ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Acta Neurobiol. Exp. 1993, 53: 451-456

The role of sexual reward in the temporal patterning of copulatory behaviour in male rats

Józef Beck and **Michał Biały**

Department of Physiology, Medical Academy of Warsaw,
26/28 Krakowskie Przedmieście St., 00-927 Warsaw, Poland

Abstract. In 8 male rats instrumental responses reinforced by contact with an estrous female with an intact or a surgically closed vagina were investigated. Contact with the female lasted until the end of the mount bout. It was observed that neither the rewarding value of the mount bout (expressed by the duration of the response) nor its arousing properties (expressed by the rate of bar presses) depended on the quality (mounts or intromissions) or quantity of the copulatory events of which it was composed. It is suggested that the temporal patterning of copulatory behaviour in male rats depends on fluctuations of sexual reward. This sexual reward can be a result of both genital stimulation as well as the performance of mounting under the influence of sign stimuli coming from the estrous female.

Key words: sexual behaviour, hereditary coordination, consummatory act, sexual reward, mount bouts, temporal patterning, rats

INTRODUCTION

The copulatory behaviour of the male rat consists of a series of intermittent mounts accompanied (intromission) or not accompanied (mount) by insertion of the penis into the vagina occurring at intervals ranging from several seconds to one minute or more and terminated by ejaculation (Larsson 1956, Dewsbury 1967). These copulatory events occur in clusters of 1-5 (mount bout) within a short period (2-10 s) separated by longer intervals called "time out periods"(Sachs and Barfield 1970, Sachs and Barfield 1976, Sachs and Garinello 1978, Sachs and Meisel 1988). Each copulatory event increases sexual arousal (Beach 1956). This increase continues up to the moment when the ejaculatory threshold is exceeded and ejaculation occurs. Sexual arousal drops then to the zero level (Kurtz and Adler 1973).

The period of sexual quiescence following each intromission has been attributed to feedback from genital sensory stimulation received during the copulatory behaviour and subsequent genital autogrooming (Beach 1956). However, when male rats were prevented from achieving intromission (Sachs and Barfield 1970, Lodder and Zeilmaker 1976), they displayed mount bouts at a rate indistinguishable from the normal copulatory rate, despite the conspicuous genital sensory deprivation.

On the basis of these results Sachs andBarfield (1976) suggested that neither the somatosensory nor the kinesthetic feedback from intromission is required for a normal pattern of mount bouts. These results support the previous suggestion of Schoelch-Krieger and Barfield (1975) that there is a copulatory clock which runs at a constant rate independently of sensory stimulation received during copulatory behaviour. However, their conclusion, that the temporal patterning of copulatory behaviour in male rat does not depend on sensory stimulation received during copulatory behaviour disregards one factor. This is the fact that the copulatory pattern in male rats consists not only of the copulatory reflex (Hart 1968, Sachs 1983) but also of the act of mounting (Barnett 1963).

It has been well established that drive can be satisfied not only during stimulation of the adequate exteroceptors (e.g taste receptors, genital receptors etc., Konorski 1970) but also during the performance of hereditary coordination under the influence of sign stimuli - the so called consummatory act (Craig 1918, Heymer 1977). The performance of the consummatory act "seems to satisfy the animal" and bring about a sudden drop in motivation (Tinbergen 1955). Thus we are dealing here with two consummatory reactions each with well expressed rewarding values. The first is related to exteroceptive stimulation and the second to kinesthetic stimulation. For the purpose of terminological convenience we denote them as "exteroceptive consummation" and "kinesthetic consummation" respectively.

Hence, during mating behaviour, the sexual drive can be satisfied in two ways: (i) by stimulation of the genital receptors and (ii) by performance of hereditary coordination under the influence of the sign stimuli coming from an estrous female. Exteroceptive consummation takes place during the intromission of the penis into the vagina whereas the kinesthetic consummation occurs during the mount and the intromission as well. The fact that male rats in a T-maze do not exhibit a clear tendency to select an intact female over a female with a closed vagina (Whalen 1961) supports this suggestion.

There is much data indicating the rewarding value of copulatory behaviour in the male rat (Sheffield et al. 1951, Kagan 1955, Beach and Jordan 1956, Ware 1968, Beck 1971, Beck 1980, Beck and Chmielewska 1976, Everitt et al. 1987, Pfaus et al. 1990) The purpose of the present study was to analyze the role of sexual reward in the temporal patterning of copulatory behaviour in male rats. Specifically, the rewarding values of the mount bouts were analyzed during the response contingent presentation of an intact estrous female or an estrous female with a surgically closed vagina.

METHODS

Animals

Eight male rats from the DA/Han/MrC strain purchased from the Center of Clinical Medicine, Polish Academy of Sciences, and twelve randomly bread female Wistar rats were used. The animals were 180 days old at the beginning of testing.They were maintained on *ad lib.* food and water and a reversed 12L:12D cycle, with light off from 9 to 21 h. Both males and females were housed 3 per standard laboratory cage.

Estrus in previously spayed females was induced by s.c. injection of 25 µg of estradiol benzoate and 500 µg of progesterone 48 and 3-6 hours before each session respectively. Two kinds of stimulus females were used: normal females (NF), and females with surgically closed vaginae (CF). The vaginae of CFs were sewed up under light ether anaesthesia 1 h before the session.

Apparatus

The apparatus (Fig.1) consisted of two compartments, a larger one 40 x 30 x 30 cm in size called the "arena" and a smaller one 20 x 30 x 30 cm called the "subject compartment" The compartments were connected by an opaque guillotine door. To permit the observation of the animals the front walls of both compartments were transparent. A 8 x 5 cm barwas attached to the front wall of the subject compartment 7 cm above the floor.

Procedure

During the sessions the male was put into the subject compartment and the stimulus female into the arena. The instrumental response consisted of 5 bar presses. When the subject had accomplished the instrumental response, the door separating him from the stimulus female was opened. The contact lasted up to the end of mount bout (MB) or it was terminated after 15 s if the copulatory behaviour was not displayed. Termination of the MB was assumed when the subject displayed any behaviour which was not directed toward the female except genital autogrooming (Sachs and Barfield 1970). After each contact the male either returned spontaneously or was forced back into the subject compartment and the next trial proceeded. The sessions with NF were carried out up to the first ejaculation, while the sessions with CF were ended after ten trials. The stimulus female for each subject was chosed randomly before each session.

The response latency (i.e., the time between the closing of the subject in its compartment and the first bar press), the burst length (i.e., the time between the first and the last bar press), as well as the sequence of copulatory events during MB were recorded on the computer (Amstrad 128). The response latencies and the burst lengths were recorded on line while the behavioural data were introduced by the experimenter. The sessions were performed once per week alternately with NF or with CF. Five sessions with CF were performed by each subject. The data obtained during these ses-

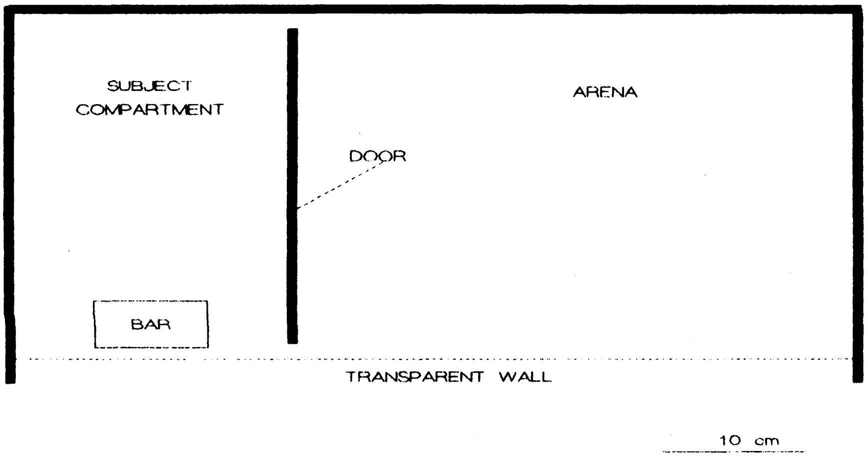

Fig.1. Apparatus for investigation of the instrumental responses with sexual reinforcement.

sions was compared with the data obtaineded during five sessions with NF.

Mount bouts classification

During the sexual contacts with females, three types of mount bouts were observed: MBs composed only of intromissions (II), MBs composed of intromissions and mounts (MI), and MBs composed only of mounts. MBs of the last type displayed during the contact with NF or with CF they were denoted as (MN) and (MC) respectively.

Data analysis

The Kolmogorov-Smirnov goodness of-fit-test, the Analysis of variance and the Pearson product-moment correlation were used to analyse the data.

RESULTS

During testing with NF six subjects displayed all three types of MBs (II - 27% , MI - 47% and MN - 26%), while in the remaining two subjects only II (55%) and MI (45%) were observed. As this last group of 2 subjects was too small for statistical analysis only the data obtained in the first 6 subjects were further analysed.

The median latencies of the instrumental responses immediately succeeding particular types of MBs are depicted in Fig 2. The analysis of the cumulative distributions of the data with Kolmogorov-Smirnov test revealed that the latencies of the instrumental responses preceded by MN, MC and MI did not differ significantly and the latencies of instrumental responses preceded by II were significantly shorter than the latencies of instrumental responses preceded by MI and MC (*P*<0.001).

The number of copulatory events per MB (M/MB) varied from 1 to 9 and differed significantly between particular types of MBs (as revealed by Kolmogorov-Smirnov test, see Fig.3).

The one-way ANOVA analysis of the bar pressing rate preceded by particular types of mount bouts revealed no significant difference (*F*=2.9, *df*=559,3, *P*>0.05).

The correlations between M/MBs and the latencies of succeeding instrumental response during testing with NF or CF revealed insignificant corre-

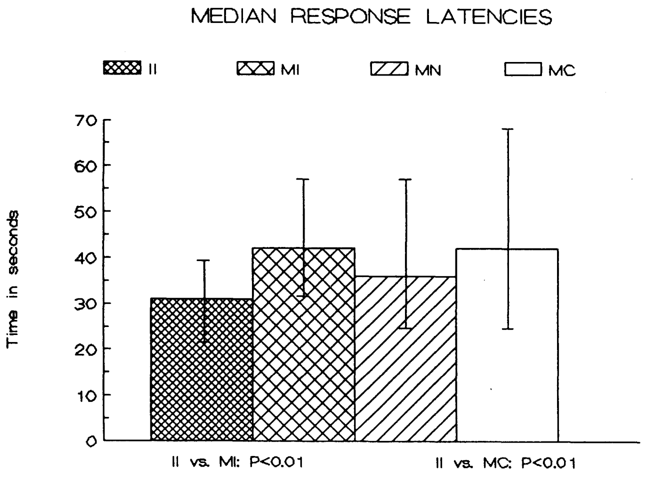

Fig.2. Medians with quartils of the latencies of the instrumental responses succeeding particular types of mount bouts. II, Mount bouts composed only of intromissions; IM, mount bouts composed of mounts and intromissions; MN, mount bouts composed only of mounts displayed during the contact with normal female; MC, mount bouts composed only of mounts displayed during the contact with the female with closed vagina. For further explanation see text.

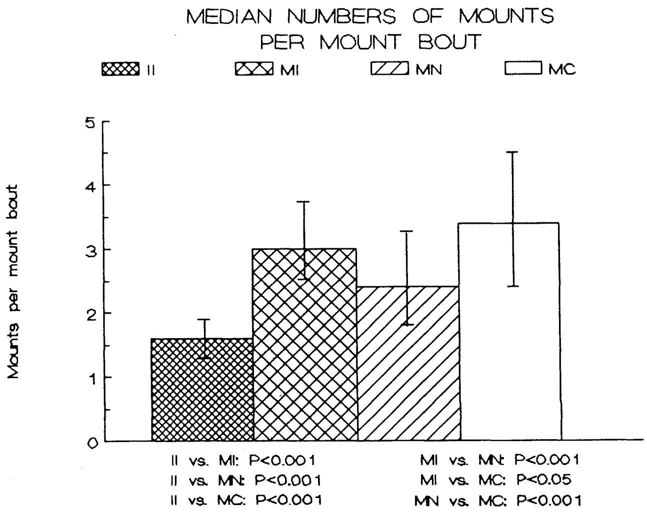

Fig.3. Medians with quartils of the numbers of mount per mount bout. Abbreviations as in Fig.2.

lations of $r_{av}= 0.099$ and $r_{av}= 0.129$ respectively. Similar results were obtained when the correlations between M/MB and the rate of bar pressing were computed, $r_{av}= 0.016$ for NF and $r_{av}= 0.005$ for CF.

DISCUSSION

The following findings of this study are particulary relevant to the understanding of the mechanism responsible for the temporal patterning of copulatory behaviour in the male rat:

- the rewarding value of a mount bout did not depend on the quality (mounts or intromissions) or quantity of the copulatory events of which it is composed.
- despite the conspicuous differences in the number of copulatory events per mount bout, the mount bouts had the same rewarding values (expressed by the duration of the latency of the succeeding instrumental response).
- the lack of correlation between the number of copulatory events per mount bout and succeeding response latencies.

Above findings indicate that the rewarding value of mount bout did not depend on the rewarding values of the particular copulatory events but on the total sexual reward accumulated during the mount bout.

On the basis of these findings, the mechanism responsible for the temporal patterning of the copulatory behaviour in male rat can be explained in the following way. During the respective copulatory events which occur in the course of a mount bout, the sexual reward resulted from both kinesthetic and exteroceptive consummations accumulates up to the moment when an optimal level of it is achieved (Fig.4). As the result of this situation, the transient inhibition of the copulatory hereditary coordination occurs. Furthermore, when, as the result of the temporal decay, the level of sexual reward decreases below a certain minimal level, this inhibition disappears. Then hereditary coordination is displayed again and a new MB commences. Such a mechanism can generate MBs composed of various numbers of copulatory events (mounts or intromissions) at intervals depending on the difference between optimal and minimal level of sexual reward and its temporal decay.

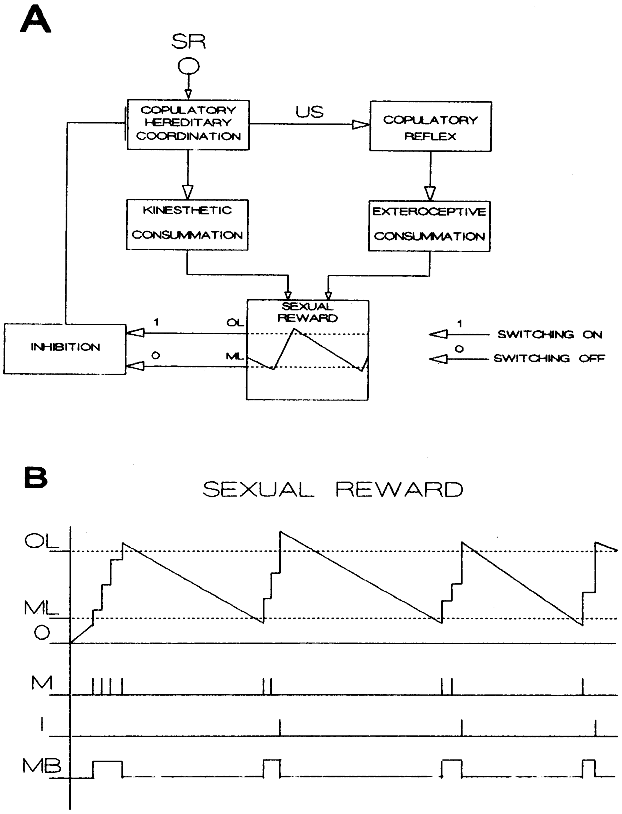

Fig.4. A, a schema representing the mechanism responsible for the pacing of copulatory behavior in male rat. B, schematic presentation of the relation between the sexual sexual reward and respective copulatory events displayed during mount bout. SR, social releaser; US, unconditioned stimulus; OL, optimal level of sexual reward; ML, minimal level of sexual reward; M, mount; I, intromission; MB, mount bout. For further explanation see text.

Both of these consummations lead also to the increase of the sexual arousal. This increase continues up to the moment when the ejaculatory threshold is exceeded and the ejaculation takes place. Sexual arousal then drops to the zero level (Kurtz and Adler 1973). The particular types of MBs exerted the same influence on the sexual arousal (reflected by the rate of bar-pressing in the succeeding instrumental response).

Some explanation is required for the fact that the latencies of the instrumental responses succeeding II were significantly shorter than the other ones. However it is not possible on the basis of the results presented here.

Summing up, the temporal patterning of copulatory behaviour in male rat seems to depend on the fluctuation of sexual reward. This sexual reward can be a result of genital stimulation as well as the accomplishment of the hereditary coordination in the stimulus situation. This explanation seems to be more parsimonious then the "copulatory clock" hypothesis. However the determination of which hypothesis is right requires further investigation.

ACKNOWLEDGEMENTS

The authors wish to thank Dr. Jerzy Chmurzyński for his valuable critical remarks and Piotr Poniński MS for his help in preparation of this manuscript.

REFERENCES

Barnett S.A. (1963) A study in behaviour. Methuen and Co., London, 288 p.

Beach F.A. (1956) Characteristics of masculine "sex drive". In: The Nebraska Symposium of Motivation (Ed. M.R. Jones). University of Nebraska Press, Lincoln, Nebraska, p. 1-32.

Beach F.A., Jordan L. (1956) Effects of sexual reinforcement upon the performance of male rats in a straight runway. J. Comp. Physiol. Psychol. 49: 105-110.

Beck J. (1971) Instrumental conditioned reflexes with sexual reinforcement in rats. Acta Neurobiol. Exp. 31: 251-262.

Beck J. (1980) A positive correlation between the male and female response latencies in the mutually reinforced instrumental sexual responses in rats. Acta Neurobiol. Exp. 38: 527-523.

Beck J., Chmielewska J. (1976) Contact with estrous female as a reward for instrumental responses in a growing male rat from the 3rd up to 14th week of life. Acta Neurobiol. Exp. 36: 535-543.

Craig W. (1918) Appetites and aversions as constituents of instincts. Biol. Bull. 34: 91-107.

Dewsbury D.A. (1967) A qualitative description of the behaviour of rats during copulation. Behaviour. 29: 154-178.

Everitt B.J., Fray P., Kostarczyk E., Taylor S., Stacey P. (1987) Studies of instrumental behaviour with sexual reinforcement in male rats (*Rattus norvegicus*): I. Control by brief visual stimuli paired with a receptive female. J. Comp. Psychol. 101: 395-406.

Freeman S., McFarland D.J. (1974) RATSEX - An exercise in simulation. In: Motivational control systems analysis. (Ed. DJ. McFarland). Academic Press, London, p. 479-504.

Hart B.L. (1968) Sexual reflexes and mating behaviour in male rat. J. Comp. Physiol. Psychol. 65: 453-460.

Heymer A. (1977) Etologishe Worterbuch. Verlag Paul Parey, Berlin, 237 p.

Kagan J. (1955) Differential reward value of incomplete and complete sexual behaviour. J. Comp. Physiol. Psychol. 48: 59-64.

Konorski J. (1970) Integrative activity of the brain. An interdisciplinary approach. Univ. Chicago Press, Chicago, 531 pp.

Kurtz R.G.,Adler N.T.(1973) Electrophysiological correlates of copulatory behavior in male rat: evidence for sexual inhibitory process. J. Comp. Physiol. Psychol. 84: 225-239.

Lodder J., Zeilmaker G.H. (1976) Effects of pelvic nerve and pudendal nerv transection on mating behaviour in the male rat. Physiol. Behav. 16: 745-751.

Larsson K. (1956) Conditioning and sexual behaviour in male albino rat. Acta Psychol. Gothoburgensia. 1: 1-269.

Lumia A.R., Sachs B.D., Meisel R.L. (1979) Sexual reflexes in male rats: Restoration by ejaculation following suppression by penile sheath removal. Physiol. Behav. 23: 273-277.

Pfaus J.G., Mendelson S.D., Philips A.G. (1990) A correlational and factor analysis of anticipatory and consummatory measures of sexual behavior in the male rat. Psychoendocrinology. 15: 329-340.

Sachs B.D. (1983) Potency and fertility: hormonal and mechanical causes and effects of penile actions in rats. In: Hormones and behaviour in higher vertebrates (Eds. J. Balthazart, E. Prove and R.Gilles), Springer Verlag, Berlin, p. 86-110.

Sachs B.D., Barfield R.J. (1970) Temporal patterning of sexual behavior in the male rat. J. Comp. Physiol. Psychol. 73: 359-364.

Sachs B.D., Barfield R.J. (1976) Functional analysis of masculine copulatory behavior in the rat. Adv. Study. Behav. 7: 91-154.

Sachs B.D., Garinello L.D. (1978) Interaction between penile reflexes and copulation in male rats. J. Comp. Physiol. Psychol. 92: 759-767.

Sachs B.D., Meisel R.S. (1988) The physiology of male sexual behavior. In: The physiology of reproduction (Eds. E. Knobil, J. Neill). Raven Press, Ltd., New York, p.1393-1485 .

Schoelch-Krieger M., Barfield R.J. (1975) Independence of temporal patterning of the mating behavior from the influence of androgen during the neonatal period. Physiol. Behav. 14: 251-254.

Sheffield F.D., Wulff J.J., Backer R. (1951) Reward value of copulation without sex drive reduction. J .Comp. Physiol. Psychol. 44: 3-9.

Tinbergen N. (1955) The study of instinct. Clarendon Press, Oxford, 228 p.

Whalen, R.E. (1961) Effects of mounting without intromission and intromission without ejaculation on sexual behavior and maze learning. J. Comp. Physiol. Psychol. 54:409-415.

Ware R. (1968) Development of differential reinforcing values of sexual responses in the male albino rat. J. Comp. Physiol. Psychol. 65: 461-465.

Received 13 April 1993, accepted 7 July 1993