Available online at www.sciencedirect.com
SCIENCE DIRECT®

Behavioural Brain Research 157 (2005) 265–272

BEHAVIOURAL BRAIN RESEARCH

www.elsevier.com/locate/bbr

Research report

A sexually dimorphic hypothalamic nucleus in a macaque species with frequent female–female mounting and same-sex sexual partner preference

Paul L. Vasey[a,*], James G. Pfaus[b]

[a] *Department of Psychology and Neuroscience, University of Lethbridge, Lethbridge, Alta., Canada T1K 3M4*
[b] *Department of Psychology, Concordia University, Montreal, Que., Canada H3G 1M8*

Received 30 March 2004; received in revised form 8 July 2004; accepted 12 July 2004
Available online 20 August 2004

Abstract

In some captive and free-ranging populations, unmanipulated female Japanese macaques (*Macaca fuscata*) routinely court, mount (with pelvic thrusting), compete for, and even prefer, on occasion, certain female sexual partners over certain males. The goal of this study was to determine if the cytoarchitecture of the dorsocentral portion of the anterior hypothalamic nucleus (AHdc), was male-typical in female Japanese macaques drawn from one such population. The AHdc is located in the medial preoptic anterior hypothalamus (MPO-AH), a region of the brain that is known to regulate sexual behaviour in primates. Despite their potential for male-typical sexual behaviour and sexual partner preference, our female subjects did not possess male-typical AHdc. The AHdc was significantly larger in males than it was in females, a difference that could be attributed to the significantly larger number of neurons in the male AHdc compared to that of the females. The AHdc of female Japanese macaques were no more male-typical in size than those of female rhesus macaques, a closely related sister species in which females rarely exhibit male-typical sexual behaviour. Although the AHdc may be involved in the regulation of sexual behaviour, this study indicates that a male-typical AHdc is not a prerequisite for the expression of male-typical sexual behaviour and sexual partner preference in Japanese macaques. This study is the first to examine the relationship between sex-atypical sexual activity and the cytoarchitecture of a hypothalamic nucleus in hormonally unmanipulated females.

Keywords: Sexual differentiation; Preoptic anterior hypothalamus; Homosexual behaviour; Primate

Mounting and sexual partner preference are two components of mating interactions that are sexually dimorphic in most species [1,6,42]. Mounting is generally considered a male-typical activity that females perform infrequently, if at all. Female mounting, when it does occur, is often enacted to facilitate adaptive social goals (i.e., dominance demonstration) or breeding strategies (i.e., proceptive behaviour in the presence of potential male mates) [7,39,49]. Sexual partner preference, in the vast majority of species, is oriented towards opposite-sex partners [42]. Females almost always prefer male reproductive/sexual partners when given the choice of a same-sex alternative, whereas, males prefer female ones. Taken together, these observations have helped establish the idea that mounting and preference for female sexual partners are male-typical activities.

Japanese macaques (*Macaca fuscata*) are unusual because, in addition to engaging in heterosexual behaviour, hormonally and neurologically unmanipulated females in certain captive and free-ranging populations frequently engage in same-sex mounting (with and without pelvic thrusting) and courtship within the context of temporary, but exclusive, sexual relationships called consortships [43]. Females will even engage in inter-sexual competition in

---

[*] Corresponding author. Tel.: +1 403 329 2407; fax: +1 403 329 2555.
E-mail address: paul.vasey@uleth.ca (P.L. Vasey).

0166-4328/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.bbr.2004.07.005

order to retain exclusive access to female sexual partners that male competitors attempt to usurp [41,45]. Moreover, they sometimes *prefer* same-sex sexual partners when given the simultaneous choice of a sexually motivated, opposite-sex alternative [41,43,47]. Accordingly, the question arises as to what extent the neural mechanisms underlying sexual behaviour in female Japanese macaques are male-typical.

A number of studies have identified the medial preoptic-anterior hypothalamus (MPO-AH) as a key brain region associated with the regulation of male-typical sexual behaviours in primates. In adult male rhesus macaques (*M. mulatta*) and common marmosets (*Callithrix jacchus*), lesions in the region of the MPO-AH reduce or completely eliminate sexual solicitations directed towards females [30,37]. Electrical stimulation of regions in the MPO-AH of adult male rhesus macaques facilitates mounting with pelvic thrusting [34]. The MPO-AH may also be involved the regulation of male-typical sexual partner preferences in primates. In adult male Japanese macaques, for example, visual presentation of a female was a sufficient stimulus to activate MPO-AH neurons in the absence of any actual sexual response [4]. Likewise, the activity of single neurons in the MPO-AH of adult male rhesus macaques is known to increase upon visual presentation of a female [31,52].

Research has also demonstrated that the MPO-AH is a key brain region associated with the regulation of female-typical sexual behaviours in primates. In adult female common marmosets, lesions in the MPO-AH virtually abolish male-directed proceptive behaviours such as tongue-flicking and staring displays [23]. Repetitive electrical stimulation of regions in the MPO-AH of intact and ovariectomized adult female rhesus macaques elicited proceptive behaviour in the form of hindquarter presentations directed at male partners [32]. Increased firing of MPO-AH neurons in intact and ovariectomized adult female rhesus macaques was associated with this same type of female-typical proceptive behaviour [32]. Single-cell recordings in the MPO-AH of female rhesus macaques indicate that excitation of neurons occurs in response to copulation with a male partner and increases with the rate and/or number of pelvic thrusts a male performs [5]. With regard to the issue of female-typical sexual partner preference, it is particularly interesting that repetitive electrical stimulation of the MPO-AH in female rhesus macaques evokes proceptive behaviour in the presence of a male conspecific, but not in the male's absence, nor in the presence of a female conspecific, a non-living object, or a human experimenter [26]. This suggests that the processing of certain sensory cues, specific to species and sex, occur in the MPO-AH prior to the manifestation of proceptive behaviour in female rhesus macaques.

In this paper, we examined one region of the MPO-AH, the dorsocentral portion of the anterior hypothalamic nucleus (AHdc) [8], in Japanese macaques. Volumetric analyses demonstrate that this nucleus is approximately 2.8 times larger in rhesus macaque males relative to females [8]. The function of the macaque AHdc is unknown. However, positional and cytoarchitectonic criteria indicates that this structure is a possible homologue of the sexually dimorphic nucleus of the preoptic area (SDN-POA) in the rat and the interstitial nucleus of the anterior hypothalamus 3 (INAH3) in humans [8]. The rat SDN-POA [14,19,38,50] and the human INAH3 [3,9,29] have both been implicated in the expression of male-typical sexual behaviour and sexual partner preference.

In light of its position within the MPO-AH, its sexually dimorphic characteristics, and its possible mammalian homologues, the macaque AHdc may participate in the regulation of male-typical sexual behaviour and sexual partner preference. The goal of this study was to determine if the cytoarchitecture of the AHdc nucleus was male-typical in female Japanese macaques drawn from a population in which unmanipulated adult females routinely mount and demonstrate same-sex sexual partner preference. To this end, we calculated the volume and total cell count of the AHdc nucleus in males and females in our sample. We then compared relative sex differences in AHdc volume between Japanese and rhesus macaques using data from a previously described rhesus macaque sample [8]. Japanese and rhesus macaques are closely related sister species in the same evolutionary clade [18]. Same-sex sexual activity occurs relatively infrequently among unmanipulated female rhesus macaques and, when it does occur, females appear to use the behaviour to facilitate an adaptive sociosexual function, namely, alliance formation [15,20,22]. In contrast, unmanipulated female Japanese macaques in the study population engaged in same-sex sexual activity frequently [43] and did not use this behaviour for the express purpose of forming alliances [40]. If female Japanese macaques in our sample have a more male-typical AHdc, then the volume of male and female AHdc should be relatively monomorphic when compared to a closely related species, like rhesus macaques, in which females do not normally exhibit male-typical sexual behaviour.

1. Materials and methods

1.1. Subjects

All of the Japanese macaque brains were obtained from individuals that were housed at the Laboratory of Behavioural Primatology at the Université de Montréal. The laboratory consisted of five indoor rooms and two large outdoor enclosures (230 m^2) furnished with swinging and climbing devices. Subjects lived in a large, mixed-sex, social group (38 individuals: 1 sexually inactive female, age 24 years; 16 sexually active females, ages 3.5–24 years; 5 sexually active males, ages 4–10.5 years; 16 sexually inactive/immature individuals, age <4 year) comprised of three unrelated matrilines. The study group's age, sex and matrilineal compositions were typical for this species as observed under free-ranging conditions [51]. Subjects were fed monkey chow, fruit, vegetables and grain on a daily basis. These food items were scattered in deep woodchip litter, which created a naturalistic foraging situation for the monkeys. Water was continuously available. All individuals were gonadally intact and had never been used for any type of invasive experimentation. Every sexually active female in this population routinely mounted, courted females and demonstrated, on occasion, same-sex sexual partner preference [43]. All sexually immature females in this group went on to engage in these same behaviours once they became sexually active.

1.2. Histology

Brain tissue was obtained from three sexually active males (ages 4–5 years), three immature males (ages 1–3 years), two sexually active females (ages 4–5 years) and two immature females (age 3 year). Subjects were euthanized with a lethal intramuscular injection of euthanyl (100 ml/kg). The brains were removed immediately from the skulls, placed in formalin and stored in the Fredrick Banting Research Center, Ottawa, Ont., Canada. Hypothalami were dissected from these brains and the blocks of tissue (approx. 3.5 cm × 2.5 cm) were re-immmersed in 10% formalin for several months prior to histological preparation. Blocks of brain tissue were frozen with dry ice, serial-sectioned at 70 μm and placed in Tris-buffered saline overnight. Sections were then mounted onto gelatin-coated glass slides and dried at room temperature overnight. The sections were defated the next day in xylene for 24 h. On the following day, the sections were rehydrated in graded alcohols (100% EtOH for 45 min, 95% EtOH for 5 min, 70% EtOH for 5 min, 50% EtOH for 5 min) and water (tap water for 5 min, distilled water for 2 min), stained with a 1% buffered thoinin for 2 min, rinsed with tap water, rehydrated in graded alcohols (50% EtOH for 5 min, 70% EtOH for 5 min, 95% EtOH until differentiated to the eye), dipped in 100% EtOH seven times, and then defated in xylene overnight. The stain sections were removed from xylene and cover-slipped with Permount the next day.

1.3. Measurements

Brain sections were coded so that analyses could be done without knowledge of the specimen's identity. The AHdc was identified using criteria outlined previously [8] at a final magnification of 300× using a Leitz DMR3 Microscope. The perimeter of each AHdc was outlined on a video monitor with a cursor. Scion Image 1.62 software calculated the area for each perimeter. Area values were multiplied by the section thickness and the square root was calculated. These adjusted area values were summed to yield nucleus volumes. Neurons were counted by focusing throughout the depth of the tissue.

2. Results

A cluster of neurons was observed within the dorsocentral portion of the MPO-AH in both male and female Japanese macaques (Figs. 1 and 2). Cytoarchitectonic and positional evidence suggests that the AHdc of the Japanese macaque is a likely homologue of the rhesus macaque AHdc [8], the rat SDN-POA [16] and the INAH3 in humans [3,9,29]. First, the

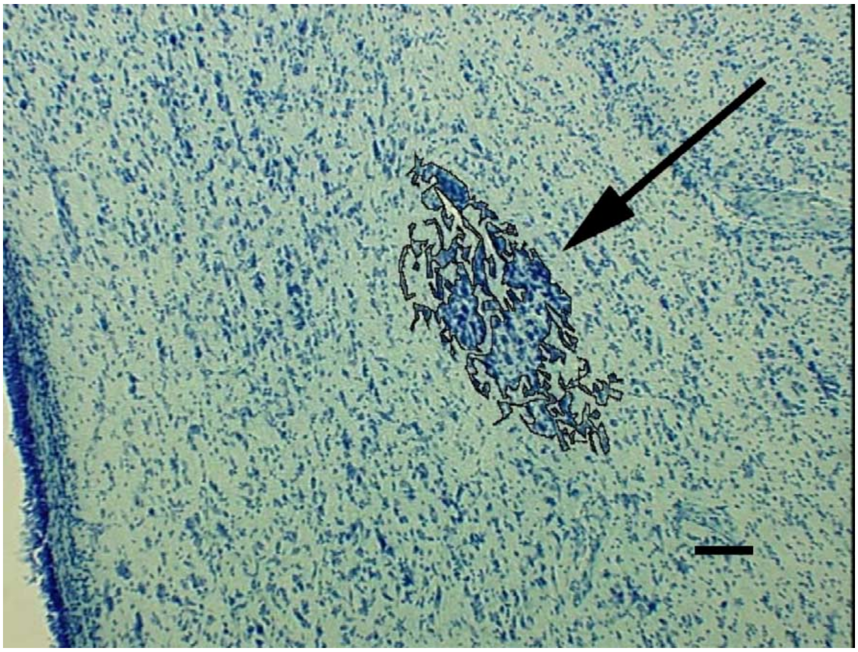

Fig. 1. The Japanese macaque dorsocentral portion of the anterior hypothalamic nucleus (AHdc). The darkly stained magnocellular region of the AHdc in the sexually active male Japanese macaque. The ependymal cell layer of the third ventricle is to the left. Final magnification of 300×. The scale bar is 100 μm in length. For more information on AHdc location see Section 2 and Ref. [8].

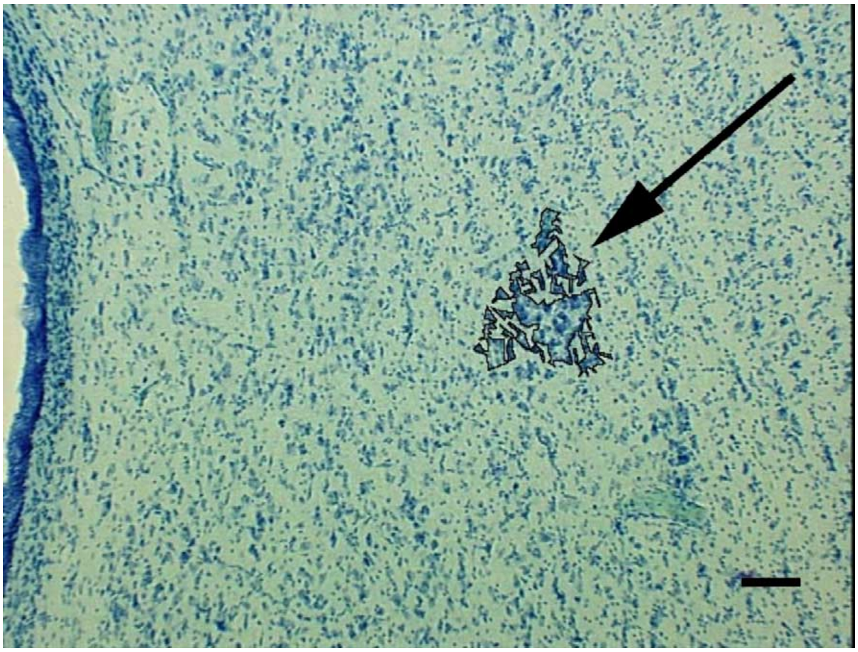

Fig. 2. The Japanese macaque dorsocentral portion of the anterior hypothalamic nucleus (AHdc). The darkly stained magnocellular region of the AHdc in the sexually active female Japanese macaque. The ependymal cell layer of the third ventricle is to the left. Final magnification of 300×. The scale bar is 100 μm in length. For more information on AHdc location see Section 2 and Ref. [8].

Japanese macaque AHdc appeared spherical or ellipsoidal in shape and appeared to contain relatively large, deeply staining, polygonal neurons. Second, the Japanese macaque AHdc was situated close to the periventricular region about 1 mm lateral to the wall of the third ventricle. It was dorsolateral to the most ventral and anterior aspect of the magnocellular division of the paraventricular nucleus. In its caudal extent, the lateral border of the Japanese macaque AHdc came in close proximity to a prominent cell group that merged posterodorsally with the bed nucleus of the stria terminalis (BNST). Unlike the human INAH 4 [3,29] the Japanese macaque AHdc was not situated in a directly lateral position to the periventricular nucleus. In fact, no structure resembling the human INAH4 was identified. At some levels, clusters of neurons were observed in the appropriate position, but these were highly variable and in no case did they coalesce into a single nucleus.

The mean AHdc volume for males ($n = 6$) was 8.84 ± 1.51 (S.E.M.) compared to a mean nucleus volume in females ($n = 4$) of 4.31 ± 0.46 (S.E.M.) (Table 1). This is a 2.05-fold difference. An analysis of variance (ANOVA) demonstrated that the volume of the AHdc was significantly larger in males compared to females ($F[1, 8] = 5.56$, $P < 0.05$). A Cohen's d-test was performed and indicated a large effect size ($d = 1.68$).

The mean total cell count of the AHdc in males ($n = 6$) was 592.2 ± 102.6 (S.E.M.) compared to a mean total cell count in females ($n = 4$) of 266.3 ± 17.2 (S.E.M.) (Table 1). This is a 2.22-fold difference. An ANOVA demonstrated that the total cell count of the AHdc was significantly larger in males compared to females ($F[1, 8] = 6.38$, $P < 0.05$). A Cohen's d-test was performed and indicated a large effect size ($d = 1.82$).

An analysis of covariance (ANCOVA) was performed for both volume and total cell count with sex as a factor using age as a covariate (Table 1). This analysis demonstrated that the volume of the AHdc was significantly larger in males than in females ($F[1, 7] = 9.89$, effect size = 0.59, $P < 0.05$). Similarly, the total cell count of the AHdc was significantly higher in males than in females ($F[1, 7] = 18.19$, effect size = 0.72, $P < 0.05$).

Table 1
AHdc nucleus volume and total neuron count in Japanese macaques

Subject	Age	Sexual status	Weight (kg)	Volume (mm^3)	Neuron count
Females					
F1	5	SA	16.2	4.41	267
F2	4	SA	15.8	3.15	222
F3	3	SI	10.2	5.39	306
F4	3	SI	10.2	4.32	270
Mean	3.75	–	13.1	4.31	266.3
S.E.M.	0.55	–	1.93	0.46	17.2
Males					
M1	5	SA	18.2	15.61	990
M2	5	SA	18.2	8.96	808
M3	4	SA	15.5	7	476
M4	3	SI	12.7	9.73	523
M5	1	SI	5.4	5.32	355
M6	1	SI	5.4	6.44	401
Mean	3.17	–	12.57	8.44	592.2
S.E.M.	0.82	–	2.64	1.51	102.6

SA: sexually active; SI: sexually inactive.

An ANCOVA was also performed for both nucleus volume and total cell count with sex as a factor using weight as a covariate (Table 1). This analysis demonstrated that the volume of the AHdc was significantly larger in males than in females ($F[1, 7] = 7.85$, effect size = 0.52, $P < 0.05$). Similarly, the total cell count of the AHdc was significantly higher in males than in females ($F[1, 7] = 12.93$, effect size = 0.65, $P < 0.01$).

A 2 × 2 ANCOVA was performed for AHdc nucleus volume with age (adult versus immatures) and sex as factors and weight as a covariate. This analysis demonstrated that there were no significant differences between older and younger individuals for AHdc nucleus volume ($F[1, 5] = 1.48$, $P = 0.28$). In addition, there was no interaction effect between age category and sex for AHdc nucleus volume ($F[1, 5] = 0.26$, $P = 0.63$). A 2 × 2 ANCOVA was also performed for AHdc total cell count with age (adult versus immatures) and sex as factors and weight as a covariate. This analysis demonstrated that there were no significant differences between older and younger individuals for AHdc total cell count ($F[1, 5] = 0.49$, $P = 0.51$). In addition, there was no interaction effect between age category and sex for AHdc total cell count ($F[1, 5] = 1.48$, $P = 0.28$).

Finally, we calculated the effect size of AHdc nucleus volume for our Japanese macaque sample ($r = 0.6405$) and the effect size for a previously described [8] rhesus macaque sample (males: $x = 0.28 \pm 0.3\,\text{mm}^3$ (S.E.M.), $n = 4$; females: $x = 0.1 \pm 0.02\,\text{mm}^3$ (S.E.M.), $n = 4$; $r = 0.6936$). We compared these different effect sizes using a Fisher's r to z transformation [24], which revealed no significant difference ($z = 0.1658$) in the AHdc nucleus volume between the Japanese macaque and rhesus macaque samples.

3. Discussion

Adult female Japanese macaques in certain populations routinely mount, thrust, court, compete for, and sometimes even prefer, some same-sex sexual partners relative to male alternatives [41,43,47]. In light of their male-typical sexual behaviour, we reasoned that the AHdc of female subjects drawn from one such population might be organized in a male-typical manner. Contrary to our predictions, our analyses indicate that the Japanese macaque AHdc is significantly larger in males than in females, independent of age and weight. This difference is due to a significantly larger number of neurons in the AHdc of males relative to females. Given the small size of our sample, it seems likely that the sex differences in AHdc volume and total cell count we found are robust ones. Age (adult versus immature) did not account for a significant amount of intra-sexual variance in AHdc nucleus volume or total cell count. This suggests that pubertal hormones do not affect growth of the AHdc nucleus. Although our female Japanese macaque subjects manifested male-typical sexual behaviour on a routine basis, their AHdc volumes and cell counts were no more male-typical than those of female rhesus macaques, a closely related sister species [18] in which females do not display male-typical sexual behaviour with any regularity [15,20,22].

The behaviour of individuals in our sample was studied extensively during a typical mating season (October 1993–February 1994) at the Université de Montréal colony, and every sexually mature female engaged in female homosexual behaviour [43]. Moreover, the majority of sexual relationships formed ($N = 95$) were homosexual (55%) relative to heterosexual (45%). Homosexual consortships could continue on and off for well over a week, or consecutively over a period of approximately 4 days. During homosexual consortships, females solicited their partners for sex an average of 28 times per hour of observation, and mounted each other an average of 31 times per hour of observation ($N = 129$ observation hours). In addition, females engaged in inter-sexual competition with males to retain exclusive access to their female sexual partners approximately once every 2.9 h of observation [41,45]. Moreover, following 92.5% of these competitive exchanges, females that were the objects of competition chose to continue to engage in sexual behaviour with their female sexual partners (the female competitor), rather than begin to engage in sexual behaviour with the male competitor. As such, multiple measures all suggest that the females in our study population routinely engaged in what most observers would define as male-typical sexual activity.

Although female–female mounting in some species is displayed as part of a social or breeding strategy [7,39,49], research indicates that same-sex mounting in female Japanese macaques is a sexual behaviour, not a sociosexual one. Sociosexual behaviours are behaviours that look sexual in terms of their outward form, but are enacted to facilitate some sort of adaptive social goal, such as dominance demonstration [49]. Female Japanese macaques do not use same-sex courting or mounting to attract male mates [17,39], impede reproduction by same-sex competitors [39], form alliances inside or outside the mating season [40], communicate about dominance relationships [46], obtain alloparental care [40], reduce social tension associated with incipient aggression [46], practice for heterosexual sexual activity (i.e., female–male mounting), or to reconcile following conflicts [44]. Like heterosexual behaviour, female homosexual behaviour is never observed outside of the species' fall-winter mating season. Moreover, these interactions do not mimic generalized patterns of social affiliation. For example, females avoid homosexual contact with close female kin, such that mounting, courtship, and consortships are never observed between mothers and daughters, sisters, or grandmothers and granddaughters [11,12]. This pattern of avoidance does not characterize other forms of social affiliation such as grooming, co-sleeping, huddling, or interventions [10,25,27]. Finally, females frequently engage in prolonged and directed clitoral stimulation during same-sex mounting either by rubbing their clitorises against the back of the mountee or by masturbating with their tails while mounting.

Previous research on perinatally hormone-treated non-primate subjects also demonstrates a lack of correlation between male-typical features of POA/AH morphology and the capacity of females to display male-typical sexual behaviour. In rats, the volume of the SDN-POA is significantly larger in females treated prenatally with testosterone propionate (TP) compared to control females [21]. Despite this neuroanatomical difference, TP-treated females rarely mounted other individuals and were no more likely to do so than control females [21]. Conversely, female ferrets treated with testosterone (T) postnatally (days P5 to P20) and for 1 month beginning after ovariectomy on P56 failed to develop the sexually dimorphic male nucleus in the dorsal preoptic/anterior hypothalamic area (MN-POA/AH), but displayed high levels of male-typical sexual behaviour nonetheless [13].

In contrast to the present study, prior research on hormonally unmanipulated subjects has demonstrated that sex-atypical sexual activity is associated with sex-atypical nuclei in the region of the MPO-AH. In humans, it has been shown that the volume of the INAH3 is smaller in homosexual males, relative to heterosexual males [9,29]. Moreover, homosexual males have a higher cell density within the INAH3, relative to their heterosexual counterparts [9]. In domestic sheep (*Ovis aries*), the volume of the ovine sexually dimorphic nucleus (oSDN) is smaller in rams that prefer male sexual partners (i.e., male-oriented rams), relative to those that prefer female sexual partners (i.e., female-oriented rams) [36]. In addition, aromatase mRNA levels are higher in the oSDN of female-oriented rams relative to their male-oriented counterparts [36].

Several factors might account for why the human [9,29] and domestic sheep [36] studies found an association between sex-atypical sexual activity and sex-atypical hypothalamic nuclei, whereas the present study did not. To begin with, prior research on humans and domestic sheep has focused on male subjects whereas our study examined female subjects. Second, although all of these studies examined superficially similar phenomenon (i.e., the expression of same-sex sexual partner preferences), in actuality, the phenomenon under investigation were fundamentally different from each other. The human and sheep research examined female-typical sexual partner preference in males, whereas our study focused on male-typical sexual partner preference in females. Third, some human males [28,48] and domestic rams [35,36] exhibit *exclusive* same-sex sexual partner preference. In contrast, our female Japanese macaque subjects exhibited *facultative* same-sex sexual partner preference, that is, they sometimes prefer female sexual partners relative to male alternatives, but this preference was not exclusive [43]. Fourth, in addition to exhibiting same-sex sexual partner preference, our female Japanese macaque subjects engaged in sex-atypical sexual behaviour (i.e., mounting), but it is questionable whether the sheep and human subjects, employed in the studies described above, did the same. Male-oriented rams mount other rams, but they do not “stand,” in the female-typical manner, to be mounted [35]. Some of the homosexual human male subjects employed in the studies described above [9,29] may have engaged in receptive anal intercourse, but it is debatable as to whether this behavioural pattern is female-typical. In light of these differences, the association between sex-atypical sexual behaviour and sex-atypical nuclei in the region of the MPO-AH may be specific to males that exhibit exclusive female-typical (i.e., androphilic) sexual partner preference.

The present study indicates that a male-typical AHdc is not a prerequisite for the expression of male-typical sexual behaviour and sexual partner preference in female Japanese macaques. However, the role of the AHdc in generating male or female sexual behaviour cannot be determined from our results. It is possible, for example, that a female-typical AHdc is sufficient to generate the male-typical sexual behaviours and sexual partner preference in question. Alternatively, the AHdc might be involved in the regulation of male-typical sexual behaviour and sexual partner preference in male Japanese macaques, but not in females. In other words, different neural mechanisms may generate ostensibly similar sexual behaviours (i.e., mounting postures, pelvic thrusting, courtship displays) and patterns of sexual partner preference (i.e., preference for female sexual partners) in male and female Japanese macaques. For example, male mounting behaviour in rats appears to be regulated by the MPO-AH [33], whereas the female mounting of sexually sluggish male rats is regulated by the ventromedial hypothalamus, not the MPO-AH [2]. Although some aspects of their sexual activity are male-typical, females in the study population also engaged in a variety of female-typical sexual behaviours. For example, they did not acquire female sexual partners in the same manner as males [45]. The female-typical AHdc that characterized our female subjects may be involved in the regulation of these sorts of female-typical sexual behaviours. Further research on this unique primate species will be needed to clarify issues pertaining to the function of the Japanese macaque AHdc.

Acknowledgements

We are very grateful to Dr. Jocelyn Fournier who furnished us with the brain material used in this study and Dr. William Byne for helpful discussions and for generously sharing his protocol for thionin staining. We also thank Jean Choi, Nadine Duckworth, Margaret Forgie, Carole Gauthier, Ellen Kapsalis, Bryan Kolb, Sergio Pellis, Anne Perkins, Drew Rendall, Terry E. Robinson, Anne Russon, John Vokey, Paul Whishaw, Sean Wright and two anonymous reviewers for helpful discussions and comments on the manuscript. Various stages of this research were funded by grants to P.L.V. from the Fonds pour la formation des Chercheurs et l’Aide de Recherche (FCAR)-Québec, the University of Lethbridge, the Alberta Heritage Foundation for Medical Research and by grants to P.L.V. and J.G.P. from the Natural Science and Engineering Research Council (NSERC) of Canada.

References

[1] Adkins-Regan E. Hormonal mechanisms of mate choice. Am Zool 1998;38:166–78.

[2] Afonso VM, Lehmann H, Pfaus JG. Brain regions associated with female mounting behaviour in the rat. Soc Neurosci Abstr 2002:28.

[3] Allen LS, Hines M, Shryne JE, Gorski RA. Two sexually dimorphic cell groups in the human brain. J Neurosci 1989;9:497–506.

[4] Aou S, Yoshimatsu H, Oomura Y. Medial preoptic neuronal responses to connatural females in sexually inactive male monkeys (*Macaca fuscata*). Neurosci Lett 1984;44:217–21.

[5] Aou S, Oomura Y, Yoshimatsu H. Neuron activity of the ventromedial hypothalamus and the medial preoptic area of the female monkey during sexual behaviour. Brain Res 1988;455:65–71.

[6] Baum MJ. Differentiation of coital behaviour in mammals. Neurosci Biobehav Rev 1979;3:265–84.

[7] Beach FA. Factors involved in the control of mounting behaviour by female mammals. In: Diamond E, editor. Perspectives in Reproduction and Sexual Behaviour. Bloomington: Indiana University Press; 1968. p. 83–131.

[8] Byne W. The medial preoptic and anterior hypothalamic regions of the rhesus monkey: cytoarchitectonic comparison with the human and evidence for sexual dimorphism. Brain Res 1998;783: 346–50.

[9] Byne W, Tobet S, Mattiace LA, Lasco MS, Kemether E, Edgar MA, et al. The interstitial nuclei of the human anterior hypothalamus: an investigation of variation with sex, sexual orientation, and HIV status. Horm Behav 2001;40:86–92.

[10] Chapais B. The role of alliances in the social inheritance of rank among female primates. In: Harcourt A, de Waal FMB, editors. Coalitions in Humans and other Animals. Oxford: Oxford University Press; 1992. p. 29–60.

[11] Chapais B, Gauthier C, Prud'homme J, Vasey PL. Relatedness threshold for nepotism in Japanese macaques. Anim Behav 1997;53:533–48.

[12] Chapais B, Mignault C. Homosexual incest avoidance among females in captive Japanese macaques. Am J Primatol 1991;23:171–83.

[13] Cherry JA, Basham ME, Baum MJ. Neonatal testosterone masculinizes sexual behaviour without affecting the morphology of the dorsal preoptic/anterior hypothalamic area of female ferrets. Brain Res 1991;546:321–8.

[14] De Jonge FH, Louwerse AL, Ooms MP, Evers P, Endert E, Van De Poll NE. Lesions of the SDN-POA inhibit sexual behaviour of male Wistar rats. Brain Res Bull 1989;23:483–92.

[15] Fairbanks LA, McGuire M, Kerber W. Sex and aggression during rhesus monkey group formation. Agg Behav 1977;3:241–9.

[16] Gorski RA, Gordon JH, Shryne JE, Southam AM. Evidence for a morphological sex difference within the medial preoptic area of the rat brain. Brain Res 1978;148:333–46.

[17] Gouzoules H, Goy RW. Physiological and social influences on mounting behaviour of troop-living female monkeys (*Macaca fuscata*). Am J Primatol 1983;5:39–49.

[18] Hoelzer GA, Melnick DJ. Evolutionary relationships of the macaques. In: Fa JE, Lindburg DG, editors. Evolution and Ecology of Macaque Societies. Cambridge: Cambridge University Press; 1996. p. 3–19.

[19] Houtsmuller EJ, Brand T, De Jonge FH, Joosten RNJMA, Van De Poll NE, Slob AK. SDN-POA volume, sexual behaviour, and partner preference of male rats affected by perinatal treatment with ATD. Physiol Behav 1994;56:535–41.

[20] Huynen MC, Taborsky T. Homosexual interactions in female rhesus monkeys *Macaca mulatta*. In: Taborsky M, Lindburg B, editors. Advances in Ethology, 32. Berlin: Blackwell; 1997. p. 211 [contributions to the XXV International Ethological Conference].

[21] Ito S, Murakami S, Yamanouchi K, Arai Y. Prenatal androgen exposure, preoptic area and reproductive functions in the female rat. Brain Dev 1986;8:463–8.

[22] Kapsalis E, Johnson RL. Female homosexual behaviour among free-ranging rhesus macaques (*Macaca mulatta*). Am J Primatol 1999;49:68–9.

[23] Kendrick KM, Dixson AF. Anteromedial hypothalamic lesions block proceptivity but not receptivity in the female common marmoset (*Callithrix jacchus*). Brain Res 1986;375:221–9.

[24] Kirk RE. Statistics: An Introduction. Fort Worth: Holt, Rinehart & Winston Inc.; 1990.

[25] Koyama N. Grooming relationships in the Arashiyama group of monkeys. In: Fedigan LM, Asquith PJ, editors. The Monkeys of Arashiyama: Thirty-five Years of Research in Japan and the West. Albany: SUNY Press; 1991. p. 211–26.

[26] Koyama Y, Fujita I, Aou S, Oomura Y. Proceptive presenting elicited by electrical stimulation of the female monkey hypothalamus. Brain Res 1988;446:199–203.

[27] Kurland JA. Kin Selection in the Japanese Monkey. Basel: S. Karger; 1977.

[28] Laumann EO, Gagnon JH, Michael RT, Michaels S. The Social Organization of Sexuality: Sexual Practices in the United States. Chicago: University of Chicago Press; 2000.

[29] LeVay S. A difference in hypothalamic structure between heterosexual and homosexual men. Science 1991;253:1034–7.

[30] Lloyd SAC, Dixson AF. Effects of hypothalamic lesions upon the sexual and social behaviour of the male common marmoset (*Callithrix jacchus*). Brain Res 1988;463:317–29.

[31] Oomura Y, Yoshimatsu H, Aou S. Medial preoptic and hypothalamic neuronal activity during sexual behaviour of the male monkey. Brain Res 1983;266:340–3.

[32] Oomura Y, Aou S, Koyama Y, Fujita I, Yoshimatsu H. Central control of sexual behaviour. Brain Res Bull 1988;20:863–70.

[33] Paredes RG, Baum MJ. Role of the medial preoptic area/anterior hypothalamus in the control of masculine sexual behaviour. Ann Rev Sex Res 1997;8:68–101.

[34] Perachio AA, Marr LD, Alexander M. Sexual behaviour in male rhesus monkeys elicited by electrical stimulation of preoptic and hypothalamic areas. Brain Res 1979;177:127–44.

[35] Perkins A, Fitzgerald JA. Sexual orientation in domestic rams: some biological and social correlates. In: Ellis L, Ebertz L, editors. Sexual Orientation: Towards Biological Understanding. Westport, CT: Praeger; 1997. p. 107–28.

[36] Roselli CE, Larkin K, Resko JA, Stellflug JN, Stormshak F. The volume of a sexually dimorphic nucleus in the ovine medial preoptic area/anterior hypothalamus varies with sexual partner preference. Endocrinology 2004;45:478–83.

[37] Slimp JC, Hart BL, Goy RW. Heterosexual, autosexual and social behaviour of adult male rhesus monkeys with medial preoptic-anterior hypothalamic lesions. Brain Res 1978;142:105–22.

[38] Turkenburg JL, Swaab DF, Endert E, Louwerse AL, Van de Poll NE. Effects of lesions of the sexually dimorphic nucleus on sexual behaviour of testosterone-treated female Wistar rats. Brain Res Bull 1988;21:215–24.

[39] Vasey PL. Homosexual behaviour in primates: a review of evidence and theory. Int J Primatol 1995;16:173–204.

[40] Vasey PL. Interventions and alliance formation between female Japanese macaques, *Macaca fuscata*, during homosexual consortships. Anim Behav 1996;52:539–51.

[41] Vasey PL. Female choice and inter-sexual competition for female sexual partners in Japanese macaques. Behaviour 1998;135:579–97.

[42] Vasey PL. Same-sex sexual partner preference in neurologically and hormonally unmanipulated animals. Ann Rev Sex Res 2002;13:141–79.

[43] Vasey PL. Sexual partner preference in female Japanese macaques. Arch Sex Behav 2002;31:45–56.

[44] Vasey PL. Pre- and post-conflict interactions between female Japanese macaques during homosexual consortships. Int J Comp Psych, in press.

[45] Sex differences in sexual partner acquisition, retention and harassment during female homosexual consortships in Japanese macaques. Am J Primatol, in press.

[46] Vasey PL, Chapais B, Gauthier C. Mounting interactions between female Japanese macaques: testing the influence of dominance and aggression. Ethology 1998;104:387–98.

[47] Vasey PL, Gauthier C. Skewed sex ratios and female homosexual activity in Japanese macaques: an experimental analysis. Primates 2000;41:17–25.

[48] Wellings K, Field J, Johnson AM, Wadworth J. Sexual Behaviour in Britain: The National Survey of Sexual Attitudes and Lifestyles. London: Penguin Books; 1994.

[49] Wickler W. Socio-sexual signals and their intra-specific imitation among primates. In: Morris D, editor. Primate Ethology. Chicago: Aldine; 1967. p. 69–79.

[50] Woodson JC, Balleine BW, Gorski RA. Sexual experience interacts with steroid exposure to shape the partner preference of rats. Horm Behav 2002;42:148–57.

[51] Yamagiwa J, Hill DA. Intraspecific variation in social organization of Japanese macaques: past and present scope of field studies in natural habitats. Primates 1998;39:257–74.

[52] Yoshimatsu H. Hypothalamic regulatory mechanisms of sexual behaviour in the male monkey. Fukuoka Acta Med 1983;74:89–100.