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Temporal Relationship of Hormonal Peaks to Ovulation and Sex Skin Deturgescence in the Baboon

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ABSTRACT. The purpose of this study was to determine the temporal relationship of peak levels of oestradiol (E_2), LH and progesterone to ovulation and sex skin deturgescence in the baboon. A total of 55 baboons were used in these studies. Hormonal levels were measured in 47 cycles and ovulation was documented by laparoscopic examination in 26 of these cycles. A temporal relationship of ovulation to sex skin deturgescence was established in 57 cycles. The mean interval from E_2 peak to ovulation was 41.4 ± 2.3 hr, the interval from E_2 peak to LH peak was 17.3 ± 2.0 hr and that from LH peak to ovulation was 18.4 ± 2.0 hr. Eleven baboons showed an LH peak on the day of the E_2 peak. The number of days to the first sign of sex skin deturgescence after ovulation was 2.07 ± 0.14 days (range 0–5 days). Nineteen cycles (33.3%) showed sex skin deturgescence 1 day after ovulation, another 19 cycles (33.3%) showed sex skin deturgescence 2 days after ovulation, and only 13 cycles (22.8%) showed sex skin deturgescence 3 days after ovulation. Sex skin deturgescence was observed on day 0, 4 or 5 postovulation in only two baboons.

INTRODUCTION

The perineal sex skin changes exhibited by the baboon during the menstrual cycle make this primate a convenient model to study reproductive physiology. HENDRICKX and KRAEMER (1969) for example found that when mating was allowed on day 3 preceding sex skin deturgescence 48% conception rate was obtained indicating that this is the optimal time for mating to achieve a conception of known age. WILDT et al. (1977) made use of laparoscopic observation for confirmation of ovulation in 52 cycles of 12 baboons and found the majority (65.4%) of all ovulations occurring on the last day of maximal turgescence or the first day of deturgescence and the remaining ovulations were found to occur anywhere from 5 days prior to sex skin deturgescence to 3 days after. This study was undertaken to obtain more data using a larger population of baboons to establish temporal relationship of ovulation to sex skin deturgescence. Furthermore, at the time this study was undertaken, there was no report to temporally correlate the increases in preovulatory E_2 to LH release and ovulation. Recently however, PAUERSTEIN et al. (1978) have shown a temporal relationship of estrogen, progesterone and LH levels to ovulation in women, rhesus monkey and baboons.

The studies reported here therefore, correlate temporally the levels of E_2, LH and progesterone to ovulation and also establish a temporal relationship of ovulation to sex skin deturgescence.

MATERIALS AND METHODS

A total of 55 baboons were studied. This group of baboons was comprised of *Papio cynocephalus* and *Papio anubis*. MAPLES (1968) places both *P. cynocephalus* and *P. anubis* in

the species *P. cynocephalus*, therefore we have made no attempts at presenting the data separately for these two species.

A perineal sex skin record of at least two years was available on these animals. However, each animal had at least one regular menstrual cycle prior to being studied. The perineal sex skin turgescence of 57 cycles was observed and recorded daily and was subjectively rated on a scale of 0 to 4 (no turgescence = 0; maximum turgescence = 4). The degree of maximum sex skin turgescence and minimum sex skin turgescence varied among individual baboons, therefore the same investigator made the observations throughout the period of this study. Daily blood samples were collected between 0800 and 1000 hr from the femoral vein of animals sedated with ketamine hydrochloride (15 mg/kg) starting about 5 to 6 days before expected sex skin deturgescence. The expected day of sex skin deturgescence was estimated from the mean lengths of maximum turgescence of the previous cycles. Daily radioimmunoassays (RIA) of E_2 and progesterone were carried out in these samples.

After detection of the estrogen surge, daily laparoscopic examinations were performed in 26 cycles until ovulation was observed. Laparoscopic examinations were also carried out daily near the expected time of ovulation in 31 cycles, and no blood samples were obtained during these observations. The morphological changes during the peri-ovulatory period as seen through the laparoscope have been described for *fascicularis* monkey by JEWETT and DUKELOW (1972), for the squirrel monkey by HARRISON and DUKELOW (1974), for the Japanese monkey by NIGI (1977), and for the baboon by WILDT et al. (1977). In some instances, when ovulation appeared imminent as judged from the appearance of the follicle such as vascularization, haemorrhagic patches on the surface or inside the thin, almost transparent dome, then another laparoscopic examination was carried out 6 to 8 hr later. Ovulation was confirmed when the follicle showed a distinct stigma which was either haemorrhagic or gave the appearance of an "eye." The follicular dome at this time had collapsed and depending on the time from ovulation to time of laparoscopic examination a clear ring of yellowish color was seen around the base of the collapsed dome, indicating that luteinization process had started. In some instances this sign of luteinization could be seen even before ovulation. In any event there were many distinct criteria as described above to confirm the occurrence of ovulation. Eight baboons underwent repeated laparoscopic examination at 6 to 8 hourly intervals until ovulation, because ovaries of these animals exhibited signs which indicated ovulation was imminent. In the remaining 18 baboons, since ovulation did not appear imminent the next laparoscopic examination was scheduled 24 hr later. At the next laparoscopic examination only 14 of these baboons showed signs of recent ovulations. However, it was very difficult to pinpoint the exact time of ovulations, and since in all likelihood most of these baboons ovulated more than 6–8 hr before laparoscopic examination, it was decided to consider the actual time of ovulation as the midpoint between the times of two laparoscopic examinations. Thus ovulation was predicted to have taken place at 3 to 12 hr before the last examination. In some instances (19 cycles), no laparoscopic examination was carried out for 2 to 4 days following detection of the oestrogen (E_2) peak. Data on these cycles were analyzed separately. A record of total cycle length (cycle day 1 = first day of menstrual bleeding), follicular phase length (cycle day 1 to day before ovulation), and luteal phase length (cycle length minus follicular phase length) and an estimate of the total length of maximum turgescence was made.

RADIOIMMUNOASSAYS (RIA)

Progesterone was measured using a specific RIA with antiserum (GDN-337) generously

supplied by Dr. G. D. NISWENDER (Colorado State University). The within assay coefficient of variation was 9.9% and between assay coefficient of variation was 19.9% with a sensitivity of 0.1 ng/ml of plasma. Cross reactions with other physiological steroids were minimal and have been reported (GOODMAN et al., 1977).

Oestradiol (E_2) was measured using a specific RIA with antiserum (E_2 TGK) kindly provided by Drs. WRIGHT and COLLINS (Emory University). The within assay coefficient of variation of oestradiol was 5.6% and between assay coefficient of variation was 11.6%, with a sensitivity of less than 10 pg/ml plasma (CASTRACANE, MOORE & SHAIKH, 1979). The RIA procedure has been reported (WU, LUNDY & LEE, 1973).

Baboon LH was measured using highly purified reagents kindly provided by Dr. V. STEVENS (Columbus, Ohio). A specific antibody generated to baboon LH (bLH) was used at a final dilution of 1/50,000. Purified baboon LH was radioiodinated with ^{125}I to a specific activity of 250 μCi per μg with a modification of the procedure of GREENWOOD, HUNTER and GLOVER (1963). The within assay coefficient of variation was 7.5% and between assay coefficient of variation was 12.0%. The limit of sensitivity of the assay was 1 to 5 ng of baboon pituitary standard per milliliter of plasma. The RIA procedure has also been reported (KOYAMA, DE LA PENA & HAGINO, 1977).

RESULTS

Menstrual cycle events and temporal relationship of hormonal peaks are shown in Table 1. The mean menstrual cycle length of 53 baboon cycles was 31.5±0.52 days with a range of 20–38 days. The follicular phase length and luteal phase length were about the same (15.6

Table 1. Menstrual cycle events and temporal relationship of hormonal peaks.

Menstrual cycle events	Mean±SE	Range
Menstrual cycle length (days), $N = 53$	31.5±0.52	20–38
Follicular phase length (days), $N = 53$	15.7±0.52	6–25
Luteal phase length (days), $N = 53$	15.6±0.35	10–20
Maximum turgescence length (days), $N = 53$	9.8±0.54	3–20
Day of cycle when E_2 peak was observed, $N = 37$	15.2±0.50	10–24
Day of cycle when ovulation was observed, $N = 26$	16.7±0.54	6–25
Number of hours to LH peak from E_2 peak, $N = 37$	17.3±2.0	0–48
Number of hours to ovulation from E_2 peak, $N = 26$	41.4±2.3	12–64
Number of hours to ovulation from LH peak, $N = 26$	18.4±2.0	0–40
Number of days to first sign of sex skin deturgescence from ovulation,[1] $N = 57$	2.07±0.14	0– 5

1) See Table 2 for details.

Table 2. Temporal relationship between ovulation and sex skin deturgescence.

Days after ovulation when sex skin deturgescence was observed (ovulation = day 0)	Number of baboons observed
0	2 (3.5%)
1	19 (33.3%)
2	19 (33.3%)
3	13 (22.8%)
4	2 (3.5%)
5	2 (3.5%)

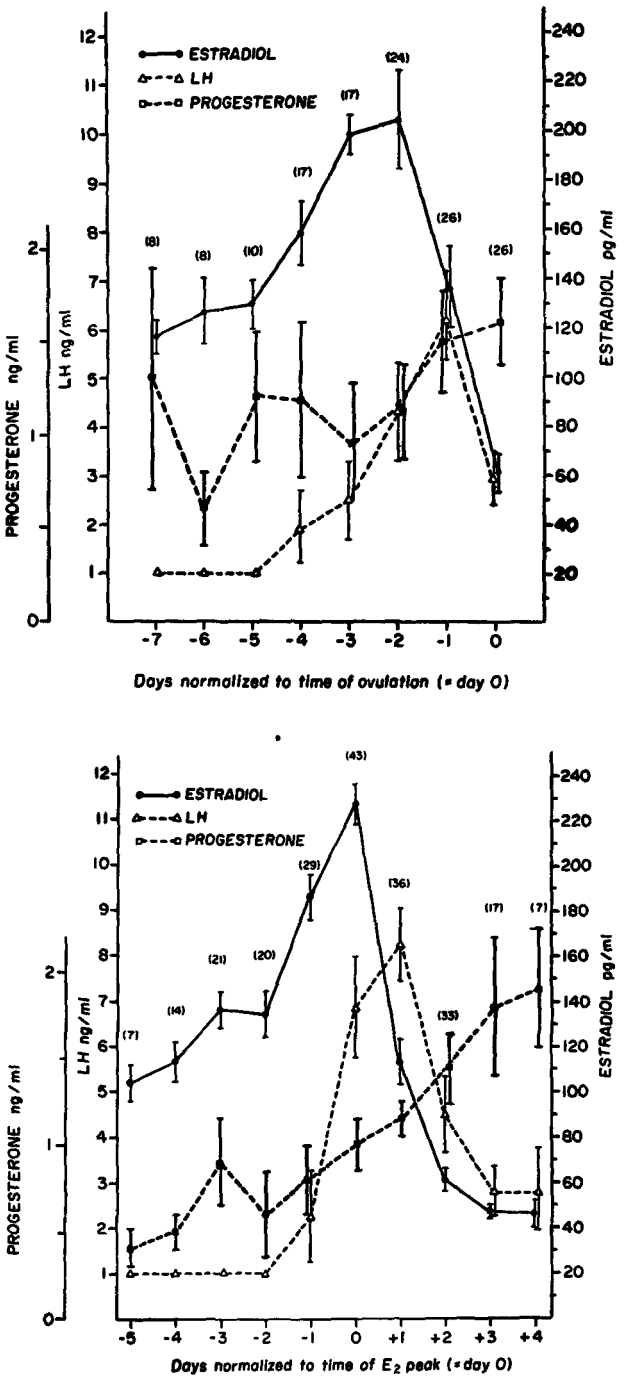

Fig. 1. Composite pattern of plasma levels of oestradiol, progesterone and LH during the periovulatory period in the baboon. Figures in parentheses indicate number of observations. **a.** The day of ovulation as confirmed by laparoscopic examination is designated day 0. **b.** The day of peak levels of oestradiol is designated day 0.

days); however, correlation analysis showed that, as the cycle length increased, the follicular phase length also increased (correlation coefficient = 0.71). Similar analysis of cycle length and luteal phase length showed poor correlation (correlation coefficient = 0.23). The length of maximum turgescence was 9.8±0.54 days.

The temporal relationship of ovulation to sex skin deturgescence is shown in Table 2. On the average, ovulation occurred 2 days before sex skin deturgescence. Table 2 shows that 66.6% of ovulations occurred either 1 or 2 days before sex skin deturgescence. The mean cycle day when ovulation was observed was 16.7±0.54 with a range of 6–25 days.

The composite pattern for LH, E_2 and progesterone curves, normalized to the day of ovulation, is shown in Figure 1a; Figure 1b shows the composite pattern normalized to E_2 peak. Figure 1b contains a larger set of data since the cycles in which time of ovulation was not confirmed by laparoscopic examination are also included. This was done to give the temporal relationship of E_2 peak to LH peak with a larger set of data than would have been possible by utilizing only the data in which ovulation was confirmed. The mean day of cycle when the E_2 peak was observed was 15.2±0.50 with range of 10–24 days. The mean interval from oestradiol peak to LH peak was 17.3±2.0 hr with a range of 0–48 hr. It must be pointed out here that of the 36 animals in which E_2 and LH peaks were recorded, 11 animals showed both peaks on the same day, which for calculation purposes was defined as "0" hr of interval between the two peaks. There was one animal which showed an LH peak 24 hr before the E_2 peak and another one which showed an LH peak 48 hr after the E_2 peak. The remaining 23 animals showed LH peaks 24 hr after the E_2 peak.

The mean interval from E_2 peak to ovulation was 41.4±2.3 hr (range 12–64 hr), and the mean interval from LH peak to ovulation was 18.4±2.0 hr (range 0–40 hr).

Figures 1a and 1b also clearly show the increases in progesterone levels before the LH peak but coincident with increases in LH levels. However, these increases were statistically not significant. After a decline at day 6 of ovulation, the progesterone levels increased at day 5 and 4 to decline again at day 3. These fluctuations, however, were also not significant.

DISCUSSION

The menstrual cycle lengths (31.5±0.52) and the maximum turgescence lengths (9.8±0.54) reported in this study (Table 1) are smaller in lengths than those reported by HENDRICKX and KRAEMER (1969) and WILDT et al. (1977) using the same species of baboons. The reasons for this discrepancy is not clear. It must, however, be pointed out that our study was conducted during the months of October through April. We have not been able to follow the cycle lengths of these animals during the summer months because they underwent various treatment regimens. However, in another group of baboons we examined the cycle lengths and the mean of 302 cycles observed was 34.8±0.29 days which is, to some extent, in agreement with the above mentioned reports. This does not however indicate that there is a seasonal effect on cycle length since not all baboons were continuously observed throughout the year. It must also be pointed out that ZUCKERMAN (1930, 1937) reported a cycle length (mean±S.D.) of 34.75±2.38 for *P. anubis* and 33.3±3.48 for *P. cynocephalus* which also are longer than those reported in this study, but none of these reported cycle lengths took into consideration any effect of the season.

The finding that the follicular phase increases with the increase in cycle length (correlation coefficient = 0.71) whereas the luteal phase is relatively constant concurs with the Ogino-

Knaus principle reported for the human (HARTMAN, 1962). However, the more recent reports of STROTT et al. (1970) and SHERMAN and KORENMAN (1974) who have shown that in the human menstrual cycle with short luteal phases, the level of progesterone declines earlier than in normal cycles without much variation in follicullar phase seems to contradict this finding. In the cynomolgus monkey, we found that the luteal phase was more variable (SHAIKH, NAQVI & SHAIKH, 1978). In the face of these conflicting observations in humans, cynomolgus monkey and baboon, the final conclusion must await analysis of the follicular and luteal phases using a much larger set of data.

The studies reported here provide useful information documenting the occurrence of ovulation and its temporal correlation to peaks of E_2 and LH (Table 1; Figs. 1a & 1b). The intervals of 41.4 ± 2.3 hr between oestrogen peak and ovulation and 18.4 ± 2.0 hr between LH peak and ovulation reported here are in agreement with the findings of PAUERSTEIN et al. (1978). However, the interval between the oestradiol and LH peaks observed in our study (17.3 ± 2.0) is not in agreement with the findings of PAUERSTEIN et al. (1978), who recorded the interval to be 23 ± 2 hr. The reason for this discrepancy could be due to our observation of 11 cycles in which the oestradiol and LH peaks occurred on the same day. Of the remaining 24 cycles, 23 showed an LH peak 24 hr after the oestradiol peak. KOYAMA, DE LA PENA and HAGINO (1977) reported LH and oestradiol peaks on the same day in six out of ten baboons. GONCHAROV et al. (1976), on the other hand, reported the LH peak to occur 1 day after the oestradiol peak in five of six baboons. HOTCHKISS, ATKINSON and KNOBIL (1971) have reported that, in the rhesus, the oestrogen and LH peaks occur on the same day. In human subjects the oestrogen peak generally precedes the LH peak (ABRAHAM et al., 1972; PAUERSTEIN et al., 1978; VANDE WIELE et al., 1970). It must be pointed out that in the studies cited, as well as in our own, blood samples were drawn once daily. It is possible that, due to this limitation, some peak values might have been missed, resulting in erroneous temporal correlations. One must also consider the possibility that the peak value is not what really triggers the events such as LH release and ovulation. Depending upon the sensitivity of individual baboons, different levels of hormones may trigger LH release and ovulation. This may be the reason for coincident LH and oestradiol peaks. We have likewise observed an LH peak on the day of ovulation in one baboon.

The positive feedback effect of oestrogen on LH secretion has been clearly established by the use of chemical antagonists (SHIRLEY, WOLINSKY & SCHWARTS, 1968; LABHSETWAR, 1970) and antiserum to oestradiol (FERIN et al., 1969) in rats and hamsters. YAMAJI et al. (1971), KARSCH, DIERSCHKE, WEICK, YAMAJI, HOTCHKISS and KNOBIL (1973) and KARSCH, WEICK, BUTLER, KIERSCHKE, KREY, WEISS, HOTCHKISS, YAMAJI and KNOBIL (1973) showed the positive feedback effect of estrogen in intact and sprayed monkeys. NILLIUS and WIDE (1971) demonstrated a similar role for estrogen in the human female. Likewise, an effect of progesterone on the timing of the LH release in the rat and hamster has been demonstrated (MCDONALD & GILMORE, 1971; SAKSENA & SHAIKH, 1974), but a role for progesterone in the timing of LH release in primates is still debatable (CLIFTON, STEINER & RESKO, 1975; KARSCH, DIERSCHKE, WEICK, YAMAJI, HOTCHKISS & KNOBIL, 1973; KARSCH, WEICK, BUTLER, KIERSCHKE, KREY, WEISS, HOTCHKISS, YAMAJI & KNOBIL, 1973). Our data clearly show increases in progesterone after onset of the LH surge, but prior to the LH peak. It can, therefore, be argued that the observed increases in progesterone were due to LH stimulation. Although human preovulatory follicles 3 to 12 mm in diameter produce progesterone in tissue culture in the absence of LH (ROSS, 1976), and rhesus ovaries produce progesterone when the largest

follicles reach a diameter of 5 to 6 mm (RESKO et al., 1975), one cannot conclude from our studies that increases in progesterone have anything to do with the release of LH or timing of the release of LH. Other studies currently under way in our laboratory involve a schedule of frequent blood sampling during the preovulatory period, and these should be useful in clarifying at least the temporal relationship of increases in progesterone to the increase in LH.

Finally, the studies reported here give useful information about the temporal relationship of ovulation to sex skin deturgescence. It is clear that most ovulations (66.6%) occur between days 1 and 2 before sex skin deturgescence (Table 2). WILDT et al. (1977) found in their study using the same species of baboons, that the majority (65.4%) of ovulations occurred on the last day of maximal turgescence or the first day of deturgescence. We recorded only 2 out of 57 ovulations (3.5%) occurring on the first day of sex skin deturgescence. WILDT et al. (1977), although observed 52 ovulations, these were repeat observations in the same group of 12 baboons. In the present study, 57 ovulations were observed in a group of 55 baboons. Thus this study represents occurrence of ovulation in relation to sex skin changes in a larger set of baboon population. HENDRICKX and KRAEMER (1969) studied optimal mating time and reported that mating for 2 to 12 hr on day 3 preceding deturgescence resulted in 48% conception rate. In their study, although it was concluded that most ovulations occur 3 days before sex skin deturgescence, one can argue, on the basis of the sperm survival time and the fact that the mating period covered 2 to 12 hr, that the majority of baboons ovulated 2 days preceding sex skin deturgescence. ZUCKERMAN (1930, 1937) and ZUCKERMAN and PARKES (1932) concluded that ovulation coincides with sex skin deturgescence, and GILLMAN and GILBERT (1946) suggested, although on a limited evidence, that ovulation may precede deturgescence by at least 2 or 3 days. Taken together all the evidence from this and other studies, it can reasonably be concluded that for maximum conception rate mating should occur either 2 or 3 days before expected sex skin deturgescence. However, for recovery of baboon embryos of precise age either for embryo transfer work or in vitro study of embryo one has to rely on preovulatory peak of oestrogen or LH. Thus these studies provide useful information not only for research involving periovulatory events, but also for pharmacological study or pro- or anti-fertility agents, where the time (and therefore, the site) of action of new agents under test must be determined as part of the study of their mechanism of action. Effectiveness of pro- or anti-fertility agents is also determined more efficiently if the timing of the occurrence of ovulation is precisely known so that drug exposure can be timed carefully in relation to these events.

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