52 , $t(3) = 0.764$, *ns*, Figure 3). We never observed erections in any pre-conditioning trials nor in the post-conditioning control trials. However erections were observed on a mean of $79.2 \pm 14.4\%$ of lemon trials postconditioning ($t(3) = 6.33$, $p = 0.008$, Figure 4). Rate of scratching did not differ between lemon and control in the pre-conditioning phase (lemon 25.1 ± 7.36 , control 18.0 ± 3.52 , $t(3) = 1.54$, *ns*) but did differ in the post-conditioning phase (lemon 41.0 ± 8.23 , control 18 ± 4.76 , $t(3) = 4.00$, $p = 0.028$, Figure 5).

Discussion

This study shows that male marmosets can be successfully conditioned to show sexual responses to an arbitrary olfactory cue, lemon scent. It is important to point out that the conditioned stimulus, lemon odor, was paired with a period of time preceding appearance of a potential mate and was not present when the female was available for copulation. The increased proximity to the stimulus box in the post-conditioning phase is similar to a

conditioned place preference demonstrated in some other studies (e.g. Meisel & Joppa, 1994). No males demonstrated an erection on any preconditioning lemon or control trial or on any postconditioning control trial. However erections were observed on a mean of 79.2 % of postconditioning trials indicating clear conditioned sexual arousal to the lemon scent in the absence of any cues from a female. Thus the marmosets displayed robust and functionally appropriate anticipatory behavioral responses to lemon odors following conditioning. This result demonstrates that marmosets are capable of associating a novel olfactory cue with access to a peri-ovulatory female.

Since the post-conditioning trials began five days after the end of conditioning and continued for four days, the effects of conditioning were relatively long-lasting. In other studies with nonhuman animals the test trials were either administered immediately following the last conditioning trials or at the latest one day following conditioning (e.g. Domjan *et al.* 1988, Hollis *et al.* 1989, Hollis *et al.* 1997; Kippin *et al.* 1998; Zamble *et al.*, 1985, 1986).

Although two of the four males in our study were sexually naïve there was no difference between these males and experienced, paired males in numbers of copulations (all males copulated to ejaculation with all females on conditioning trials) nor were there any clear behavioral differences in post-conditioning trials. Sexually naïve marmosets were as aroused and as easy to condition as sexually experienced males.

A somewhat puzzling result is the significant increase in scratching behavior on lemon trails post-conditioning. Scratching has been identified as a behavior indicative of anxiety in studies on a closely related species ((Barros *et al.* 2000). One possible reason for increased scratching rate on post-conditioning lemon trials is that during conditioning males have been expecting to copulate with a female after the presence of lemon odor and then in postconditioning trials no females are present in the box and therefore none are available for copulation. Additional study will be needed to better understand this result.

Both common marmosets and cotton-top tamarins have been observed to distinguish between odors of peri-ovulatory and non-ovulatory females with increased sexual arousal and testosterone release (Smith & Abbott, 1998, Ziegler *et al.* 1993, 2005). Peri-ovulatory odors can activate the medial preoptic area and anterior hypothalamus in common marmosets as shown through functional magnetic resonance imaging (Ferris *et al.*, 2001).

However, the demonstration of sexual conditioning to an arbitrary odor helps resolve an apparent paradox about common marmosets. In both captive and field studies (Anzenberger, 1985, Digby, 1999; Evans, 1983; Lazaro-Perea, 2001) common marmosets engage in courtship behavior and extra-pair copulation with animals from other groups, yet a close pair bond appears to be essential for the successful rearing of young since fathers engage in extensive parental care. Under such circumstances behavior that would communicate certainty of paternity would be important. Male sexual behavior with other females in captivity is constrained when males have visual access to their mates (Anzenberger, 1985) and in the wild, although adult males have been observed in extra-group copulations when dependent infants are not present, breeding females do not engage in extra-group copulations (Lazaro-Perea, 2001), some non-breeding females participating in extra-group copulations may get pregnant but are not able to successfully rear any infants that result (Digby 1995; Roda & Medes Pontes 1998; Lazaro-Perea *et al.* 2000; Melo *et al.* 2003; Arruda *et al.* 2005; Sousa *et al.* 2005; Bezerra *et al.* 2007), providing certainty of paternity. The additional facts that (1) fathers are unresponsive to odors from novel, peri-ovulatory females by showing neither behavioral interest and lack of increase in testosterone as shown by non-father males (Ziegler *et al.*, 2005) and (2) odors of novel females induce the activation of

brain areas involved in memory, motivation and evaluation (Ferris et al. 2004) both suggest that male marmoset sexual behavior is not driven simply by an arousing pheromone secreted by a peri-ovulatory female. Instead other processes must be involved.

We suggest (as Goldfoot (1981) did for macaques) that the cues that stimulate male marmoset sexual behavior are multivariate and involve a male's social condition, whether single or paired, a father or not a father and also that males learn about specific cues related to their own mates not only odor specific cues but also vocal and visual cues as well. Note that Anzenberger (1985) found that the visible presence of a mate was sufficient to inhibit courtship of a novel female.

Studies of several species of marmosets and tamarins have reported individual recognition by odor alone (see Epplé, 1986 for review) and the current study demonstrates that males can learn to associate arbitrary odor cues with sexual experience suggesting that males may learn cues identifying their mate through sexual interactions. It will be an interesting and important topic for future research to examine neural responses of male marmosets to odors and other sensory cues of their own mates and of novel females as a function of male social status.

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Figure 1.
Timeline of habituation and testing.

Figure 2.

Mean box-directed behaviors per trial (look at, sniff, touch) in pre-conditioning and post-conditioning phases. Box-directed behaviors in post-conditioning phase lemon trials are significantly greater than on the control trials ($p = 0.018$).

Figure 3. Mean locomotor behavior per trail in pre-conditioning and post-conditioning phases. There are no significant differences between lemon and control trials for either phase.

Figure 4. Mean percent of trials pre-and post-conditioning trials where an erection was observed. There were significantly more sessions with erection to lemon than to control in postconditioning trials ($p = 0.008$).

Figure 5. Mean scratch rate per trial in pre-conditioning and post-conditioning phases. There were significantly more scratches on lemon trials than control trials in the post-conditioning phase ($p = 0.028$).