Hormones and Behavior 105 (2018) 166–176

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Hormonal contraceptive affects heterosexual but not homosexual behavior in free-ranging female Japanese macaques over 17 mating seasons

Jean-Baptiste Leca[a,*], Noëlle Gunst[a], Keiko Shimizu[b], Michael A. Huffman[c], Yukio Takahata[d], Paul L. Vasey[a]

[a] Department of Psychology, University of Lethbridge, Lethbridge, Japan
[b] Department of Zoology, Okayama University of Science, Okayama, Japan
[c] Primate Research Institute, Kyoto University, Inuyama, Japan
[d] School of Policy Studies, Kwansei Gakuin University, Sanda City, Japan

ARTICLE INFO

Keywords:
Hormonal contraception
Chlormadinone acetate
Putative fertile period
Attractivity
Proceptivity
Consortship
Heterosexual behavior
Homosexual behavior
Japanese macaque

ABSTRACT

We assessed the effect of a progestin-based contraceptive treatment (chlormadinone acetate) on female heterosexual and homosexual behaviors in a free-ranging group of Japanese macaques (*Macaca fuscata*) living at Arashiyama-Kyoto, Central Japan. The data included estimated intensity of fertility cues, sexual solicitations and mounting behaviors collected daily during 17 consecutive mating seasons (1995–2012) from 159 females. Females that were on contraception: (1) exhibited less intense cues of putative fertility and for shorter periods; (2) were solicited by fewer males, and those males that did solicit them did so less often (i.e., lower heterosexual attractivity); (3) solicited fewer males and when they did perform sexual solicitations they did so less often (i.e., lower heterosexual proceptivity); (4) engaged in shorter heterosexual consortships with fewer male partners (i.e., lower heterosexual receptivity), compared with females that were not on contraception. In contrast, contraceptive treatment had no significant effect on the prevalence, occurrence, frequency, or duration of female homosexual behaviors. Even though heterosexual and homosexual behaviors can both be considered sexual in character and under hormonal control, our results suggested they are, to some extent, dissociable. Because females engaging in homosexual interactions showed less intense cues of putative fertility than those engaging in heterosexual interactions, regardless of contraceptive treatment, we argued that the hormonal threshold required for the expression of heterosexual behavior by females was associated with elevated sex hormones levels compared to homosexual behavior. We discussed the hormonal correlates of sexual behavior and partner preferences in Japanese macaques.

1. Introduction

Since progestin-based oral contraceptives (OCs) were first introduced as hormonal birth control in human populations, their reported effects on sexual behavior, desire and satisfaction have been contradictory (Davis and Castaño, 2004). Some studies have reported negative side effects (e.g., reduction in sexual desire: Wallwiener et al., 2010; depression: Kulkarni, 2007). Other studies have reported positive outcomes (e.g., higher sexual satisfaction with male partners: Little et al., 2002). Whether negative or positive, effects of OCs on sexual behavior support the view that OCs alter the normal cyclicity of sex hormone secretion, which plays a major role in the expression of sexual behavior (Sherwin, 1988). Overall, by changing women's bodies such that they experience a state of hormonal pseudo-pregnancy, progestin-based contraceptives reduce peak fertility and affect female attractivity, proceptivity, and receptivity (Macrae et al., 2002). Finally, other studies showed either no significant effect of OCs on women heterosexuality (Fortenberry and Hensel, 2011), only transient effects (Grounds et al., 1970), or substantial individual differences in response to OCs, leading to inconclusive results (Graham et al., 2007).

Potential sources of contradictory results may be related to experimental design differences or pre-existing hormonal variation between women (Graham et al., 2007). However, the main confounds in investigating the effects of OCs on women sexuality probably lie in uncontrolled differences in the way sexual desires and behaviors were evaluated. Because patterns of heterosexual arousal and behavior in women may be more determined by cognitive, psychosocial, emotional and cultural components than hormonal factors, it is difficult to

* Corresponding author.
E-mail address: jeanbaptiste.leca@uleth.ca (J.-B. Leca).

https://doi.org/10.1016/j.yhbeh.2018.08.009
Received 24 February 2018; Received in revised form 18 August 2018; Accepted 24 August 2018

objectively measure their responses to OCs (Fortenberry and Hensel, 2011; Wallen, 1990; Welling et al., 2012). Even though many lesbians are on OCs to help regulate the hormonal cycle and reduce pain during menstruation (Marrazzo and Stine, 2004), we are not aware of any reports on the effect of OCs on female homosexuality in humans – probably because lesbians are not concerned about conception during their typical sexual interactions.

The objective and systematic collection of behavioral data from appropriate non-human primate models may circumvent the problems associated with the reliance on self-reports in the study of OCs in humans. It is well known that endogenous and exogenous changes in sex steroid hormones affect the social and sexual behavior of a variety of animal taxa, including non-human primates (Dixson, 2012). In many primates species, female heterosexual attractivity, proceptivity, and receptivity are mediated by behavioral cues (i.e., sexual solicitations) and non-behavioral cues (i.e., visual-morphological signals such as genital swelling, and chemical signals such as genital odors from vaginal secretions), which are associated with particular phases of the ovarian cycle and corresponding changes in a female's hormonal state (Beach, 1976).

In non-human primates, female exposure to exogenous hormones, such as the administration of progestin-based contraceptives or the natural consumption of plant steroids, not only reduced reproductive function by interfering with reproductive physiology, but also had an inhibitory effect on sexual behavior, either directly by attenuating female attractivity, proceptivity, and/or receptivity, or indirectly through reduced female agonistic behavior occurring in the context of mate competition (e.g., common marmosets, *Callithrix jacchus*: Kendrick and Dixson, 1985; chacma baboons: *P. ursinus*: Saayman, 1973; olive baboons, *Papio hamadryas anubis*: Higham et al., 2007; pigtailed macaques, *Macaca nemestrina*: Pazol et al., 2004). For example, injections of medroxyprogesterone acetate considerably reduced female-to-male solicitations in pigtailed macaques (Pazol et al., 2004), and male-to-female solicitations and mounts in stumptailed macaques (*M. arctoides*: Linn and Steklis, 1990). Likewise, progesterone implants decreased female approaches and follows of males in chacma baboons (Saayman, 1973) and virtually abolished proceptive and receptive tongue-flicking and significantly increased mount refusals in common marmosets (Kendrick and Dixson, 1985). Interestingly, the natural diet of primates sometimes contains phytochemicals and steroid-like substances that may affect female sexual behavior, influence the timing of fertility, or function as contraceptives (Higham et al., 2007; Strier, 1993).

It should also be noted that hormonal influences on sexual behavior in non-human primates varied considerably with social and environmental conditions (e.g., laboratory studies of pairs or trios of subjects versus studies of social groups of individuals housed in outdoor enclosures), and were more evident as socio-ecological conditions approached those natural for the species under study (Linn and Steklis, 1990). In addition to hormonal factors, investigations of the effect of contraceptive on sexual behavior should consider socio-ecological variables and physiological state of subjects such as age, dominance relationships, availability of potential sexual partners, and likelihood of fertile period (e.g., Linn and Steklis, 1990; Pazol et al., 2004).

Although female homosexual behavior is part of the sexual repertoire of numerous primate species (reviewed in Sommer and Vasey, 2006), information on the hormonal state of both intact and hormonally manipulated females engaged in homosexual interactions is scarce and contradictory. Female homosexual behavior in rhesus macaques (*M. mulatta*) appeared to vary as a function of menstrual cycle stage. Akers and Conaway (1979) determined menstrual phase visually on the basis of face coloration, genital swelling and menses and found that female-female mounting occurred more frequently during the periovulatory phase than during the luteal phase. Conversely, female homosexual interactions in stumptailed macaques were not associated with any particular cycle phase, suggesting minimal if any hormonal control (Chevalier-Skolnikoff, 1976). However, this could also be due to the fact that, in this species, heterosexual and homosexual interactions are more influenced by social factors than ovarian hormones (Slob et al., 1978). Overall, the effects of hormonal contraceptive on female heterosexual and homosexual behaviors in non-human primates remain insufficiently documented and poorly understood. Further research is needed to better comprehend the hormonal correlates of sexual behavior and partner preferences.

Females within certain populations of Japanese macaques (*M. fuscata*) showed a relatively high prevalence and frequency of homosexual behavior and facultative same-sex sexual partner preference (Vasey, 2006). In Japanese macaques, most female-female mounting occurs in association with genital stimulation (Vasey and Duckworth, 2006), but appears to serve no sociosexual function (Vasey, 2004a; Vasey et al., 1998). Structurally, the homosexual and heterosexual patterns of behavior exhibited by adult female Japanese macaques were very similar with respect to courtship, mount postures, inter-mount activity, partner retention, incest avoidance, and consortship formation (i.e., formation of, temporary, but exclusive, sexual associations; Vasey, 2004b).

Several lines of evidence indicate that both female homosexual and heterosexual behaviors are similarly influenced by sex steroid hormones. First, like male-female mounting, female-female mounting occurred more frequently during the periovulatory period than during the luteal phase (O'Neill et al., 2004; O'Neill, 2012). Second, a relationship between hormonal state, proceptive behaviors, and homosexual activity in female Japanese macaques has long been suggested (Fedigan and Gouzoules, 1978; Wolfe, 1984) and was recently confirmed by hormonal analyses, although the sample size was small ($N = 3$ subjects: O'Neill et al., 2004). Third, like heterosexual behavior, female homosexual behavior was confined to the mating season and occurred when females showed signs of higher fertility, such as a reddening of the face and genital swelling (Wolfe, 1984). Therefore, because female homosexual behavior is part of the sexual repertoire of certain populations of Japanese macaques, and has been found to mirror heterosexual behavior in many respects, hormonal contraceptives are likely to produce similar effects on homosexual and heterosexual behaviors in this species.

The goal of this study was to assess the effect of a hormonal contraceptive treatment on the heterosexual and homosexual behaviors of female Japanese macaques living in a large free-ranging social group. Based on these previous findings, we hypothesized inhibitory effects of the hormonal contraceptive treatment on 1) heterosexual and homosexual attractivity (measured by the intensity and duration of cues of putative fertile periods, and solicitations received by females from male and female partners), 2) heterosexual proceptivity (measured by female-to-male solicitations) and receptivity (measured by male-female consortships), and 3) homosexual proceptivity (measured by female-to-female solicitations) and female's readiness to allow female mounts (measured by female-female consortships). We tested a series of predictions derived from these three hypotheses (Table 1), and discussed the implications of our results in terms of hormonal correlates of sexual behavior and partner preferences in non-human primates and humans.

2. Methods

2.1. Study group and species

The following observations were conducted on the free-ranging provisioned Arashiyama-E troop of Japanese macaques at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture, Japan. The Arashiyama group of Japanese macaques is one of the longest continuously studied non-human primate populations in the world (Huffman et al., 2012). Long-term records on individually identified monkeys (including longitudinal data sets on sexual behavior) are available from years of collaborative research between observers working at this site (Leca et al., 2012). During the study period (1995–2012), the size and composition of the Arashiyama-Kyoto group