Photoperiod and ovulatory menstrual cycles in female macaque monkeys

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Summary. Macaques (Macaca mulatta and M. assamensis) which had been maintained on a 12L : 12D light cycle for the previous 4 years and had 25–35-day menstrual cycles were randomly assigned to two groups. Those in Group 1 were kept in 12L : 12D for 13 months. Those in Group 2 were subjected to three successive 5-month periods of 20L : 4D, 4L : 20D and 20L : 4D. There were no significant differences between the two groups in the frequency, duration and percentage of ovulatory menstrual cycles, suggesting that photoperiod is not the sole regulator of seasonal breeding in these animals.

Introduction

Several reports have established the seasonal character of breeding activity in some species of macaques (Hartman, 1932; Vandenbergh & Vessey, 1968; Michael & Zumpe, 1971; Drickamer, 1974; Roberts, 1978). In the northern hemisphere the vast majority of conceptions occur between October and December, a period of decreasing or short daylight. Although various factors such as precipitation, availability of food, and photoperiod have been suggested as the regulatory factors, none has been conclusively demonstrated.

In numerous species (Hoffman, 1973), including some prosimians (Petter-Rousseaux, 1970; Van Horn, 1975; Reynolds & Van Horn, 1977), photoperiod has been shown to regulate seasonal breeding. Based on these observations we have undertaken a series of experiments to determine what role photoperiod has in regulating reproductive function in female macaques.

Materials and Methods

All of the monkeys used in this study were purchased from various commercial sources which had obtained the animals by capturing them in their natural environment. The monkeys had been maintained under laboratory conditions for at least 4 years. The conditions consisted of individual housing in a temperature-controlled (19–22°C) room with 12 h light : 12 h dark (12L : 12D) lighting schedule (lights on at 08 : 00 h). The animals received monkey chow once daily and fresh fruit 3 times per week. Water was available at all times.

Nine intact female rhesus monkeys (Macaca mulatta) and 10 intact Assamese monkeys (M. assamensis) were used. All of these animals had demonstrated regular menstrual bleeding (25–35-day intervals) for at least 4 months before the experiment. Beginning in March 1979 animals of each species were randomly assigned to two groups. Those in Group 1 (N = 9) were subjected to a 12L : 12D lighting schedule for a 13-month period. This provided data on the occurrence of normal ovulatory menstrual cycles within the colony. Those in Group 2 (N = 10) were subjected to three 5-month periods of altered photoperiod: two periods of long light (20L : 4D, lights on at 08 : 00 h)

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separated by one period of short light (4L:20D, lights on at 08:00 h). Rooms were completely sealed from external light throughout these experiments. All animal husbandry was performed between 08:00 and 11:00 h. Menstruation was checked daily by insertion of a cotton tipped applicator into the vaginal orifice. The caged females were also trained to present a leg to the investigator who then obtained a 1-ml blood sample via the saphenous vein. Samples were taken 2 or 3 times a week.

Serum progesterone was determined by the method of Abraham, Swerdloff, Tulchinsky & Odell (1971). Progesterone was purchased from Sigma Chemical Co. (St Louis, Missouri), progesterone antiserum, raised against progesterone-11α-BSA, was purchased from Accurate Chemical and Scientific Corp. (Hicksville, New York), and [1,2,6,7-3H]progesterone was purchased from New England Nuclear (Boston, Massachusetts). Cross-reactivity with possible interfering steroids was less than 1%. Recovery of progesterone added to serum was 84–97% and assay sensitivity (a displacement of 2.086 times the s.d. of the 0 dose) was 25 pg. Within- and between-assay coefficients of variation were 7% and 13%, respectively. Menstrual cycles were considered to be ovulatory when progesterone concentrations were elevated (~1–8 ng/ml) for at least 7 days. Statistical comparisons were made by analysis of variance (Dixon et al., 1981).

Text-fig. 1. Periods when serum progesterone concentrations were indicative of ovulation (> 1 ng/ml, □) and when menses occurred (■) in (a) 9 macaque monkeys maintained in a 12L:12D lighting schedule and (b) 10 macaques maintained in 2 photoperiods of long light (20L:4D) separated by 1 period of short light (4L:20D). An R preceding the monkey number indicates a rhesus monkey (Macaca mulatta) and an A indicates an Assamese monkey (M. assamensis).
Results

In the 9 monkeys subjected to a 12L:12D lighting schedule, 92% of the menstrual cycles (n = 106) were ovulatory (Text-fig. 1a). Ovulatory menstrual cycle lengths averaged 30 ± 2 (s.e.m.) days, while overall menstrual cycles were 31 ± 3 days long.

The results obtained from Group 2 are illustrated in Text-fig. 1b: 70% of the 44 menstrual cycles were ovulatory during the first long photoperiod, 78% of the 37 menstrual cycles were ovulatory during the short photoperiod, and 96% of the 46 menstrual cycles were ovulatory during the second long photoperiod. The lengths of the ovulatory menstrual cycles were 34 ± 5, 40 ± 3, and 31 ± 1 days, and the overall menstrual cycle lengths were 38 ± 6, 40 ± 3, and 31 ± 1 days in the 20L:4D, 4L:20D and 20L:4D lighting schedules, respectively. None of these values were statistically different from each other or from the values obtained in Group 1.

When evaluated on an individual basis (Text-fig. 1a, b), 6 of the control monkeys demonstrated normal ovulatory menstrual cycles throughout the entire 13-month period studied. Of the remaining three, Monkey R633 was oligomenarchic and Monkeys A693 and A697 demonstrated distinct periods of ovulation/anovulation. In Group 2, 4 females remained ovulatory throughout the experiment, regardless of the light schedule. The other 6 monkeys became anovulatory while exposed to the initial 20L:4D photoperiod; 4 resumed ovulatory menstrual cycles within 70 days after being exposed to the 4L:20D photoperiod and the other 2 within 45 days after being exposed to the second 20L:4D photoperiod.

Discussion

In macaques, the vast majority of fertile menstrual cycles occur between October and December (Vandenbergh & Vessey, 1968; Roberts, 1978), a period of decreasing or short daylight. The corollary of this is that there is a quiescence of reproductive function during increasing or long daylight. To test the hypothesis that photoperiod regulates these changes in reproductive function, we subjected monkeys to varying light:dark cycles. We selected a rather extreme period for the light:dark cycle in the belief that if we chose a moderate cycle (e.g. 18L:6D) and obtained negative or inconclusive results, we would still wonder if an extreme cycle would provide more conclusive data.

The observation that 6 of the 10 monkeys subjected to varying photoperiods became anovulatory during the first long photoperiod initially suggested some influence of photoperiod. However, only 4 of the animals resumed normal ovulatory menstrual cycles during the short photoperiod. Furthermore, when the light:dark cycle was returned to the 20L:4D schedule, there was no inhibition of ovulatory menstrual cycles in any of the animals. In fact, the 2 monkeys that had remained anovulatory during the short light photoperiod resumed normal reproductive function during this long photoperiod.

If these variable results are taken to indicate an effect of photoperiod on reproductive function in female macaques, it is unclear why only 50% of the treated animals responded to changes in photoperiod. This was probably not due to the animals of one species responding differently (see Text-fig. 1a, b). It is possible that long days have to coincide with a particular phase of an endogenous free-running annual rhythm. If such is the case, then one would expect some animals to be in phase (i.e. respond) and some to be out of phase (i.e. not respond) with the photic stimulation at the time of the experiment. Although this is what we observed, experiments to prove the existence of an endogenous rhythm would be very difficult. The equivocal response to photoperiod may also have been due to photorefractoriness, but data from other species indicate that exposure for 5 months would have been sufficient to overcome the refractory period.

Since our results indicate that light alone does not regulate seasonal breeding in macaques, other factors must be considered. Vandenbergh & Vessey (1968) reported that seasonal breeding in a
troop of free-ranging rhesus monkeys was correlated with rainfall and vegetation. Jayaraman, Hurkadli & Gopalakrishnan (1979) reported that bonnet monkeys (M. radiata) which had been anovulatory for periods of up to 40 months demonstrated normal menstrual cycles within 2 months after the addition of alfalfa to their diets. It is probable that the regulation of seasonal breeding in macaques involves the integration of numerous external stimuli. Barsotti, Abrahamson, Marlar & Allen (1980) have reported that housing macaques under conditions that closely simulate the temperature, humidity and lighting in the natural environment during the breeding season resulted in establishment of ovulatory menstrual cycles within 2 months in animals recently obtained from their natural environment.

Two of the control animals demonstrated distinct periods of anovulation between the months of March–August. This is similar to the defined period of reproductive quiescence for macaques both in the wild and in the laboratory (May–September, Erikson, 1964; Riesen, Meyer & Wolf, 1971). This may reflect persistence of the annual reproductive cycle in animals captured from the wild even though they have been isolated from environmental cues, as has been shown for male rhesus monkeys in which the annual cycle of serum testosterone continues for long periods after isolation from normal environmental cues (Michael & Bonsall, 1977).

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References


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