THE EFFECTS OF THE MATING PATTERN OF THE MOUSE ON THE FORMATION OF CORPORA LUTEA

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Summary. Female mice were placed with males and subjected to three different treatments. One group experienced a low number of pre-ejaculatory thrusts, the ejaculatory reflex and the formation of a copulatory plug. A second group experienced a variable number of pre-ejaculatory thrusts, the ejaculatory reflex and the formation of the copulatory plug which was immediately removed. The third group experienced a variable number of pre-ejaculatory thrusts only. The results indicated that a large number of pre-ejaculatory thrusts is neither necessary, nor sufficient, for the induction of luteal activity in the female mouse. The ejaculatory reflex and the formation of the copulatory plug are sufficient to induce luteal activity regardless of the number of pre-ejaculatory thrusts. The results are compared with those of similar work on the rat.

INTRODUCTION

Quantitative aspects of the pattern of sexual behaviour of the male mouse have been shown to differ according to genotype (McGill, 1962; McGill & Blight, 1963; McGill, 1965). Since the laboratory populations studied were originally derived from wild populations, it is perhaps reasonable to assume that genetic variation in these traits exists in wild populations and, further, that these traits have been subjected to the pressures of natural selection. If this is correct, it would appear that natural selection has resulted in the evolution of a comparatively long and complex pattern of behaviour which, superficially at least, would be expected to reduce rather than increase fitness. This communication is concerned with the examination of a possible mechanism for the correlation between this aspect of behaviour and fitness, but before discussing the problem further it is necessary to describe the pattern of behaviour both qualitatively and quantitatively.

The pattern of sexual behaviour in the male mouse (*Mus musculus*) consists of a series of mounts and mounts-with-intromission (called 'intromissions'). This series normally ends in ejaculation (which can be identified by the male clutching the female with all four limbs and falling to his side) and the formation of the copulatory plug which remains in the female's vagina for about 18 hr.

The work already cited indicates that for the particular strains studied

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ejaculation took place after an average of 425 thrusts, with a mean mating time of 1500 sec. It has also been shown (McGill, 1963) that if a male has ejaculated in the previous 28 hr, both these parameters are reduced to about 20% of the above values.

One possible reason for the evolution of this pattern of behaviour is found in the physiology of the females. It is well known that ovulation occurs spontaneously during the oestrous cycle of both the rat (*Rattus norvegicus*) and the mouse (Asdell, 1964). However, in the absence of copulation, or similar stimulation, functional corpora lutea are not formed and the oestrous cycle does not have a true luteal phase. It is obvious, therefore, that the male mouse must somehow provide appropriate stimulation to the female during a normal mating in order to induce the luteal phase. Three sources of stimulation from the male may be either sufficient or necessary for the induction of the luteal phase. These are: (1) a minimum number of pre-ejaculatory thrusts, (2) the ejaculatory reflex and the formation of the copulatory plug and (3) the subsequent presence of the plug in the vagina. The present experiment was designed to study the relative importance of these three factors.

MATERIAL AND METHODS

Subjects were 10- to 20-week-old male and female mice of the outbred Q-strain which is maintained at the Institute of Animal Genetics, Edinburgh. They had been kept on a reversed light-dark cycle (08.00 hours–20.00 hours) for 6 weeks before the beginning of the experiment. Observations were made in the early afternoon under normal room illumination.

Sexually experienced males were placed individually in plastic cyclinders 10 in. in diameter and 20 in. in height. Two females were then introduced into each cylinder and about 15 min allowed for the initiation of sexual behaviour. Some females, even though in oestrus would reject, or be rejected by a particular male, and consequently, if mating did not occur, the females were offered to a second male, and two new females introduced into the cylinder of the first male.

Matings were carefully observed and controlled to prepare the following groups of females: (a) females which received a relatively low number of thrusts (6 to 55), the ejaculatory reflex and the formation of the copulatory plug; (b) females which received a variable number of thrusts (24 to 135), the ejaculatory reflex and the formation of the copulatory plug which was immediately removed (this is not easily done and one can never be sure that all the plug has been extracted); and (c) females which received a variable number of thrusts (15 to 156) only, i.e. these females did not experience the male's ejaculatory reflex or receive a copulatory plug.

Following the experimental treatment the females were caged singly for 48 hr. At the end of this period a sexually experienced 'indicator-male' was placed in the female's cage. The female was subsequently examined each afternoon for the presence of a copulatory plug and/or for the birth of a litter.

The birth of a litter was recorded in order to ensure that the number of days from treatment to mating was indeed the number of days taken to return to true oestrus, which enabled us to discount such problems as behavioural oestrus

Four females which did not give birth to a litter around 19 to 21 days after mating were discarded.

RESULTS

Since we are interested in both the effects of the treatments and the effects of the number of thrusts within a treatment, the results are presented as a histogram (Text-fig. 1). Each female is represented by a number which indicates

TEXT-FIG. 1. The number of days before return to fertile oestrus after experimental treatment. Each mouse is represented by a number which indicates the number of thrusts it received. (a) Normal mating; (b) normal mating, plug removed; (c) pre-ejaculatory thrusts only.

the number of thrusts it received. The abscissa shows the number of days before return to fertile oestrus. All females impregnated by the treatment are therefore indicated on Day 0. Days 1 and 2 were the aforementioned isolation days which insured that the Day 0 oestrus had passed before the introduction of the indicator males.

The results presented in Text-fig. 1 indicate that the number of thrusts without ejaculation [group (c)] has little effect on the number of days between treatment and subsequent oestrus. Most of the females returned to fertile oestrus 4 days after treatment, as would be expected if the oestrous cycle was unaffected by the treatment. By contrast, none of the females which had received a plug [groups (a) and (b)] returned to oestrus after the normal interval of time. All were either pregnant, or, with the possible exception of one female in group (a) that returned to oestrus after 7 days, pseudopregnant.

DISCUSSION

These results permit the following conclusions regarding the induction of luteal activity in female mice.

(1) A large number of pre-ejaculatory thrusts seems neither necessary nor sufficient, for the induction of luteal activity. It should be noted that while the number of thrusts received by the females in this study was only about 10 to 25% of that preceding ejaculation in the fully-rested (13 days) male, the treatments are similar to the number of thrusts preceding ejaculation in the fertile copulation of a male who has recently ejaculated.

(2) The observation that females of groups (a) and (b) became either pregnant or pseudopregnant regardless of the number of pre-ejaculatory thrusts they received indicates that the ejaculatory reflex, together with the formation of the plug, is sufficient for the establishment of luteal activity and that the removal of the plug only affects the proportion which become pseudopregnant rather than pregnant. The present study cannot separate the effects of the ejaculatory reflex from the effects of plug formation, but these two factors could be differentiated by the use of males which have been surgically deprived of their coagulating glands.

In the rat, intromissions are very brief, and most frequently consist of a single thrust, (Bermant, 1965). Wilson, Adler & Le Boeuf (1965) have studied the effects of number of intromissions before ejaculation on successful pregnancy in the female rat. They found that nine out of ten female rats who received four or more intromissions before ejaculation became pregnant; whereas only two out of nine females who received three or fewer intromissions became pregnant. Since an average of eleven intromissions occurs before the first ejaculation in a rested male rat (Beach & Jordan, 1956), one may conclude that at least one-third of the normal number of intromissions is necessary for the induction of a luteal phase in the oestrous cycle of the rat.

It would appear, therefore, that there is a fundamental difference between the physico-endocrinological relationships of the rat and the mouse. This indication is supported by the fact that although there is abundant evidence for the establishment of pseudopregnancy following cervical stimulation in the rat, Stone & Emmens (1964) and Finn (1965) reported that electrical and mechanical stimulation of the cervix of the mouse did not result in pseudopregnancy.

The results of this study indicate that a large number of pre-ejaculatory thrusts are not, in themselves, sufficient to initiate the neuro-hormonal reflexes

which result in a luteal phase in the oestrous cycle of the mouse. By contrast, however, the ejaculatory pattern of the male, together with the formation of a copulatory plug, appears to be adequate for the induction of the formation of functional corpora lutea, regardless of the number of pre-ejaculatory thrusts. Consequently, the relationship between fitness and the complex mating pattern of the mouse does not appear to be dependent on the induction of the formation of functional corpora lutea.

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