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Stimulation of Mounting Behavior but not Lordosis Behavior in Ovariectomized Female Rats by p-Chlorophenylalanine[1]

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Mounting Lordosis PCPA Monoamines

WHEN tested with sexually receptive female rats normal female rats show a considerable amount of mounting behavior, i.e. the sexual behavior pattern typical of normal male rats [23]. Ovariectomy decreases and subsequent replacement treatment with estradiol increase the display of mounting behavior by female rats [23], suggesting that ovarian hormones, possibly estrogens, may play a role in the hormonal regulation of mounting behavior in female rats. Estrogens, formed in the rat brain from circulating testosterone [19], may also be involved in the activation by hormones of the sexual behavior of male rats (see [7]). Recently, we found that treatment with the 5-hydroxytryptamine (5-HT) synthesis inhibitor p-chlorophenylalanine (PCPA) [16] induced sexual behavior in hormonally untreated castrated male rats [27]. It seems possible, therefore, that one of the many possible mechanisms whereby gonadal hormones activate the sexual behavior of castrated male rats may involve an action on brain monoamine, possibly 5-HT, neurotransmission. In the present study we examined to what extent PCPA treatment of ovariectomized rats stimulates the display of mounting behavior. Since the importance of ovarian estrogens for the display of lordosis behavior, i.e. the sexual behavior pattern typical of normal female rats, is well known (see [28]), we also investigated the possible effects of PCPA treatment on lordosis behavior in ovariectomized rats.

METHOD

Animals

Female Wistar rats (Möllegård Breeding Laboratories, Ejby, Denmark) were used. The rats were maintained with continuous access to food and water in an air conditioned temperature-controlled colony room with the lights out between 1100–2300 hr. All rats were ovariectomized at about 90 days of age and they were used in experiments 40–60 days later weighing approximately 280 g.

Procedure

Twenty-six ovariectomized rats were randomly divided into 2 groups and injected with 126 mg/kg p-chlorophenylalanine methyl ester HCl (n = 13) (PCPA, H 69/17, Hässle, Mölndal, Sweden) or NaCl (n = 13) daily for 3 days. The rats were tested for mounting behavior and lordosis behavior in response to manual stimulation 24 hr after the last injection.

Forty-two ovariectomized rats were randomly divided

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into two groups and injected daily with 40 mg/kg PCPA (n = 21) or NaCl (n = 21) for 10 days. The rats were tested for mounting behavior and lordosis behavior in response to manual stimulation on treatment Days 2, 4, 6, 8 and 10. Eight randomly selected PCPA- and NaCl-treated rats were killed and 2 cm of each uterine horn from the cervix were out off and weighed. Eight other randomly selected females from each treatment group received 0.5 mg progesterone at 1000 hr on treatment Day 11 and were tested for lordosis behavior in response to male mounting 6 hr later.

Twenty-three ovariectomized rats received daily injections of 40 mg/kg PCPA (n = 13) or NaCl (n = 10) for 19 days. Commencing on Day 7 of treatment daily treatment with 2.0 μg/kg estradiol benzoate (EB) was added to the PCPA treatment. The rats were tested for lordosis behavior in response to male mounting on treatment Days 10, 12, 14, 16 and 18. All rats received 0.5 mg progesterone at 1000 hr on treatment Day 19 and were tested for lordosis behavior with males 6 hr later. PCPA was dissolved in 0.9% NaCl and injected IP in a volume of 2.0 ml/kg at 1000 hr. Estradiol benzoate was dissolved in peanut oil and injected SC in a volume of 0.5 ml/kg at 1000 hr.

Behavioral Tests

Mounting behavior. Female rats, of course, do not possess a genital structure comparable to the rat penis. Even so, however, when tested with a receptive stimulus female they display the overt behavior patterns comparable to mounts (i.e. mount with pelvic thrusting) and intromissions (i.e. mount with intromission) displayed by normal male rats [23]. In this study we also observed females showing behavior patterns that were indistinguishable from that of the behavior of an ejaculating male rat (i.e. mount with a final deep intromission, slow dismounting and genital grooming). The behavior patterns of the females in the present study have been termed *mounts, intromission patterns* and *ejaculation patterns* to indicate that they differ from the corresponding behavior patterns in male rats in that no penile insertion or emission of seminal fluid occurs. The frequency of these behavior patterns were observed in tests with stimulus females which were made sexually receptive by sequential injections of estradiol benzoate (20 μg/rat, 48 hr before testing) and progesterone (0.5 mg/rat, 6 hr before testing). Testing took place in circular (50 cm dia.) Plexiglas cages in which the rats were allowed to adapt for 2–5 min before the stimulus female was introduced. The latency to the first intromission pattern, *intromission pattern latency,* the interval from the first intromission patterns to an ejaculation pattern, *ejaculation pattern latency,* and the time from an ejaculation pattern to the following intromission pattern, *post-ejaculatory interval,* were recorded. Tests were ended if the intromission pattern latency was > 15 min, if the ejaculation pattern latency was > 30 min, or if the post-ejaculatory interval was > 15 min. In the final test, i.e. on treatment Day 10, three of the rats that received daily injections of 40 mg/kg PCPA displayed ejaculation patterns. Testing of these rats was prolonged and the frequency of mounts, intromission patterns and ejaculation patterns as well as the response latencies was measured in three consecutive ejaculatory series.

Lordosis behavior. The rats were tested for lordosis behavior (concave back flexion, lateral tail deviation and neck extension, see picture in [25]) immediately after the mounting behavior tests. Lordosis was tested both in response to manual stimulation or in response to mounting by male rats. The manual stimulation procedure is described elsewhere [25]. In tests with stimulus males each female was presented to a cage adapted sexually vigorous male rat and remained with the male until mounted 10 times. The number of lordosis responses were recorded and a lordosis quotient (no. of lordosis responses/no. of mounts × 100) was calculated.

Statistical Procedures

Percentage of responding rats were compared with the Chi^2 test or the Fisher exact probability test. Since testing time differed according to whether or not a rat showed intromission patterns response frequencies were expressed as mounts/min or intromission patterns/min and the groups were compared with the Mann-Whitney U test.

RESULTS

Effects of Treatment with 126 mg/kg of PCPA for Three Days on Mounting and Lordosis Behavior

Mounting behavior. Table 1 shows that treatment with 126 mg/kg of PCPA for 3 days stimulated the display of mounting behavior.

One PCPA-treated rat showed an ejaculation pattern after 34 mounts and 11 intromission pattern with an ejaculation pattern latency of 22.8 min and a post-ejaculatory interval of 0.7 min.

Lordosis behavior. None of the rats showed lordosis behavior in response to manual stimulation.

TABLE 1

MOUNTING BEHAVIOR DISPLAYED BY OVARIECTOMIZED RATS TREATED WITH 126 mg/kg P-CHLOROPHENYLALANINE (PCPA) OR NaCl FOR THREE DAYS AND TESTED 24 HR AFTER THE LAST INJECTION

Treatment	No. of rats	Mounts	% showing Intromission patterns	Ejaculation patterns	Mounts/min*	Intromission patterns/min*
PCPA	13	92.3	53.8	7.7	0.8 ± 0.1	0.3 ± 0.1
NaCl	13	30.8	0	0	0.2 ± 0.1	–
p†		<0.01	<0.01	NS	<0.02	

*Non-responders excluded.
†Fisher exact probability test or Mann-Whitney U test. NS, $p > 0.05$.

TABLE 2

MOUNTING BEHAVIOR DISPLAYED BY OVARIECTOMIZED RATS TREATED DAILY WITH 40 mg/kg P-CHLOROPHENYLALANINE (PCPA) OR NaCl FOR 10 DAYS AND TESTED EVERY SECOND DAY OF TREATMENT

Treatment	No. of rats	Mounts	% showing Intromission patterns	Ejaculation patterns	Mounts/min*	Intromission patterns/min*
PCPA	21	81.0	71.2	28.6	0.7 ± 0.1	0.3 ± 0.1
NaCl	21	38.1	23.8	0	0.4 ± 0.1	0.06 ± 0.01
p†		< 0.05	< 0.01	<0.05	< 0.05	<0.02

*Non-responders excluded.
†Chi^2 test or Mann-Whitney U test.

TABLE 3

MOUNTING BEHAVIOR DISPLAYED BY SIX OVARIECTOMIZED RATS TREATED DAILY WITH 40 mg/kg P-CHLOROPHENYLALANINE FOR 10 DAYS. THE VALUES ARE MEANS ± S.E.M. OF TESTS WHEN THE RATS SHOWED EJACULATION PATTERNS

Mounts	Intromission patterns	Intromission pattern latency (min)	Ejaculation pattern latency (min)	Post-ejaculatory interval (min)
20.5 ± 4.3	9.9 ± 1.5	3.7 ± 0.9	19.8 ± 3.2	2.3 ± 0.6

TABLE 4

MOUNTING BEHAVIOR DISPLAYED IN THREE CONSECUTIVE EJACULATORY SERIES BY TWO INDIVIDUAL OVARIECTOMIZED RATS TREATED DAILY WITH 40 mg/kg P-CHLOROPHENYLALANINE

Behavioral parameter	Rat	Ejaculatory series 1	2	3
Mounts	1	4	1	1
	2	31	17	4
Intromission pattern	1	13	2	2
	2	19	7	3
Ejaculation pattern latency (min)	1	17.1	4.4	4.5
	2	26.7	14.3	9.0
Postejaculatory interval (min)	1	3.7	3.0	1.3
	2	3.6	1.6	2.5

Effects of Daily Treatment with 40 mg/kg of PCPA on Mounting and Lordosis Behavior

Mounting behavior. Table 2 shows that daily treatment with 40 mg/kg of PCPA stimulated the display of all parameters of mounting behavior.

Rats treated with PCPA also showed mounts and intromission patterns in significantly more tests than NaCl-treated rats (mounts: 2.6 ± 0.4 (mean ± SEM) vs 1.4 ± 0.4, $p<0.02$, intromission patterns: 1.9 ± 0.4 vs 0.4 ± 0.2, $p<0.002$).

Six PCPA-treated rats displayed ejaculation patterns in 1, 1, 1, 3, 3 and 4 tests respectively. Table 3 shows the response frequencies and latencies of these females.

Two of the three rats that showed ejaculation patterns in the final test displayed repeated ejaculatory series. Table 4 shows the variation in response frequencies and latencies in these two individual rats. The gradual reduction of the mount and intromission frequencies and of the ejaculation latency which are seen in male rats testes with similar procedures [17] were also seen in the PCPA-treated rats.

Lordosis behavior. Manual stimulation failed to stimulate lordosis behavior in any of the rats. Lordosis in response to male mounting was not observed after progesterone treatment.

Uterine and body weights at autopsy. At the time of autopsy the uterine weight of the PCPA-treated rats was 69.7 ± 8.4 g (mean ± SEM) (n = 8), which was not different from 63.2 ± 4.2 g (n = 8) for the controls. There was no group difference in body weights (234.8 ± 7.4 g for PCPA-treated vs 248.1 ± 4.7 g for NaCl-treated rats).

Effect of Daily Treatment with PCPA on the Induction of Lordosis Behavior by Estradiol Benzoate

Table 5 shows that there was no significant difference in lordosis response to daily treatment with 2.0 μg/kg estradiol benzoate between rats receiving daily injections of 40 mg/kg of PCPA or NaCl.

All rats with the exception of one NaCl-treated rat showed lordosis to all mounts 6 hr after administration of 0.5 mg progesterone in the final test (Table 5).

DISCUSSION

This study has shown that treatment with the 5-HT synthesis inhibitor PCPA stimulates the display of mounting behavior by ovariectomized hormonally untreated female rats. In a previous study [27], we found that the same doses and injection schedules of PCPA as used in this study induced the complete pattern of sexual behavior in several, but not all, castrated male rats. The PCPA treatment not only reduced brain levels of 5-HT and

TABLE 5

LORDOSIS BEHAVIOR DISPLAYED BY OVARIECTOMIZED RATS TREATED DAILY WITH 40 mg/kg P-CHLOROPHENYLALANINE (PCPA) OR NaCl FOR 19 DAYS. DAILY TREATMENT WITH 2.0 μg/kg ESTRADIOL BENZOATE WAS ADDED ON DAY 7 AND THE RATS WERE TESTED FOR LORDOSIS EVERY SECOND DAY COMMENCING ON DAY 10. 0.5 mg/RAT PROGESTERONE WAS ADMINISTERED TO ALL RATS 6 HR PRIOR TO THE TEST ON DAY 19

	Treatment	No. of rats	Treatment days 10	12	14	16	18	19
Lordosis	PCPA	13	40.0 ± 0.0	36.3 ± 10.3	61.0 ± 5.0	57.5 ± 7.7	71.5 ± 5.9	100.0 ± 0
quotient*	NaCl	10	23.3 ± 8.8	45.0 ± 10.4	45.6 ± 10.6	55.0 ± 8.3	47.8 ± 10.4	90.0 ± 10
% showing	PCPA		15.4	61.5	76.9	100	100	100
lordosis	NaCl		30	80	90	100	90	90

*Mean ± S.E.M., non-responders excluded.

inhibited 5-HT synthesis in the castrated males but also affected brain catecholamine (CA) levels and synthesis [27]. It seemed most likely, however, that the stimulatory effects of PCPA on sexual behavior in the male rats were related to the effects of PCPA on 5-HT neurotransmission, since administration of the 5-HT precursor DL-5-hydroxytryptophan inhibited the behavioral effects of PCPA and restored brain 5-HT levels to normal. The administration of the CA precursor L-DOPA, on the other hand, had no inhibitory effect on the sexual behavior of the PCPA-treated male rats and treatment with the CA synthesis inhibitor α-methyl-p-tyrosine did not stimulate the sexual behavior of castrated male rats [27]. Although no biochemical analyses of brain monoamines were made in the present study it seems highly likely that the stimulatory effects of PCPA on the mounting behavior of the ovariectomized female rats which is reported in this study also resulted from the effects of PCPA on 5-HT neurotransmission. Evidently, interference with brain 5-HT neurotransmission stimulates the display of mounting behavior in gonadectomized male and female rats in the absence of exogenous supply of gonadal hormones.

The induction of all aspects of mounting behavior, including ejaculation patterns, by PCPA in ovariectomized rats deserves special emphasis since display of ejaculatory behavior by normal female rats previously has been reported in only one study [12]. The present results agree with that study in showing that the neuromuscular mechanisms necessary for display of the complete pattern of masculine copulatory behavior are present and functional in at least some normal female rats. This was further evidenced by a detailed analysis of the pattern of mounting behavior which was displayed by the two females in the present study that showed repeated ejaculatory series in the final test. Both these rats showed the progressive reduction of mounts, intromission patterns and ejaculation pattern latency which is characteristically displayed by normal male rats during ad lib copulation [17]. However, the post-ejaculatory intervals of the females in the present as well as the previous study [12] were much shorter than those shown by males of our strain [27]. Interestingly, the same brief postejaculatory refractory period has been reported with regard to female rat lordosis behavior [20]. The pattern of mounting and lordosis behavior in female rats is thus characterized by short refractory periods. Abnormal shortening of the postejaculatory interval in male rats has been reported after lesions in the junction of the diencephalon and mesencephalon [2, 9, 15], presumably destroying ascending monoamine pathways [10]. It is possible, therefore, that monoamines are involved in the control of the temporal aspects of rat sexual behavior. However, it is unadvisable to speculate further on this issue in the absence of additional experimental evidence.

In contrast to the clear stimulatory effect of PCPA on mounting behavior no stimulation of lordosis behavior by PCPA treatment was found under any of the present conditions. Three daily injections of a moderately high dose of PCPA or daily treatment with a lower dose of PCPA failed to stimulate lordosis behavior even when exogenous progesterone was supplied. Estrogen and progesterone are well known to synergize in the hormonal induction of lordosis behavior in ovariectomized female rats [4,8] but it seems unlikely that PCPA treatment, i.e. a reduction of brain 5-HT levels, can substitute for estrogen in this paradigm. Daily treatment with PCPA also failed to affect the progressive increase in lordosis behavior which is known to occur in ovariectomized female rats as a response to daily estrogen treatment [11]. Supply of exogenous progesterone to the PCPA + estrogen- or NaCl + estrogen-treated rats stimulated lordosis responding in all but one of the rats and no group differences were detected. Similar results of PCPA treatment on the estrogen-progesterone activation of lordosis behavior have previously been reported [14,22]. We conclude, therefore, that doses and injections schedules of PCPA that stimulate mounting behavior in ovariectomized female rats exert no effects on lordosis behavior or on the induction of lordosis behavior by a low dose of estrogen. However, monoamines have been suggested to be involved in the regulation of lordosis behavior in female rats (see [1,18]). The present data are not necessarily contradictory to this research since in most previous studies drugs affecting monoamine neurotransmission were given to estrogen-primed females to replace progesterone in the estrogen-progesterone induction of lordosis. In this study PCPA was given in an attempt to mimic the effects of estrogen rather than progesterone on lordosis behavior.

Monoamines are involved in the neural control of the anterior pituitary [13]. It is possible, therefore, that the effects of PCPA on mounting behavior which are reported in this study resulted from an ACTH-induced secretion of adrenal androgens and estrogens rather than from a direct effect of PCPA on the neural mechanisms which control mounting behavior. However, androgens and estrogens

stimulate lordosis behavior and uterine weight in ovariectomized rats [5,6], and neither of these effects were found after treatment with PCPA in the present study.

A previous study reported that estrogen-induced mounting and lordosis behavior in ovariectomized female rats were differently affected by the administration of an antiestrogen [24] leading to the speculation that estrogen possibly activates mounting and lordosis via different mechanisms (see also [3]). The present results also show that mounting and lordosis behavior can be dissociated by PCPA injections and support the suggestion that these patterns of rat reproductive behavior are differently regulated in individual animals [21,26], perhaps by activating different neurotransmitter mechanisms.

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