SEXUAL BEHAVIOUR, SWELLING OF THE SEX SKIN AND PLASMA PROGESTERONE IN THE PIGTAIL MACAQUE

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(Received 30th September 1971, accepted 11th April 1972)

Summary. The sexual behaviour of heterosexual pairs of eight female and six male adult pigtail monkeys, *Macaca nemestrina*, was observed for a 15-min testing period on alternate days of a complete menstrual cycle. The behaviour was correlated with changes in swelling of the sexual skin and in plasma progesterone. A close relation between the peak of sex skin swelling and the time of ovulation was established by laparotomy. Aggressive behaviour was spasmodic and there was very little display of social patterns of behaviour, such as grooming or pouting. 'Presenting' by the female was significantly more frequent in the follicular phase but the majority of other behaviour patterns, including female 'reaching back', frequency of mounting and intromission by the male and number of pelvic thrusts per intromission, did not differ significantly between follicular and luteal phases of the menstrual cycle. The proportion of tests on which ejaculation occurred rose during the follicular phase and reached a maximum at the time of peak sex skin swelling. During the luteal phase, a rise in ejaculatory latency and a marked decline in the incidence of ejaculation, coincided with detumescence of the female's sex skin and elevation of her plasma progesterone. The reduced incidence of ejaculation in these time-limited tests was accompanied by a decrease in the rate of intromission and rate of pelvic thrusting. The ejaculatory behaviour of the male was sensitive to the hormonal status of the female and was inhibited by the presence of progesterone in her blood.

INTRODUCTION

Although sexual behaviour in primates occurs throughout the menstrual cycle, evidence has accumulated that expressions of sexual behaviour in monkeys vary with the stage of the female's menstrual cycle. The literature on *Macaca mulatta* has been reviewed by Luttge (1971). Responses of the female to the male, such as grooming, 'presenting' and sexual receptivity, and frequency of

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mounting by the male and achievement of ejaculation all reach a peak at about mid-cycle, the presumed time of ovulation (Michael, Saayman & Zumpe, 1967; Bullock, Paris, Resko & Goy, 1969).

In *Macaca nemestrina*, the pigtail macaque, an external indicator of ovarian condition is provided by the perineal or sexual skin. In the baboon, tumescence of the sex skin can be brought about by oestrogen and detumescence by progesterone (Gillman, 1938, 1940a, b). The peak of sex skin swelling may, therefore, be regarded as an index of the approach of ovulation.

We have studied the sexual behaviour of heterosexual pairs of pigtail macaques throughout the menstrual cycle in the hope that concurrent measurements of the sex skin would enable us to make a closer correlation of changes in behaviour with physiological events in the menstrual cycle than is possible in some other species. This paper describes our findings and relates them to levels of progesterone in the female, determined throughout the menstrual cycle.

MATERIALS AND METHODS

Eight adult female pigtail macaques were each paired with a given male of the same species and studied for sexual behaviour on alternate days of a complete menstrual cycle. Six vasectomized males were available, so that two males were used twice. Testing was performed in a large solid-sided cage (290 × 150 × 210 cm) with a transparent plexiglass front through which observations were made. The animals were carried from their nearby home cages in small transport boxes and the female was admitted to the testing cage first. The test was timed to start from the introduction of the male and lasted for 15 min. The animals had previously been habituated to the testing procedure.

Observations were made simultaneously by two investigators and the frequency of different behaviours was recorded on a score sheet divided into 1-min segments, the elapsed time being automatically indicated by a time clock which also signalled the end of the test. Thirty-six patterns of behaviour were scored, including aggressive-submissive patterns, such as threatening or grimacing, and social patterns, such as grooming and proximity, in addition to a wide range of sexual patterns, from genital contact and presenting to mounting and ejaculation.

Daily measurements of sex skin diameter were taken, using calipers placed along an imaginary line drawn over the upper edge of the ischial callosities. Spots were tattooed at the extremities of this line and the calipers were always placed on the same marks. Although seemingly crude, this procedure allowed measurements to be duplicated to within 1 mm.

On the day of behavioural testing, 5 ml blood were withdrawn from a femoral vein into a heparinized syringe. The plasma was separated by centrifugation in the cold and stored frozen until assayed. Progesterone concentration was determined by a modification of the competitive protein-binding method of Neill, Johansson, Datta & Knobil (1967), employing a globulin fraction of dog serum, obtained by precipitation with 50% ammonium sulphate, as the binding protein.

Assays were performed with single samples of 1 ml plasma from the follicular

phase and 0.5 ml from the luteal phase. Each assay included a standard curve (0 to 8 ng recrystallized progesterone), two blank samples of ovariectomized-adrenalectomized plasma and two samples containing a trace amount of tritiated progesterone for concurrent estimation of recovery. The unknown samples were corrected for the blank and for recovery, and progesterone concentration was expressed in ng/ml.

Laparotomy was performed under Fluothane anaesthesia, beginning 2 days before the expected peak of sex skin swelling and continuing daily for 5 days or until ovulation was seen to have occurred. Surgery was carried out during the menstrual cycle immediately following the one in which behavioural observations and progesterone determinations were made.

RESULTS

Of the five animals subjected to laparotomy, the developing follicle was ruptured during surgery in one animal and, in two others, it was prudent to discontinue surgery before ovulation although detumescence had begun. For

TEXT-FIG. 1. Relationship of phases of swelling to duration of the menstrual cycle in the pigtail macaque. ●, Tumescence; ○, detumescence.

the remaining two females, ovulation occurred between the day of peak swelling and the first day of detumescence of the sex skin. In ovulatory cycles, this day provided an index of the beginning of the luteal phase and a ready means of dividing the cycle into its follicular and luteal phases.

In the eight cycles studied, the interval between menstruations ranged from 26 to 40 days (mean 32.9 ± 5.0 S.D.). As shown in Text-fig. 1, duration of cycle length was more highly correlated with the duration of the follicular (tumes-

cent) phase ($r = 0.987$), which varied from 12 to 24 days compared to a range of from 14 to 17 days for duration of the luteal phase ($r = 0.737$). Text-figure 2

TEXT-FIG. 2. Changes in sex skin swelling (○) and plasma progesterone (●) during the menstrual cycle of eight pigtail macaques. Arrows indicate days on which ejaculation occurred when the female was paired with the male.

shows the changes in sex skin swelling and concentration of plasma progesterone for a complete menstrual cycle of each of the eight females. In every case, the rise in plasma progesterone coincided with the onset of sex skin detumescence,

the presumed time of ovulation. It was difficult to establish exactly when the peak of plasma progesterone occurred as some samples had to be discarded when their content exceeded the upper limit of the linear portion of the standard curve (8 ng), e.g. Female 601. Three animals (Females 2516, 601 and 2514) showed small, transient rises in plasma progesterone during the follicular phase. These three animals were also the ones with the longest menstrual cycles (40, 35 and 39 days, respectively) and the duration of the follicular phase in each of these cycles was 23, 20 and 24 days, respectively. Moreover, the pattern of ejaculatory behaviour differed markedly in these animals compared with the other five females.

For Females 2516, 601 and 2514, the average proportion of tests in the follicular phase on which males achieved ejaculation was 0.36 (range 0.18 to 0.50), whereas the corresponding proportion for females with shorter cycles was 0.88 (range 0.71 to 1.00). In the case of Female 2516, the deficiency in

TABLE 1
FREQUENCY OF SEXUAL BEHAVIOUR PATTERNS IN PAIRED MALE AND FEMALE
PIGTAIL MACAQUES DURING THE MENSTRUAL CYCLE

<i>Behaviour</i>	<i>Follicular phase</i>	<i>Luteal phase</i>
	<i>Average frequency/animal/test</i>	<i>Average frequency/animal/test</i>
♂ mounting	9.6 ± 2.8*	7.7 ± 4.5
♂ intromission	8.5 ± 3.3	7.6 ± 4.8
♂ pelvic thrusts per intromission	14.6 ± 1.6	13.5 ± 2.2
♀ presenting	16.1 ± 10.5	9.1 ± 7.5
♀ reaching back	8.9 ± 2.7	6.7 ± 4.4

* Mean ± standard deviation.

ejaculatory performance did not seem to be attributable to the male. When the same male (2504) was paired with Female 2509, the ejaculatory performance was regular and comparable to that of all other males paired with females undergoing shorter cycles.

In the thirteen separate assays of progesterone used in this study, the average plasma blank was 0.45 ± 0.08 ng. The mean and standard deviations for recoveries were 67.6 and 7.0%, respectively. The coefficient of variation for the determination of 5 ng was about 15%. Even after correction for the plasma blank, the assay gave a positive systematic error of about 30% in the estimation of 5 ng authentic progesterone. We do not, therefore, regard the values of progesterone presented in this paper as absolute estimates but rather as true indications of changes in concentration during the menstrual cycle.

The majority of the patterns of sexual behaviour studied showed little change in frequency with stage of the menstrual cycle. Aggressive patterns were spasmodic and there was very little display of social patterns, such as grooming or pouting. By dividing the cycle into its follicular and luteal phases, a significant difference was found between the two phases in the frequency of 'presenting' by the female ($P < 0.05$), but not in frequency of mounting, intromission or number of pelvic thrusts per intromission by the male (Table 1).

During copulation, the female often displayed a characteristic 'reaching back' motion to grasp either of the male's legs with one hand while turning her head to gaze at him. This behaviour occurred a total of 1047 times over all tests, and the difference in average frequency per female per test between the follicular and luteal phases failed to reach the 5% level of probability (Table 1). Although 'reaching back' occurred in 93% of ejaculatory intromissions (49/53) compared to 74% of non-ejaculatory intromissions (734/999), of all intromissions in which 'reaching back' occurred, only 6% (49/783) were associated with ejaculation.

TEXT-FIG. 3. Changes in ejaculatory latency of the male with stage of the female's cycle in the pigtail macaque. Number of ejaculations in parentheses.

The event which varied markedly with the stage of the female's cycle was the ejaculatory behaviour of the male. Ejaculatory latency, defined as the time from start of the test to first ejaculation, declined during the follicular phase, reached a minimum close to the time of peak sex skin swelling and rose rapidly after the onset of sex skin detumescence (Text-fig. 3). During the follicular phase, latency was positively related to number of intromissions ($r = 0.629$, d.f. = 40, $P < 0.001$). The number of ejaculations also rose during the tumescent phase but ejaculation during the 15-min test practically ceased after detumescence began. For each of the eight pairs tested, there was a decrease in the incidence of ejaculation during luteal tests compared with follicular tests ($P < 0.01$). The average percentage of follicular tests in which ejaculation occurred was 56 (45/81), whereas only 8.3% (5/60) of all luteal tests were associated with ejaculation.

The incidence of ejaculation, defined as the proportion of tests in which the male achieved ejaculation, reached a maximum coincident with the peak of sex skin swelling, and is shown in Text-fig. 4, together with the pattern of change in plasma progesterone. As the level of progesterone began to rise, the incidence of ejaculation rapidly declined.

Text-figures 5 and 6 show the changes in rate of intromission and rate of pelvic thrusting in relation to incidence of ejaculation and ejaculatory latency. The average rates (number per minute) of intromission and pelvic thrusting were significantly higher in the follicular than in the luteal phase ($P < 0.05$) and

TEXT-FIG. 4. Incidence of ejaculation by the male (○) and level of plasma progesterone in the female (●) in relation to sex skin swelling in the pigtail macaque.

TEXT-FIG. 5. Incidence of ejaculation and rate of intromission at different stages of female sex skin swelling in the pigtail macaque. Rate of intromission was determined by dividing the total number of intromissions by ejaculatory latency or total test-time when ejaculation did not occur.

both rates showed an abrupt decrease after the onset of sex skin detumescence. The rise in ejaculatory latency and decline in incidence of ejaculation were thus accompanied by decreased rates of intromission and pelvic thrusting.

Mounting rate, defined as the frequency of mounts per test divided by time to ejaculation or to end of test when ejaculation failed to occur, also varied

significantly ($P < 0.02$) with the phase of the cycle. During the follicular phase, the mean mounting rate was 9.7 ± 1.2 (S.D.), and in the luteal phase it was 4.2 ± 0.5 (S.D.). This difference in mounting rates reflects the low frequency of ejaculation during the luteal phase. Although mounting frequency did not vary with the cycle (Table 1), the frequencies obtained for most luteal tests were distributed over total testing time, whereas similar frequencies during the follicular phase were distributed over the shorter interval terminated by ejaculation.

TEXT-FIG. 6. Rate of pelvic thrusting and ejaculatory latency in relation to swelling of the sex skin in the pigtail macaque. Rate of pelvic thrusting was determined by dividing the total number of thrusts to ejaculation by the latency to ejaculation or total test time when ejaculation did not occur.

DISCUSSION

Changes in sex skin size during the menstrual cycle of *M. nemestrina* followed the pattern previously reported for the baboon (Gillman, 1935) and resembled that of the chimpanzee (Yerkes & Elder, 1936; Young & Yerkes, 1943; Clark & Birch, 1948). Our data confirmed those of Zuckerman (1937) regarding the relative constancy of the length of the luteal phase. Laparotomy provided evidence suggesting a close connection between time of ovulation and the peak of sex skin swelling in *M. nemestrina*, as reported for the chimpanzee by Young & Yerkes (1943). The existence of this external indicator of ovulation gives the pigtail macaque a marked advantage over the rhesus monkey as a species for research on reproduction in non-human primates.

The qualitative pattern of changes in plasma progesterone in our animals was similar to that reported for the rhesus monkey (Neill, Johansson & Knobil, 1967; Kirton, Niswender, Midgley, Jaffe & Forbes, 1970). Although some animals showed transient rises in plasma progesterone during the follicular phase, the sampling interval (48 hr) was too long to determine whether progesterone was present in plasma before ovulation, as reported for the rat

(Feder, Resko & Goy, 1968a), guinea-pig (Feder, Resko & Goy, 1968b) and rhesus monkey (Johansson, Neill & Knobil, 1968). In the three animals (Females 2516, 601 and 2514) which showed small increases in progesterone during the tumescent period, it appeared that the secretion of progesterone lengthened the duration of the follicular phase of the cycle, possibly by interrupting follicular growth. One animal (Female 2511), however, showed a cycle of average length although the concentration of progesterone in the follicular phase was elevated compared with that of other females showing similar cycles of average length.

We have no information about the changes in levels of oestrogens during the menstrual cycle of *M. nemestrina*, but it is unlikely that collapse of the sex skin is due to oestrogen withdrawal alone. Work on the spayed baboon showed that withdrawal of oestrogen will bring about detumescence but injection of oestradiol benzoate is not able to prevent the normal course of detumescence in the intact animal (Gillman, 1938). Exogenous progesterone, given during the follicular phase, causes premature collapse of the sex skin and can overcome the effect on perineal swelling of concurrently administered oestradiol (Gillman, 1942).

In contrast to the findings of Michael, Herbert & Welegalla (1966) in the rhesus monkey, grooming by either the male or female was virtually absent in our tests and bore no relation to the female's menstrual cycle. 'Presenting' by the female to the male occurred either without contact ('presenting' at a distance) or in response to the male's manual contact. Although a 'paired-*t*' test revealed that 'presenting' at a distance was less frequent in the luteal phase ($P < 0.05$), there was considerable variation from animal to animal.

A behaviour similar to 'reaching back' by the female was described in the rhesus monkey by Zumpe & Michael (1968) as the 'clutching reaction' and was reported to occur most frequently in conjunction with ejaculation by the male, being likened by these authors to the female orgasm. In our study, female 'reaching back' occurred throughout the cycle and, in contrast to the rhesus monkey, was not strongly associated with ejaculation.

This paper reports in detail for the first time changes in primate sexual behaviour correlated with concurrent monitoring of changes in endogenous hormone levels. In the rhesus monkey, mounting of the female by the male is most frequent at mid-cycle (Michael, Saayman & Zumpe, 1967) and declines during the luteal phase (Michael & Welegalla, 1968). In the pigtail monkey, we found that mounting and intromission continued throughout the cycle. However, an abrupt decline in the incidence of ejaculation was observed after the onset of detumescence of the sex skin and coincident with the rise in plasma progesterone. Ejaculatory latency reached a minimum at the time of peak swelling so that both the highest frequency and fastest attainment of ejaculation were closely related to the time of ovulation. Similar findings have been reported for the rhesus monkey (Michael, Herbert & Welegalla, 1967), for the chimpanzee (Yerkes & Elder, 1936; Young & Orbison, 1944) and for the baboon (Rowell, 1967). A maximum rate of conception has been reported from matings taking place around mid-cycle in the rhesus monkey (Hartman, 1932; Van Wagenen, 1945).

It is not clear how information about the female's hormonal status is conveyed to the male. Swelling of the sex skin may be a visual clue, although other factors may be involved, such as olfactory signals (Michael & Keverne, 1968, 1970).

The changes brought about by luteal progesterone which render the male no longer able to achieve ejaculation in the 15-min testing period remain conjectural. Conceivably, a longer testing period might have allowed ejaculation to occur. Tokuda, Simons & Jensen (1968) reported times to ejaculation which exceed 15 min, but the data were collected in a group living situation and were not analysed according to stage of the cycle. An inhibitory effect of progesterone on ejaculation has previously been reported in the rhesus monkey by Michael, Herbert & Saayman (1966) and Michael, Saayman & Zumpfe (1968). Progesterone has also been shown to antagonize oestrogen-induced sexual behaviour in non-primate species such as the sow (Baker, Ulberg, Grummer & Casida, 1954), the cow (Melampy, Emmerson, Rakes, Hanka & Eness, 1957) and the guinea-pig (Goy, Phoenix & Young, 1966), an antagonism akin to the action of these hormones on the sex skin of the baboon (Gillman, 1942).

The reduced incidence of ejaculation in the luteal phase may be due to a change in the amount of penile stimulation experienced by the male. This is suggested by the findings that the average rates of intromission and pelvic thrusting were significantly lower in the luteal than in the follicular phase and that both rates showed a decline immediately after the onset of detumescence. Such an explanation is consistent with the current hypothesis that, in lower mammals, successive intromissions lead to a cumulative increase in penile stimulation until an ejaculatory threshold is reached (Beach, 1967). Our data do not suggest an explanation for the change in rate of intromission alone, but it is possible that alterations in the morphology of the vagina or in the nature of its secretions may affect the quality of the penile stimulation experienced during intromission. Quality of penile stimulation rather than quantity may also be a factor in the mechanism controlling ejaculatory latency, since changes in this behavioural measure during the follicular phase were not found to be related to rate of intromission and were in fact positively correlated with its frequency.

ACKNOWLEDGMENTS

We are grateful to Dr C. W. de Lannoy for performing the surgical procedures and thank Dr J. A. Resko for his interest and Mr Jan Ploem for technical assistance. The work was supported by funds from NIH Grants MH 08634 and MH 21312. Predoctoral training funds for C. A. Paris were provided by Grant GMO 149503. Publication No. 544 of the Oregon Regional Primate Research Center, supported in part by NIH Grant FR 00163.

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