Brain Research, 86 (1975) 97–108

CHARACTERISTICS OF EXAGGERATED SEXUAL BEHAVIOR INDUCED BY ELECTRICAL STIMULATION OF THE MEDIAL PREOPTIC AREA IN MALE RATS

ARIEL MERARI AND AVITAL GINTON

Department of Psychology, Tel-Aviv University, Tel-Aviv (Israel)

(Accepted October 23rd, 1974)

SUMMARY

Twenty-two sexually experienced male rats were implanted with lateral preoptic (LPO) and medial preoptic (MPO) electrodes. Following surgery, the 22 MPO and 18 LPO electrodes were screened for the induction of stimulation-bound copulation in the presence of estrus females. Stimulation through 5 of the MPO electrodes induced highly exaggerated, stimulation-bound sexual behavior. Ten MPO electrodes produced escape behavior, 2 electrodes aggression and one electrode induced sexual behavior intermingled with aggression. The tips of all the electrodes which effected exaggerated copulation were located within a small preoptic region, less than 1 mm lateral to the midline. LPO electrodes had either inhibitory effects on mating behavior or none at all. The increase in copulatory activity by MPO electrodes' stimulation was expressed in a great enhancement in the number of ejaculations, and marked decreases in the latency to ejaculation, the post-ejaculatory refractory period, and in the number of intromissions preceding an ejaculation. It is concluded that the electrical stimulation affected both the sexual arousal mechanism and the intromission–ejaculation mechanism involved in mating behavior.

INTRODUCTION

During the last decade a few studies have shown that electrical stimulation applied to the hypothalamus or preoptic area may facilitate sexual behavior in male rats. Although stimulation-bound copulation has been reported for both posterior hypothalamic[3–5], and anterior or preoptic electrode placements[15,18,19], only the latter placements yielded highly exaggerated sexual behavior.

Within the preoptic area, medial electrodes seem to be more successful than lateral ones in producing stimulation-bound, supernormal copulatory behavior. In the

studies of Van Dis and Larsson[18] and Malsbury[15] electrical stimulation applied to the medial preoptic area (MPO) resulted in stimulation-bound, supernormal copulatory behavior in some of the subjects. On the other hand, the only report of a markedly augmented sexual behavior due to lateral stimulation is the study of Vaughan and Fisher[19]. These authors reported that the electrode tips in 3 male rats which showed a dramatic increase of copulatory behavior upon electrical stimulation, were located in the dorsolateral aspects of the anterior hypothalamus. Unfortunately, the exact localization of the electrodes was not reported in this study. Madlafouek *et al.*[14] were able to induce a mild facilitation of some copulatory measures by electrically stimulating the lateral preoptic area (LPO). The changes in mating behavior obtained in this study were much less drastic than the greatly exaggerated, stimulation-bound copulation[15,18,19]. Malsbury failed to find facilitatory effects of LPO stimulation on mating behavior.

The differences between the effectiveness of MPO and LPO manipulations in controlling mating behavior are further stressed by studies which used lesion and hormone implantation techniques. Larsson and Heimer[12], and Giantonio *et al.*[10] found that whereas MPO lesions resulted in a complete or severe loss of mating behavior in the majority of the subjects, LPO lesions had only minor deleterious effects or none at all. Similarly, Davidson[7] found that the copulatory behavior of castrated male rats could be restored by the implantation of small amounts of testosterone propionate in the MPO, but not in the LPO. Comparable results were obtained by Lisk[13].

Although there can be no doubt regarding the possibility of obtaining facilitatory effects on mating behavior via preoptic stimulation, subjects showing very dramatic augmentation of copulatory activity are quite rare. In the study of Vaughan and Fisher, for example, only 3 out of 30 males showed this effect. A possible explanation for this low rate of success is that the relevant preoptic neural substrate is rather circumscribed and very small deviations of the electrode are sufficient to eliminate or considerably reduce the strong facilitatory effect on sexual behavior.

The main purpose of the present investigation, therefore, was to attempt to achieve a better localization of the preoptic regions that have stimulatory effects on copulation. Another aim of the experiment was to analyze the facilitatory effects of preoptic stimulation on sexual behavior in terms of the functional mechanism or mechanisms which it activates.

METHODS

Subjects

Twenty-two albino male rats of a local Wistar strain, 70–100 days of age at the onset of the experiment, served as subjects. They were housed 4 in a cage and received water and food *ad libitum*. The temperature in the animal rooms was maintained at 22 °C, and the light–dark cycle was reversed. Light was given from 7 p.m.–7 a.m.

Stimulus females for the mating tests were taken out of a group of 60 ovariectomized Wistar females. Estrus was induced by intramuscularly injecting 25 μg of

estradiol benzoate (Di-oestrogyn, Assia Ltd.) 48–72 h, and 400 μg of progesterone (Progestin, Assia Ltd.) 4–6 h prior to the mating tests.

Mating tests

These tests were conducted in semicircular plywood cages with a transparent front, 40 cm high and 80 cm in diameter. Five minutes before the beginning of each test the male was placed in the observation cage for adaptation. The estrus condition of the female was examined by placing her with a non-experimental male. Only females which displayed vigorous lordosis responses were used in the mating tests. The timing and frequency of mounts, intromissions and ejaculations were recorded on a Monsanto model 512 A counterprinter with an attached electronic timer. In addition to these standard measures of copulatory behavior, the occurrence of incomplete mounts was recorded whenever the male performed a mount without a proper clasp or pelvic thrusting.

Surgery

The subjects were anesthetized with pentobarbital sodium (Nembutal, Abbott Ltd.) supplemented by ether. Each male was unilaterally implanted with 2 monopolar electrodes, one of them aimed at the MPO and the other at the LPO. The electrodes were stainless steel wires 0.2 mm in diameter, insulated except for the cross section of the tip. The implantation was performed stereotaxically, using a Kopf Small Animal Stereotaxic Instrument. The 2 electrodes were always implanted ipsilaterally. Implantation coordinates for MPO electrodes were 1.5 mm anterior to bregma, 0.0–0.5 mm lateral to the midline, and 8.5 mm below the skull. LPO electrodes were implanted 1.5 mm anterior to bregma, 2.5–3.0 mm lateral to the midline, and 8.5–9.0 mm below the skull. A jeweler's screw, which reached the upper surface of the cortex, was placed posteriorly at about an equal distance from the lateral and medial electrodes, to serve as a reference electrode.

General procedure

At the beginning of the experiment each male was given 2 mating tests, 7–14 days apart, for the purpose of acquiring sexual experience. Each test was terminated at the first intromission following an ejaculation. Males which successfully performed these preliminary tests were implanted with the intracranial electrodes. Following 14 days of recovery the subjects were given another mating test in which they were allowed to copulate *ad libitum* ('exhaustion test'). The test was discontinued when 30 min had elapsed without an intromission, or one hour without an ejaculation. These exhaustion tests were taken as the subjects' baseline copulatory performance to be compared with mating activity under electrical stimulation. The males were then allowed another 14 days of rest before the screening of electrical stimulation was initiated.

For the purpose of screening, the male was placed in the observation cage with an estrus female and allowed to perform one intromission before the current was turned on. In the event that no intromission was performed within 15 min, stimulation was applied nevertheless. The electrical stimulator output was a trapezoid, biphasic

50 Hz current. This current was applied via a pulse generator to give a pulse duration of 20 msec and interpulse interval of 80 msec. The initial current intensity in the screening procedure was 10 μA, and it was raised in 5–10 μA steps. At each intensity the current was delivered for about 30 sec, followed by a 30 sec off period. The maximal intensity used was 300 μA, but in many cases this level was not reached because of the appearance of motor seizures or interfering behavior, such as aggression towards the female or escape behavior. Stimulation periods at intensities which produced a marked facilitation of copulatory behavior were repeated a few times and their duration was increased up to 90 sec.

Six males showed supernormal, stimulation-bound sexual behavior in the screening session. However, one of them lost his electrodes before additional testing could be performed, and another one displayed a mixture of stimulation-bound copulation and aggressive behavior. Stimulus females which were tested with this last mentioned male were so badly wounded that proper examination of his sexual behavior was impossible. The remaining 4 males had a 14 day rest period before the final mating test under electrical stimulation took place. During this test the current intensity which proved to be effective in inducing stimulation-bound sexual behavior in the screening test was applied at a rate of about 60 sec on–60 sec off. The intensity was gradually raised when the electrical stimulation at the initial current no longer produced a clear enhancement of copulatory behavior. The test was terminated an hour after its start, unless it was interrupted by interfering behaviors.

The following measures of copulatory activity were used in analyzing the effects of electrical stimulation upon sexual behavior: (1) latency to the first event (LEV) — the time from the onset of current to the occurrence of the first incomplete mount, complete mount, or intromission; (2) ejaculation latency (EL) — the time from the first intromission until the following ejaculation; (3) post-ejaculatory interval to intromission (PEI–I) — the time from ejaculation until the following intromission; (4) post-ejaculatory interval to the first event (PEI–EV) — the time from ejaculation to the first consecutive incomplete mount, mount, or intromission; (5) the number of intromissions to ejaculation (I/E) — the number of intromissions preceding an ejaculation; (6) the combined rate of intromissions and ejaculations per min (I + E/min); and (7)

TABLE I

DISTRIBUTION OF STIMULATION-BOUND BEHAVIORAL EFFECTS OF POA ELECTRICAL STIMULATION ACCORDING TO LATERAL DISTANCE OF ELECTRODE FROM THE MIDLINE

Behavioral effect	*Distance from midline (mm)*					*Total*
	0–1	*1–2*	*2–3*	*3–4*	*4–5*	
None	2	2	6	10	2	22
Escape	9	1				10
Sex	5					5
Aggression	2					2
Aggression + sex	1					1
Total	19	3	6	10	2	40

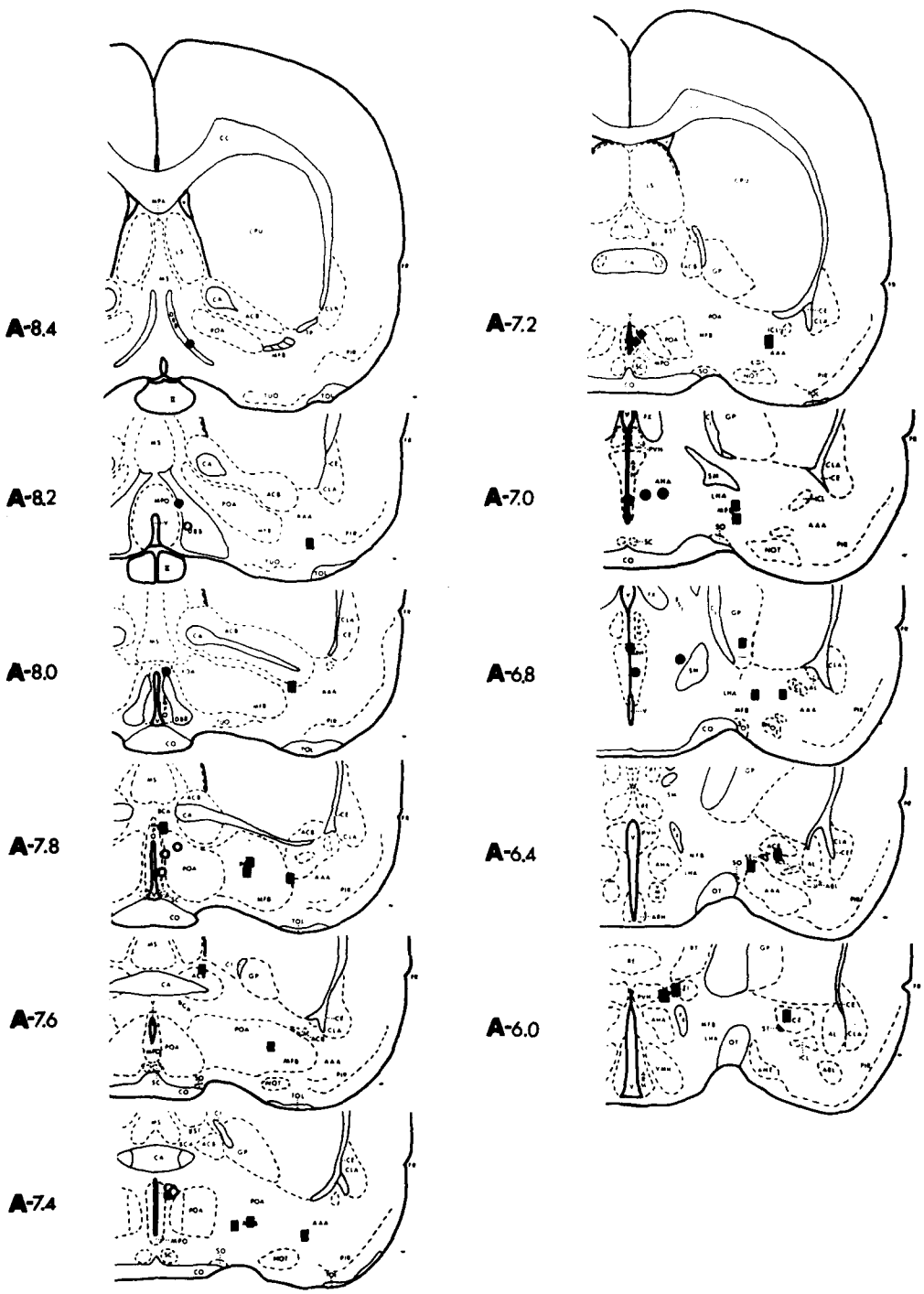

Fig. 1. Distribution of electrode tips according to the behavioral effects of stimulation. ●, escape; ○, sexual behavior; ◆, aggression; ◇, sex and aggression; ■, inhibition of sexual behavior, or no effect at all. Drawings of brain sections were adapted from Pelligrino and Cushman[17]. The number at the left of each section is the anterior distance from the interaural line.

the rate per min of all copulatory events including incomplete and complete mounts, intromissions and ejaculations (EV/min).

Following termination of the electrical stimulation tests, small brain lesions were produced around the tips of each one of the intracranial electrodes, in order to facilitate the identification of their loci. Lesioning was carried out by the application of anodal current at 2 mA for 20 sec. The animals were anesthetized 48 h later and perfused through the heart with saline followed by a solution of 10% formalin in saline. The brains were then removed and soaked for a week in the formalin solution. Coronal sections (50 μm) were cut through the electrode tracks and photographed by the technique described by Guzman-Flores *et al.*[11]. In most of the cases the lesion at the site of the electrode's tip was less than 0.5 mm in diameter.

RESULTS

Table I summarizes the behavioral results of the screening tests for 18 LPO and 22 MPO electrodes. It is clear that the lateral distance of the electrode tip from the midline had a great importance for the behavioral effects under the present experimental conditions. While no stimulation-bound behavioral effects were observed for the 18 lateral electrodes whose tips lay more than 2 mm lateral to the midline, 17 of the 19 electrodes whose tips lay less than 1 mm away from the midline produced some behavioral response.

Since the main purpose of the present investigation was to study sexual behavior, no attempt was made to quantify or systematically study the aggressive or escape behaviors which were produced by some of the electrodes. Nevertheless, these behaviors were highly stereotyped and were clearly generated by the electrical stimulation, appearing as soon as the current was turned on, and terminating immediately upon its cessation. The aggression was expressed as a sudden and savage attack on the estrus female, accompanied by biting and shaking her head and neck region. Despite the female's squeaks and attempts to escape, this behavior did not stop until the current was turned off. The stimulation-bound escape behavior consisted of rapid running around the observation cage with repeated jumps against the plexiglass wall. Quite often, the speed of running seemed to increase as the current intensity was raised.

The exact locations of the electrode tips as found upon autopsy and their behavioral effects are presented in Fig. 1.

It can be seen that the 3 aggression-producing electrodes were located within a very small area of the MPO, 7.2–7.4 mm anterior to the interaural line and less than 0.5 mm lateral to the midline. The area in which escape behavior could be aroused was much less confined, ranging from 6.8 to 8.4 mm anterior to the interaural line and from 0.0 to 1.4 mm lateral to the midline.

None of the 18 LPO electrodes produced stimulation-bound sexual behavior. On the contrary, electrical stimulation through all of these electrodes had an almost complete inhibitory influence on copulation when current intensities were at or above the level which created searching behavior. In 14 of the animals, elevation of the cur-

rent beyond this intensity was accompanied by clear motor disturbances, such as rotation to one side, shaking or seizures. The remaining 4 subjects displayed searching behavior without apparent motor effects, but showed no copulatory activity as well, in spite of the constant presence of an estrus female during the screening tests.

Six of the 22 medial electrode placements resulted in an exaggerated, stimulation-bound sexual behavior. This behavior was characterized by almost no copulatory activity while the current was off, as opposed to a considerably augmented sexual behavior at the times when the current was on. The boundaries of the area in which stimulation resulted in supernormal sexual behavior are 7.4–8.2 mm anterior to the interaural line, 0.2–0.8 mm lateral to the midline, and 7.6–8.5 mm below the dura. Besides the six 'sexual' rats, only 3 more males had their electrode tips located within these 3-dimensional borders, and all of them exhibited escape behavior upon electrical stimulation.

One of the stimulation-bound copulators had lost his electrodes after the screening session, before a more systematic record of his behavior was taken, but one could not mistake his supernormal, stimulation-bound sexual activity. Another stimulation-bound copulator exhibited bouts of aggression interchangeably with exaggerated copulatory behavior within the same range of current intensities. Because of severe damage inflicted upon the stimulus female, it was impossible to examine his behavior under stimulation for sufficiently long periods, but here again, there was no doubt regarding the supernormal performance of this male's copulatory behavior.

The results for the remaining 4 males are shown in Table II.

All of the copulatory activity during the stimulation tests for these rats occurred while the current was on, except for one incomplete mount for males Nos. 25 and 39. Male No. 24 failed to copulate during the control exhaustion test which followed electrode implantation. His behavior toward the female resembled that of some sexually naive males on their first encounter with a receptive female, namely, prolonged anogenital sniffing and a few incomplete mounts, with an absence of complete mounts. The stimulation test for this rat was started with a 15 min off period. During this time the male exhibited only one complete mount without an intromission. Upon stimulation onset, however, the subject immediately displayed supernormal sexual behavior.

The most striking phenomenon demonstrated in Table II is the great increase in the number of ejaculations that took place during the stimulation tests, as compared to the prestimulation (baseline) tests. It should be noted that whenever the stimulation tests were long enough (rats Nos. 24 and 25), the number of ejaculations markedly exceeded the normal figure which can be obtained by a rat before being exhausted.

The application of electrical stimulation resulted in a dramatic decrease in the EL, PEI–I, and PEI–EV. The greatest change occurred in the PEI–EV, whose grand mean dropped from 627 sec in the control sessions to 21 sec in the stimulation tests. Thus, there was practically no post-ejaculatory refractory period under stimulation conditions. It is important to note that the means for the stimulation tests presented in Table II are based on both on and off periods. Since practically all copulatory activity occurred during the on periods, these means underestimate the effects of

TABLE II

COPULATORY ACTIVITY OF MALE RATS DURING MPOA STIMULATION SESSIONS (S) AND CONTROL SESSIONS (C)

Male	*Effective current intensity in μA*	*Mean latency to 1st EV from switching ON the current (sec)***	*Duration of stimulation session (min)****	*No. of ejaculations*		*Mean ejaculation latency (sec)***	
				S§§	*C**,§	*S*§§§	*C*†
24	60–120	10.1 (4–18)	60 (26.8)	13	0 (0)	56.3 (0–245)	—
25	165–260	6.8 (2–20)	60 (30.1)	20	5 (7)	74 (0–341)	228 (68–555)
26	120–130	15 (7–22)	9 (5.4)	4	1 (7)	45 (5–159)	154 (118–250)
39	60	7.67 (7–8)	3.3 (2.2)	2	1 (7)	46 (16–76)	81.5 (49–114)
Mean				9.7	2.3	55.3	154.5

* For matter of comparison, in control session, only events which occurred within the same limits of time as the stimulation session are counted.

** In brackets, the range of latencies for each rat.

*** Consists of alternating on and off periods. The total on periods alone is given in brackets. The short durations for rats Nos. 26 and 39 were due to occurrence of motor seizures which terminated the tests.

§ In brackets, the total number of Es which were achieved by the rats in the control session before exhaustion.

§§ Rats Nos. 25 and 26 had ejaculated 2 more times under sub-threshold stimulation intensities before the stimulation-bound intensities were reached.

§§§ Including off periods.

† For comparison matters the means for rat No. 26 in the control session were calculated from 4 series only, starting from the third, and for rat No. 39 from the first two series (see remarks 3 and 5).

†† In brackets, frequencies/min during on periods only.

electrical stimulation on copulation. For example, when an ejaculation was performed 5 sec before termination of the on period, the PEI for that series would register as at least 65 sec, because the 60 sec off period intervened between the ejaculation and the resumption of copulatory activity upon the onset of the consecutive on period.

Two weeks after the stimulation test, rat No. 24 was tested for sexual performance under a continuous stimulation of a constant current intensity for 7 min. During the first 5 min the male ejaculated 11 times, and 8 of them were executed without any preceding intromissions. The mean PEI–I was about 30 sec for these 11 series, as compared to 114 sec for the same rat in the standard stimulation session, which included off periods. The occurrence of ejaculations without preceding intromissions was also observed during the standard stimulation sessions in about half of the series for males Nos. 24 and 25 (6 and 12 such ejaculations, respectively). This is the reason why the mean number of intromissions per ejaculation was less than 1.00 for these rats.

The means of the frequency/min of copulatory events reveal the very high density of mating activity which took place while the current was on. The almost total absence of refractory periods produced difficulties concerning the females' willingness to mate.

*Mean PEI-I (sec)***		*Mean PEI-EV (sec)***		*Mean No. of intromissions to ejaculation***		*I + E* *min*		*EV* *min*	
S§§§	*C*†	*S*§§§	*C*†	*S*	*C*	*S*††	*C**	*S*††	*C**
114.2 (18–384)	—	39.2 (2–122)	—	0.77 (0–2)	—	0.38 (0.85)	—	2.11 (4.73)	—
121.4 (12–624)	724 (383–1385)	19 (3–103)	719 (383–1385)	0.85 (0–4)	2.57 (1–5)	0.61 (1.22)	0.31	3.01 (6.01)	0.9
76.5 (14–207)	803.5 (493–1447)	15.25 (5–46)	797 (379–1447)	1.25 (1–2)	4.75 (3–7)	1.00 (1.66)	0.67	2.77 (4.62)	1.55
15 (15)	329 (329)	14 (8–20)	367 (322–413)	2.5 (2–3)	4.5 (3–6)	2.12 (3.18)	1.25	9.39 (14.09)	2.84
81.7	618.8	21.8	627.6	1.34	3.94	1.03 (1.72)	0.74	4.32 (7.36)	1.76

This problem was partially solved by using 4–5 females in turn for each male, each female serving for about one min. The authors were aware of the possibility that this procedure may lead to an increase in the copulatory activity merely by replacing an 'old' female by a new one (Fisher[8]). Nevertheless, the facilitatory influence of the rapid exchange of females is negligible in comparison with the increase in the density of copulation observed in the present study[2,9,20] and, more importantly, its effect should not be limited to the on periods, as was clearly the case during the stimulation sessions.

While observing rats Nos. 24 and 25 which were tested for a relatively long period of time, it has become apparent that following a few ejaculations under a certain current intensity the males stopped intromitting but continued to mount at a high rate. A similar phenomenon was seen in the continuous stimulation session for male No. 24. During the last 2 min of stimulation no intromission was achieved, although many mounts were performed. In such cases in the stimulation tests, raising the current intensity resulted in a resumption of intromissions and ejaculations. The intensity was increased 5 μA whenever no intromission had been performed during one or two stimulation periods. This manipulation was effective in all cases.

The upper limits of stimulation intensities were dictated by the occurrence of motor seizures (rats Nos. 25, 26 and 39), or by the appearance of competing behavior (in the case of rat No. 24, who showed vigorous aggressive behavior at intensities higher than 120 μA). The intensity thresholds for motor seizures tended to decrease with repeated stimulation, and for rats Nos. 26 and 39 they became lower than the thresholds for stimulation-bound copulation. It was found, in male No. 26, that the intraperitoneal administration of 1 mg/kg of diazepam (Valium, Hoffman La-Roche) 45 min prior to the onset of the stimulation test, prevented the motor seizures and thus enabled the rat to exhibit stimulation-bound copulation again.

DISCUSSION

The results of the present study once again demonstrate the complexity of the preoptic area in controlling motivational and emotional behaviors. Sexual behavior, aggression and escape were facilitated by adjacent and sometimes overlapping electrode placements. Nevertheless, a close inspection of the anatomical localization of electrodes which produced these effects reveals that the areas in which sexual behavior or aggression could be aroused are much more circumscribed than the region that produced escape behavior.

The present investigation supports the notion that at least part of the difficulty in producing stimulation-bound, exaggerated sexual behavior is due to the small anatomical area in which this effect can be produced. All of the successful electrodes were located in a region whose longitudinal, lateral and vertical measures were 0.8 mm $\times$ 0.6 mm $\times$ 0.9 mm, respectively. Within this block of brain tissue, 66% of the electrodes generated highly augmented copulatory behavior.

In accordance with the study of Malsbury[15] and contrary to the work of Madlafousek *et al.*[14], no facilitatory influence of LPO stimulation on copulatory behavior was observed in the present study. This result is also in general agreement with lesion and hormone implantation studies[7,10,12,13], which showed that attempts to affect sexual behavior by manipulation of the LPO were much less successful than MPO interventions. It should be mentioned, however, that whereas in the present study the authors looked for stimulation-bound sexual behavior and raised the current until this behavior was observed or a motor disturbance appeared, Madlafousek *et al.*[14] used a relatively low, constant-level current which did not lead to motor disturbances. While under the conditions of the present investigation most LPO electrodes effected suppression of copulation, it is still possible in principle that the use of a prolonged sub-threshold current would have yielded the slight facilitation of copulatory measures, similarly to the results of Madlafousek *et al.*[14].

An analysis of the effects of MPO stimulation on sexual behavior shows that all measures of copulation were affected. The most salient feature of sexual performance under electrical stimulation was the great increase in the frequency of copulatory activity, especially the much augmented density of ejaculations. In the course of normal mating behavior in the male rat, relatively fixed periods of rest intervene between consecutive intromissions and ejaculations[1]. These pauses in mating activity virtually disappeared in the animals which showed increased sexual behavior under electrical stimulation.

In 1956 Beach[1] suggested that two different mechanisms form the basis of masculine copulatory behavior, namely the sexual arousal mechanism (SAM) and the intromission and ejaculatory mechanism (IEM). The role of the former is to arouse the male's interest in the female and to increase his sexual excitement to a degree that will suffice to motivate him to initiate mounting. The IEM, on the other hand, maintains or increases the level of sexual excitation by repeated insertions, until the threshold of ejaculation is reached. Beach also suggested some measures of mating behavior that seem to reflect the action of each one of the proposed mechanisms. Thus, the latency

to the first intromission or to the first mount and the post-ejaculatory refractory period depend on the SAM, while the ejaculation latency and intromission frequency depend on the IEM. Assessment of the results of the present investigation reveals that measures which represent both the SAM and the IEM were concurrently affected by the electrical stimulation. Thus, a very dramatic shortening of the PEI–I and PEI–EV as well as a great increase in the frequency/min of copulatory events which stand for the arousal mechanism according to Beach's classification occurred together with a considerable decrease in the latency to ejaculation and the number of intromissions that preceded an ejaculation. The two last-mentioned changes are correlates of the IEM, as described by Beach[1].

It should be concluded, therefore, that in the same locus of stimulation both the IEM and the SAM were simultaneously activated. This does not necessarily mean that the same neural tissue mediates these two components of mating behavior. It is highly probable, however, that at the very medial aspects of the preoptic area of the male rat, there is a neural pathway which controls all aspects of copulation.

A differential effect of the current on the SAM and the IEM was demonstrated in the cases where, after prolonged stimulation, the males stopped intromitting and ejaculating, but kept on mounting at a high rate. The fact that insertions were resumed once the current was raised indicates that under certain conditions the two mechanisms have different thresholds of activation. The possibility of reactivating the IEM by increasing the current is especially interesting in view of the similarity between the present situation and the process of deterioration in mating behavior following castration. In both cases, mounts — which attest to the existence of sexual motivation — can be observed long after the disappearance of intromissions and ejaculations[6,16]. That is to say, at least the initial decline in sexual performance after castration is due to impaired IEM. However, finer experimental techniques are necessary in order to reveal the neural processes underlying the impairment of this mechanism and the ways in which it was reactivated in the present study by the crude method of electrical stimulation.

ACKNOWLEDGEMENT

The authors thank Mrs. Mayana Lewinstern for skillful technical assistance, and Mr. Jacob Rinetski for preparation of the figure.

REFERENCES

1 BEACH, F. A., Characteristics of masculine 'sex drive'. In M. R. JONES (Ed.), *Nebraska Symposium on Motivation*, Univ. of Nebraska Press, Lincoln, Nebr., 1956, pp. 1–32.
2 BEACH, F. A., AND RANSOM, T. W., Effects of environmental variation on ejaculatory frequency in male rats, *J. comp. physiol. Psychol.*, 64 (1967) 384–387.
3 CAGGIULA, A. R., Analysis of the copulation–reward properties of posterior hypothalamic stimulation in male rats, *J. comp. physiol. Psychol.*, 70 (1970) 399–412.
4 CAGGIULA, A. R., AND HOEBEL, B., 'Copulation reward site' in the posterior hypothalamus, *Science*, 153 (1966) 1284–1285.

5 CAGGIULA, A. R., AND SZECHTMAN, H., Hypothalamic stimulation: a biphasic influence on copulation of the male rat, *Behav. Biol.*, 7 (1972) 591–598.
6 DAVIDSON, J. M., Characteristics of sex behavior in male rats following castration, *Anim. Behav.*, 14 (1966) 266–272.
7 DAVIDSON, J. M., Activation of the male rat's sexual behavior by intracerebral implantation of androgen, *Endocrinology*, 79 (1966) 783–794.
8 FISHER, A. E., Effects of stimulus variation on sexual satiation in the male rat, *J. comp. physiol. Psychol.*, 55 (1962) 614–620.
9 FOWLER, H., AND WHALEN, R. E., Variations in incentive stimulus and sexual behavior in the male rat, *J. comp. physiol. Psychol.*, 54 (1961) 68–71.
10 GIANTONIO, G. W., LUND, N. L., AND GERALL, A. A., Effect of diencephalic and rhinencephalic lesions on the male rat's sexual behavior, *J. comp. physiol. Psychol.*, 73 (1970) 38–46.
11 GUZMAN-FLORES, C., ALCARAZ, M., AND FERNANDEZ-GUARDIOLA, A., Rapid procedure to localize electrodes in experimental neurophysiology, *Bol. Inst. Estud. méd. biol. (Méx.)*, 16 (1958) 29–31.
12 LARSSON, K., AND HEIMER, L., Mating behavior of male rats after lesions in the preoptic area, *Nature (Lond.)*, 202 (1964) 413–414.
13 LISK, R. D., Neural localization for androgen activation of copulatory behavior in the rat, *Endocrinology*, 80 (1967) 754–761.
14 MADLAFOUSEK, J., FREUND, K., AND GROFOVA, I., Variables determining the effect of electrostimulation in the lateral preoptic area on the sexual behavior of male rats, *J. comp. physiol. Psychol.*, 72 (1970) 28–44.
15 MALSBURY, C. W., Facilitation of male rat copulatory behavior by electrical stimulation of the medial preoptic area, *Physiol. Behav.*, 7 (1971) 797–805.
16 MERARI, A., SHOHAM, V., MOLAD, G., AND PERRI, H., Long-range effects of castration on mating behavior in the male rat, *Bull. Psychon. Soc.*, 2 (1973) 215–216.
17 PELLIGRINO, L. J., AND CUSHMAN, A. J., *A Stereotaxic Atlas of the Rat Brain*, Appleton Century Crofts, New York, 1967.
18 VAN DIS, H., AND LARSSON, K., Induction of sexual arousal in the castrated male rat by intracranial stimulation, *Physiol. Behav.*, 6 (1971) 85–86.
19 VAUGHAN, E., AND FISHER, A. E., Male sexual behavior induced by intracranial electrical stimulation, *Science*, 137 (1962) 758–760.
20 WILSON, J., KUEHN, R., AND BEACH, F. A., Modification in the sexual behavior of male rats produced by changing the stimulus female, *J. comp. physiol. Psychol.*, 56 (1963) 636–644.