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THE MATING MOVEMENTS OF MALE DECORTICATE RATS: EVIDENCE FOR SUBCORTICALLY GENERATED MOVEMENTS BY THE MALE BUT REGULATION OF APPROACHES BY THE FEMALE

IAN Q WHISHAW and BRYAN KOLB

Department of Psychology, University of Lethbridge, Alta (Canada)

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The study shows that although many features of copulation in decorticate male rats are normal, copulatory success is importantly dependent upon the control of approaches exerted by the normal female rat. Copulation by neonatally decorticated adult rats and normal adult rats was studied in cohabitation and videotaped tests. Seven of 10 decorticate rats and 6 of 6 normal rats sired pups in the cohabitation test. When initially paired with ovariectomized and primed female rats, in the videotaped tests, all normal rats, but only one decorticated rat, copulated. All decorticate rats made movements indicative of sexual interest including treading on the female's back, passing over the female, and sniffing the female's genitals. After activating stimulation, 5 of 6 remaining decorticated males copulated. After one successful mount the remaining copulatory patterns proceeded relatively normally. Numbers of mounts, intromissions, ejaculations, postejaculatory songs, and the intromission and ejaculatory patterns were like those of control rats, although the decorticate rats had fewer mount bouts and showed abnormalities in the execution of movements. Precopulatory movements were notated, using the Eshkol–Wachmann system, and compared with copulatory movements. Non-copulatory and copulatory approaches were similar, except that clasping appeared to be the key movement involved in the transition of an approach movement into a copulatory movement. The analysis also showed that the females' movements of hopping, turning, and kicking were important for regulating the males' approaches, and were instrumental in the success achieved by the decorticated males. The study shows that although the cortex, insofar as it facilitates the appearance of certain movements and contributes to their efficiency, is involved in male sexual activity, in its absence well organized sexual activity is possible, although this is dependent, in part, upon the behaviour of the female.

INTRODUCTION

Male rats with neocortex or neocortex plus limbic cortex removed are able to copulate sufficiently well to sire pups³⁷. This result was established indirectly by collecting evidence that issued from long periods of cohabitation between decorticated male and normal female animals. Since no direct observation of the mating activity of totally decorticate male rats has been made, the central purpose of this study was to describe the mating activity of male decorticate rats. Observations of

copulation were thought to be important for the following reasons. First, they would be relevant to Beach's^{2–5}, now classic, dual-factor model of sexual arousal. The model postulates that mating is under the control of a sexual arousal mechanism, which is responsible for bringing the male to the threshold for copulation, and an intromission and ejaculatory mechanism, which regulates subsequent sexual activity. In his seminal paper on the behaviour of partially decorticated male rats, Beach² suggested that cortical lesions reduce the responsiveness of the male rats by decreasing

Correspondence I Q Whishaw, Department of Psychology, University of Lethbridge, Lethbridge, Alta, Canada T1K 3M4

their sexual arousal. His conclusion that complete decortication abolishes sexual arousal completely was, of course, only inferential because his largest ablation removed only 79% of the neocortex, and thus was not complete, and also because copulatory behaviour was not observed in the animals with the largest ablations. It is possible that his rats with large ablations had some other, perhaps subtle, but critical, abnormality that escaped analysis. Since it has now been demonstrated that decorticated rats can copulate, observations of their behaviour may produce results that can bear upon this issue.

A second reason for observing copulation is to obtain information about the contribution of cortex to the control of complex motor behaviour. It has been suggested that the absence of sexual behaviour in male rats, as opposed to female rats, is attributable to the complexity of this species-typical behaviour⁷. Without examination, however, it is not possible to specify whether this species-typical behaviour is abnormal. Also, some species-typical behaviours, e.g., nest building, seem to depend upon the integrity of the cortex^{19,36}, whereas others, e.g., grooming, do not^{36,43}. Thus, it is becoming clear that before generalizations about the neural control of various complex behaviours can be made, cortical involvement in all species-typical movement sequences should be examined. Copulatory behaviour is particularly interesting because it is one of the male rats' most complex motor sequences, involving as it does, the integration of movements that include locating a female, following her, performing a series of copulatory acts, grooming, etc., all of which must be appropriately timed and integrated and which may continue repeatedly, in sequence, for a number of hours³³. If the cortex is thought of as being involved in controlling complex motor activity, then it would be predicted that the male rats' copulatory behaviour would be disorganized. If copulatory behaviour is relatively normal, the results would suggest that complexity per se is not a characteristic of behaviour that necessarily indicates cortical mediation.

A third reason for examining decorticate rats is to contrast their behaviour with the behaviour of normal rats. A powerful way of gaining insight

into the behaviour of normal animals is to compare their actions with the actions of animals that have had brain damage. The errors, omissions, changes and simplifications of behaviour that characteristically follow brain transections frequently provide key insights into the principles underlying the integration of normal behaviour^{19,36-44}.

The rats were decorticated at one day of age. This procedure was used because optimal performance of many surviving behaviours is seen after neonatal, as contrasted with adult, decortications^{8,19,40}. Therefore, if copulation did occur it would be representative of the optimal capacities of the residual brain. If copulation did not occur, the result might suggest that neonatal decortication imposes upon the rat a type of isolation that deprives it of the benefits of socialization and learning that might be conferred by an intact cortex^{3,16,34,35}. For the purposes of comparison with our previous work³⁹, normal and neonatally decorticated male rats were screened to see if they would sire litters. Then they were placed with ovariectomized and estradiol benzoate and progesterone-primed female rats and their behaviour was videotaped. Subsequent analysis was directed towards obtaining a complete description of all sexual behaviour.

METHODS

Subjects

Twenty adult male rats and 16 adult female rats were used. In 14 male rats, obtained from 3 separate litters, all of the neocortex was removed when they were one day of age. Six of the female rats were ovariectomized a month prior to testing. Except when assigned to specific test procedures, the rats were housed individually in hanging wire mesh cages (20 × 25 × 18 cm high). Water was freely available through a metal spout and Purina Rat Chow pellets were left on the floor of the cage. The animal room had a 12-h-on, 12 h-off lighting schedule, and testing was done during the first half of the dark cycle.

Surgical procedure

Surgery was performed using conventional techniques¹⁹. A few hours after birth the male

pups were placed in a cooling chamber set at 0 °C until anaesthesia was achieved. Then a small aperture was opened on each side of the dorsal surface of the skull. The cortex, all tissue above the rhinal fissure, including the cingulate cortex was visualized, using a dissecting microscope, and removed by suction (glass pipette, approximately 1 mm in diameter). The hippocampus was spared. The wound was then sutured. The pups were rewarmed under a heat lamp, after which they were returned to their mothers. Ovariectomies in the adult female rats were performed in the conventional manner⁸.

Histological procedure

At the conclusion of the experiments, the male rats were deeply anesthetized and perfused through the heart with a solution of 0.9% NaCl and 10% formalin. Brains were removed, weighed, photographed, embedded in celloidin, and cut in 20 µm sections. These were mounted on glass slides and stained with cresyl violet. The sections were examined with a light microscope and projected onto a magnetic graphics tablet that was attached to an Apple II plus microcomputer. By tracing on the image with a metal stylus, the extent of neocortex, hippocampus, or subrhinal cortex remaining was calculated by comparing the area of tissue in the brain-damaged rats with that in control rats. The measures were obtained from 20 sections per rat at locations approximating those illustrated previously (ref 37, Fig 1).

Testing procedures

When the male rats were 150 days old, 10 decorticated and 6 normal rats were each paired with an adult female rat. When the females became pregnant, they were transferred to maternity cages. At parturition the latency between initial pairing and birth was calculated. The male rats were then given further tests in an observation room. The test room was dimly illuminated with red light and testing took place during the first 3 h of the laboratory dark cycle. The male rats were individually placed in a circular Plexiglas observation cage (38 cm diameter and 28 cm high) for 24 h of habituation. Then an ovariectomized, and estradiol benzoate- and progesterone-primed, fe-

male rat was introduced. Priming was achieved by administering 10 µg of estradiol benzoate subcutaneously 48 h and 24 h before testing and 500 µg of progesterone 3 h before testing. Behaviour was videotaped using a Sony Betamax recorder (Beta III mode). One hour of copulatory activity was taped from all rats and 5 h was recorded from one control and one decorticate rat. If a rat did not copulate in the test session, it was given a second test and if necessary a third test.

To determine how sexually naive decorticate rats responded to non-sexually receptive female rats, 4 sexually naive decorticate male rats were given two 1-h tests. Two males were paired first with a receptive female and then with a non-receptive female. The sequence was reversed for the other two males.

BEHAVIOURAL ANALYSIS

Latency to pup birth

The ability of the decorticate rats to copulate was determined by whether the cohabitant female became pregnant. Male efficiency was inferred from the number of days between pairing and parturition.

Counts and measures of copulatory behaviours in observation tests

The following measures of behaviour were taken from the video recordings, using either the standard or slow-motion playback feature^{10,11,34}.

Latency to initiate the first copulatory mount

Latency to the first mount was the time from initial pairing to the time when the male made a definitive mount with accompanying pelvic thrusting. It was found that the probability of making a decorticate rat copulate was greatly increased by sensory stimulation, i.e. hand waves or palpation of the hindquarters (see below). Therefore, if a rat had not mounted within 1 h, sensory stimulation was administered.

Precopulatory behaviour The rats made a variety of non-copulatory social contacts with the females. Three of these were identified and counted: (a) genital sniffing, the male sniffed the area around the base of the female's tail, (b) treading, the male reared up and made tread-

ing movements with the front paws on the side or back of the female, and (c) passes, the male passed, or climbed, over the female's back

Mounts, intromissions, ejaculations and other social contacts Mounts were often difficult to discriminate from intromission patterns. In case of doubt a behaviour was classified as a mount if a rat did not groom immediately after a mount, or if it immediately attempted another mount, or if it walked away from the female and lay down. Intromissions were identified by the males' post-mount rapid back flip and immediate initiation of genital grooming. Ejaculations were reliably identified by the males' long post-pelvic thrusting clasp and by the following long refractory period.

Latency to ejaculate Latency to ejaculate was the time between the first mount of a copulatory series and ejaculation.

Timing of mounts, intromissions and ejaculations Intervals between mounts, intromissions and ejaculations were measured and compared.

Number and duration of mount bouts Mount bouts were identified as a series of mounts (mounts, intromissions, or ejaculations) that were not fractionated by a non-sexually directed behaviour (body grooming, walking away and exploring, lying down and resting, etc.)³²

Temporal dimensions of intromission and ejaculatory patterns To compare the time dimensions of the copulatory acts of normal and decorticate rats the following measures were made on intromissions and ejaculations: (a) intromission pattern duration: the time between the start of a mount (the male's pelvis is positioned over the female's rump) and the termination of the forelimb clasp. Twenty intromissions were chosen at random for measurement from the videotape record of each rat, (b) ejaculation pattern duration: 3 separate measures were taken. First, the pelvic thrusting duration was measured. This was defined as the time that elapsed between the start of the mount (the male's pelvis is positioned over the female's rump) to the terminating period of immobility (the male stops thrusting). Second, the duration of clasp that followed the end of pelvic thrusting was recorded: the time between the cessation of pelvic thrusting and the point at which the forelimb clasp was terminated. Third, the

period of post-ejaculatory immobility was measured: the period during which the male stood immobile, after releasing the female.

Post-ejaculatory song recording To determine whether the male decorticate rats emitted a post-ejaculatory song¹, a high frequency microphone was connected to an amplifier and FM-recorder. Recordings were taken from two normal and two decorticate rats. The record was replayed at a reduced speed to make the high frequency sounds audible to the experimenters.

Movement notation. Sample behaviours were subjected to frame-by-frame (30 frames/s) analysis to clarify the temporal relations between the movements made by the male and by the female, the topographic relation that the male and female maintained with respect to each other, the partnerwise relations, i.e., contacts, that they made, and the actual movements that they made. Movements were recorded using a notation procedure based on the Eshkol-Wachmann movement notation method^{15,17,30}

RESULTS

Cohabitation test

Seven of the 10 female rats, which had been paired with decorticate rats, and 6 of the 6 female rats, which had been paired with normal male rats, produced litters of pups. The time from pairing to pup birth was 35 days (range 28–59 days) for females paired with decorticate males vs 31 days (range 25 vs 42 days) for females paired with normal males. This difference approached, but did not quite reach, significance (two-tailed *t*-test, $P > 0.05$). When the females that had been paired with the 3 remaining male decorticate rats had not become pregnant after 80 days of cohabitation, they were replaced with 3 different females. After a second 80 days of cohabitation, none of these females had become pregnant.

Videotaped tests

Latency to initiate copulation

In the videotaped tests, 6 out of 7 of the decorticated rats and 6 out of 6 of the normal rats mated

with the primed female rats. The most obvious difference in the behaviour of the two groups of male rats was the decorticate rats' long latency to initiate copulation. In addition, 5 of the 6 required sensory stimulation before they began to copulate (Table I). The latency means and standard deviations were: decorticates = 105.4 ± 74.9 min vs controls = 8.5 ± 8 min. This difference was significant, $t(10) = 3.01$, $P < 0.02$.

The latency difference, however, does not fully describe the differences between the two groups. The first decorticate rat to be filmed initiated mating after 59 min, and had it not done so we may have terminated the study after examining the behaviour of the remaining rats: none of them initiated mating within the 1-h test. Accidentally, however, we discovered that the decorticated rats could be induced to copulate with activating stimulation. Just before removing the third rat from the test chamber, we were cleaning the Plexiglas chamber with a cloth, to improve viewing, and found that we had apparently induced mating by the rat with the cleaning movements. We therefore retested the second rat. After 1 h had elapsed, without copulation taking place, we made rapid hand movements in front of it. The movements failed to induce copulation, but we were able to induce copulation by delivering a series of light, rapid pinches to the animal's rump. Of the

remaining 4 rats, one was induced to copulate by hand movements and 3 were made to copulate by pinches. When the decorticated rats were retested, only the first rat (latency = 54 min) spontaneously initiated copulation within 1 h. The remaining 5 rats only initiated copulation after receiving activating stimulation. None of the remaining 4 decorticate rats initiated copulation in either of two tests, even after receiving activating stimulation.

Pre-copulatory behaviour of decorticate male rats

Although the decorticate rats were slow to initiate copulation, they were active and they were responsive to the female rats. As soon as a female was introduced they approached her, engaged in genital sniffing, made pawing movements on her back (treading) and climbed over her (passes), repeatedly. We counted each of these behaviours through the first 1 h of filming. The results are summarized in Table I. The males contacted the females an average of twice each minute, and made an average of 157.7 contacts prior to copulating. The control rats made similar responses toward the females, but the number of instances of each behaviour was much lower, obviously because their latency to initiate copulation was so much shorter. The control rats made an average of 3.6 genital sniffs (one rat made no sniffs), 2.5 treading movements (2 rats made no treading movements), and only one control rat made a pass (4 times) over a female.

The movements of sniffing, treading, and passing made by the male decorticate rats towards the female rats before copulation began could have been movements quite unrelated to sexual activity. To evaluate this possibility, 4 sexually naive decorticate rats were paired with non-primed female rats for one 1-h observation session and with a primed female rat for a second 1-h observation session (two rats were paired with non-primed females first and then with primed females, and for the other two rats the order of pairing was reversed). The incidence of treading and passes, but not genital sniffing, was significantly higher when the primed females were present. They made a mean of 63 ± 22 vs 36.3 ± 20 treading movements on the primed as compared with the

TABLE I

Contacts made by male decorticate rats with female rats prior to initiating copulation

Rat	Sniff	Tread	Pass	Latency to first mount
1	36	99	113	58.46
2	34	56	40	84.48
3	33	123	4	63.05
4	26	116	42	65.20
5	16	38	8	90.58
6	20	65	34	253.39
7	19	200	10	60.00*
8	21	121	14	60.00*
9	11	95	29	60.00*
10	14	106	33	60.00*
Mean	23	102	32.7	105.04

* Did not mate

non-primed females, $t(3) = 8.5$, $P = 0.002$, a mean of 12 ± 6 passes vs 4 ± 3 passes over the primed as compared with the non-primed females, $t(3) = 4.9$, $P = 0.14$, and a mean of 16.5 ± 7.5 sniffs of the primed females vs 9.2 ± 6.5 sniffs of the non-primed females, $t(3) = 1.73$, $P = 0.17$. The result demonstrates that the social movements were made towards non-primed female rats, but their incidence did increase toward females in oestrus. Although none of the 4 rats spontaneously initiated copulation, it is likely that they were representative of those tested in greater detail, because when later cohabitated with female rats 3 of the 4 sired litters.

Number of mounts, intromissions and ejaculations

A summary of the number of mounts, intromissions, ejaculations, and other contacts made by the decorticate and control male rats during

TABLE II

Incidence of mounts, intromissions, ejaculations and other contacts made by decorticate and control male rats to primed female rats during the first hour following the first mount

Rat	Mounts	Intromission	Ejaculations	Other
<i>Decorticate*</i>				
1	21	23	3	12
2	10	28	1	10
3	25	34	2	20
4	11	26	3	26
5	8	13	2	18
6	12	25	3	40
Mean	14.5	24.8	2.3	26
<i>Control</i>				
1	31	25	3	37
2	21	28	3	27
3	21	21	3	10
4	52	30	3	4
5	9	23	4	0
6	21	14	1	5
Mean	25.8	23.5	2.8	9.8

* t -tests, $P > 0.05$

the 1 h of copulation is given in Table II. Overall, the incidence of each behaviour in the two groups was similar. The decorticate rats made somewhat fewer mounts, but the difference was not significant, $t(10) = 1.05$, $P = 0.32$. There was no significant difference in the number of intromissions, $t(10) = 0.365$, $P = 0.68$, or the number of ejaculations, $t(10) = 0.96$, $P > 0.52$, made by the two groups.

Counts were also made of the number of non-copulatory contacts (sniffing, treading, passes) that the male rats made with the females (Table II). The decorticate rats made significantly more 'other' contacts with the females than did the control rats, $t(10) = 2.19$, $P < 0.025$, and most of these contacts consisted of treading (110 of 116 in decorticate rats and 32 of 54 in control rats).

Latency to ejaculation

A summary of latencies to successive ejaculations after the occurrence of the first mount in each copulatory sequence is given in Table III. Analysis of latency showed that the decorticate rats had slightly longer latencies than the control rats, but the difference was not significant, $t(10) = 0.9$, $P = 0.4$. Similarly, the mean times between the first and second ejaculations were not different, $t(8) = 0.9$, $P > 0.67$, nor were the times between the second and third ejaculations different, $t(7) = 0.9$, $P = 0.41$. Finally, the latency between the first mount to ejaculation for all ejaculations considered together was also not significant, $t(31) = 1.06$, $P = 0.28$.

TABLE III

Latency (mean \pm S D in s) to ejaculation after the first mount in successive copulatory sequences by decorticate and control male rats

Group	Ejaculation number		
	1	2	3
Decorticate	$24.6 \pm 13^*$	$17.5 \pm 4^*$	$15.7 \pm 5^*$
Control	16.2 ± 11	16.3 ± 5	15.3 ± 3

* t -tests, $P > 0.05$

Timing of mounts and intromissions

A measure that did show differences between the two groups was the latency between successive mounts and intromissions. We compared the intermount latencies and the interintromission latencies for both groups of rats, and in addition, since these measures are somewhat artificial and arbitrary, we also calculated the latency between each mount or intromission. For all mounts, the mean interval between mounts for decorticate rats was 120.8 ± 153 s vs 61.4 ± 67 s for control rats, a difference that was significant, $t(220) = 4.1$, $P < 0.001$. Similarly, the mean interval between intromissions for decorticate rats was longer than was the mean interval between intromissions for control rats: decorticate rats = 81.9 ± 54.9 vs control = 66.6 ± 52.8 , $t(280) = 2.38$, $P = 0.017$. To gain a better idea of the differences between the distribution of mounts and intromissions for the two groups, the latencies between mounts and intromissions were pooled. The mean interval between successive mounts or intromissions for control rats was 33.9 ± 29 s vs 58.6 ± 43 s for decorticate rats, a difference that was highly significant, $t(573) = 8.5$, $P < 0.001$. A probability distribution of these latencies is shown in Fig 1. It can be seen from Fig 1 that 33% of control mounts occurred within 15 s following a mount and 50% of mounts occurred within 31 s. The comparable values were 0.8% and 21% respectively for the decorticate rats. In summary, these measures demonstrated that the control rats returned to make a mount or intromission much more quickly than did the decorticate rats. Examination of the behaviour of the two groups of rats

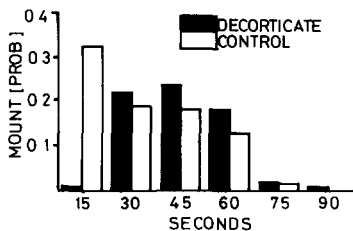


Fig 1 Probability distribution of intermount intervals for control and decorticate rats. Note that the decorticate rats were less likely to remount within 15 s of a previous mount, which was the interval within which control rats were most likely to remount.

TABLE IV

Mounts per mount bout and mount bout durations (mean \pm S D) for decorticate and control rats

Group	n	Mounts (n)	Durations (s)
Decorticate	124	$2.03 \pm 1.7^*$	$82.8 \pm 78^{**}$
Control	162	2.59 ± 2.5	61.5 ± 74

* t -test, $t = 2.14$, $P = 0.03$

** t -test, $t = 2.30$, $P = 0.02$

suggested that these differences occurred because the decorticate rats were slow to locate the female and less accurate in making successful approaches. That is, the control rats made quick, accurate, successful approaches while the decorticate rats approached the females from the wrong direction, were too slow, or made an inaccurate approach (see below), each of which caused the female to move and necessitated repetition of the approach.

Mount bouts

Copulatory efficiency was measured by calculating the number of mounts (mounts or intromissions) that occurred in succession before a rat engaged in some non-copulatory activity, such as exploring, rearing, lying down or grooming (other than genital grooming). Sachs and Barfield³² have called this unit of behaviour a mount bout and they suggest that it is a basic unit of the male rats' sexual behaviour. The number of mounts per bout and the mean duration of the mount bouts are summarized in Table IV. As is shown here, the control rats made significantly more mounts per mount bout, $t(284) = 2.14$, $P = 0.03$, and their mount bouts lasted significantly longer, $t(283) = 2.34$, $P = 0.02$ than those of the decorticate rats.

Temporal dimensions of intromissions and ejaculations

Pelvic thrusting durations were measured during both intromissions and ejaculations by counting the number of frames that occurred from the completion of a mount to the end of pelvic thrusting. Frames were measured on the slow-

TABLE V

Pelvic thrusting durations during intromission and during ejaculation made by decorticate and control rats (mean \pm S D)

Group	n	Intromission	n	Ejaculation
Decorticate	60	0.547 \pm 0.113	23	1.167 \pm 0.253*
Control	61	0.544 \pm 0.134	18	1.013 \pm 0.269**

* *t*-test, *t* = 0.13, *P* = 0.611

** *t*-test, *t* = 1.80, *P* = 0.077

motion mode of the recorder (30 frames/s) and the frame counts were then converted to seconds. Both visual inspection of the patterns of mounts and pelvic thrusts and the frame-by-frame measures showed no obvious differences between the control and the decorticate rats. Table V summarizes the mean durations of pelvic thrusting during intromission and during ejaculation. There were no significant differences in durations during intromission, *t*(19) = 0.13, *P* = 0.6, or during ejaculation, *t*(39) = 1.79, *P* = 0.08, between the two groups, but quite obviously the durations of pelvic thrusting during ejaculation were almost twice as long as they were during intromission.

Following intromission the male rats released the females and almost immediately began genital grooming, but following pelvic thrusting during an ejaculation they continued to clasp the female for variable periods of time or else they released the female and remained motionless before beginning genital grooming. The clasp durations and the immobility durations that occurred during the first 3 ejaculations were measured. Clasp duration was slightly longer in the decorticate rats, 1.85 \pm 2.80 s, than in the control rats, 0.499 \pm 0.72 s, but the difference was not quite significant, *t*(36) = 1.91, *P* = 0.057. Immobility durations after the female was released were also slightly longer in the decorticate rats, 3.94 \pm 3.24 s vs 2.06 \pm 1.02 s in the control rats, and this difference was significant, *t*(36) = 2.36, *P* = 0.022. Total immobility (the sum of clasp duration and immobility after release) following ejaculations was significantly longer in the decorticate rats than in the control rats, *t*(36) = 2.63, *P* = 0.012. These slight differences in immobility are difficult to interpret given the observations of

TABLE VI

Pelvic thrusting duration, post-thrusting clasp duration, and post-clasp release immobility durations (s) obtained from successive ejaculations made by one decorticate rat during a 5 h mating session

No	Time	Thrusting	Clasp	Post-release
1	2.04	1.030	0.033	3.963
2	2.29	0.830	0.865	3.896
3	3.00	0.899	1.030	3.263
4	3.36	1.300	11.289	6.690
5	3.59	1.260	4.795	6.993
6	4.29	1.260	7.493	4.995

Peirce and Nuttall²⁹ that the duration of sexual contact increases in normal rats with successive ejaculations. According to their measure total contact is little more than a second during the first 3 ejaculations, but it then increases to over 3 s for subsequent ejaculations. Since most of the observations in our study were limited to the first 3 ejaculations we cannot provide comparable observations; however, one control and one decorticate rat were observed for longer time periods. The control rat ejaculated 7 times during a 5-h observation period and the immobility durations with clasp duration did increase from a mean of less than 0.1 s during the first 3 ejaculations to more than 1 s during the remaining ejaculations. In this rat the immobility following release was rather constant at about 2 s. The results from the decorticate rat are shown in Table VI. It can be seen from Table VI that the duration of pelvic thrusting increased only slightly in successive ejaculations, but the duration of immobile clasp duration increased dramatically in the last 3 ejaculations and in addition the duration of post-release immobility also showed a tendency to increase. Thus, although the measures obtained from this rat are considerably larger than the mean values reported by Peirce and Nuttall²⁹, the pattern towards increased durations of contact with successive ejaculatory patterns is consistent with the major findings of their study with control rats.

Post-ejaculatory songs

The number and duration of post-ejaculatory songs¹ were recorded from two decorticate rats

and from two control rats. Animals from both groups produced a number of vocalizations, lasting from 2 to 5 s after ejaculation. We were unable to detect any obvious differences in the songs emitted by animals in the two groups. The female rats also appeared to respond to songs from both groups in similar ways; that is, by standing still facing the male, with ears directed toward the male.

Movement notation

The movement notation analysis was done on the non-copulatory interactions between the rats as well as the copulatory acts. Three general features of the interactions were described: (1) the topographic relation between the two rats indicated the location of the male with respect to the female. Beginning at the female's nose, which was labelled 0, 45° interval points around the circumference of the female were numbered from 1 to 7, in a clockwise direction. Points of contact were indicated by labels standing for the body part touched. Thus, 4P would designate that the male was behind the female touching her pelvis, 6S would indicate that its head was to the left of the female touching her shoulder, etc.; (2) the pairwise relations between the two rats indicated the orientation of the male with respect to the female. The direction of orientation of the male's head, when the male is placed schematically within the circle surrounding the female, indicated its pairwise relation with respect to her. Thus, 0 would indicate that the male is oriented in the same direction as the female and 2 would indicate he is oriented at 90°, facing across her from left to right, etc.; (3) the order of movements made by the two animals was designated frame-by-frame by specifying the beginning and end of each movement made by the animal or by a body part.

Non-copulatory interactions

It had been our expectation that the male decorticate rats would make many errors in their approach and interactions with the female rats, but in all of the mating encounters we observed only 5 major interactive errors, all made by one rat. These consisted of the male mounting the

female from the front on two occasions and the male missing a mount and making pelvic thrusts on the sawdust substrate on 3 occasions. Frame-by-frame analysis of the interactions of the male and female rats provided an explanation for the absence of errors in approach. The regulation of the relationship between the two animals seemed to be largely under the control of the female rats. This regulation was maintained both during precopulatory interactions as well as during copulatory encounters, in such a way that the male was confined to a relatively restricted pattern of movements that he could make towards the female. In fact, once we had clarified this interactive relation, it became clear that the precopulatory acts of sniffing, rearing up and treading on the female's back, and passing over the female, and the copulatory acts of approaching and mounting and clasping, were all terminal variations of a common approach forced upon the male by the movements of the female. The terminal acts, themselves, were no doubt mainly under the control of the male. With the failure in the execution of clasping, it seemed possible to identify a failure of a movement that may have been essential to initiating copulation. The various aspects of these behavioural interactions are described below.

Fig 2 shows a sequence of movements made by a male decorticate rat and a primed female, which culminated in the male making a pass over the female's back. Briefly, the sequence begins with the male and female standing still in an 'initial position', with the female in front of and facing away from the male. The male initiates the approach. As the male approaches, the female makes a number of movements which culminate in the male making a final approach toward the female's rump, from an angle of about 45° to one side. The interaction terminates when the male's movement carries him over the female's back toward the female's head, that is, at this point the female turns reinstating the 'initial position' between the two animals. The actual details of the movement sequence are shown in Fig 3, and can be followed with reference to Fig 2. At frame 1 both animals are motionless and the male is positioned behind and facing away from the female. The male moves first (frame 2) and his movement

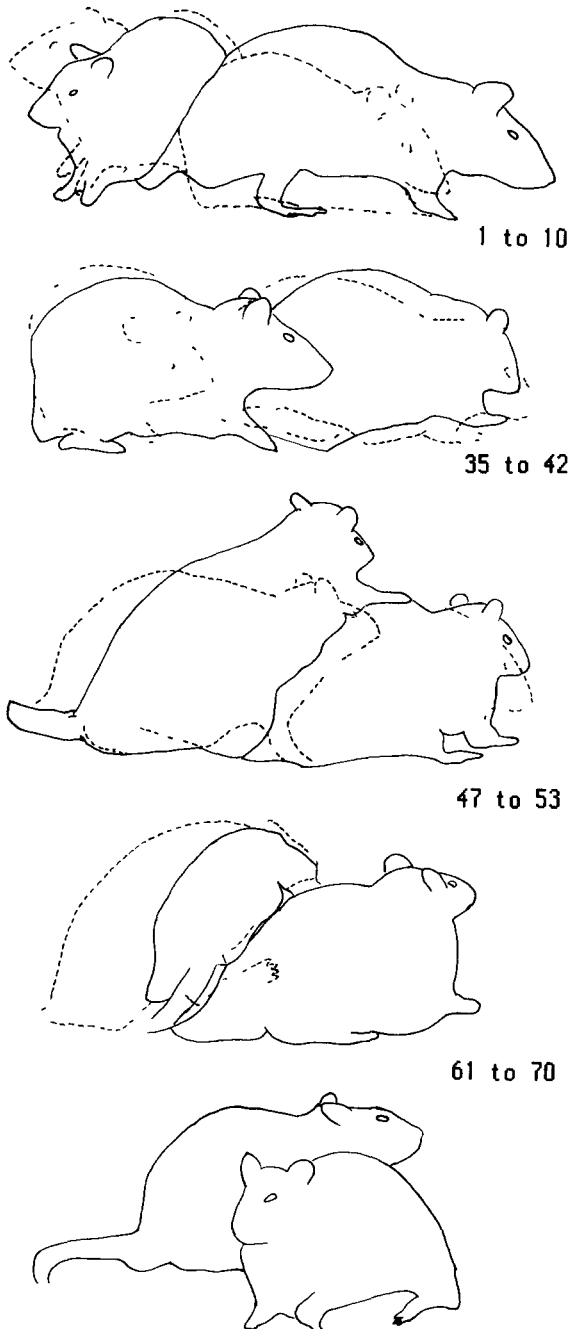


Fig 2 Tracing from a videotaped sequence (30 frames/s) in which a male decorticate rat passed over the back of a primed female rat. Dotted outlines illustrate initial frame position and solid lines illustrate terminal frame position. In the sequence the male moves first and serves as the stimulus inducing the female to hop forward (1–10). The female's movements carry her in a circle away from the male and she kicks twice with her rear feet when the male is directly behind her, forcing him to continue to circle (35–42). When the male

will carry him in a 180° arc which ends at frame 50. In initiating this movement the male steps on the tail of the female with his left paw and later steps on the right rear paw of the female. Both the visual aspects of the male's movements and these contacts may have contributed to initiating and maintaining the female's subsequent movements. The female begins to move at frame 6 and hops in a 90° turn which lasts through to frame 13. At this point she makes two rapid kicks with her rear legs, forcing the male, now almost directly behind her, to raise his head and continue his circling movement. The female then hops, in one motion, directly forward (frames 36–50). At this point the male is now approaching from her left rear, head up (frame 54). As the male contacts the female, he rears up, placing his forepaws on her back, and simultaneously makes a number of alternating treading movements with his forepaws on her back (frames 54–61), and then continues his forward movement so that he passes over her back. During this contact the female flattens her back and raises her head (this movement is not notated in Fig 3). As the male completes the pass over the female's back his left rear leg is slightly extended and dragged in a somewhat stereotyped manner. As the male's head comes into view in the female's right visual field, and as he contacts her vibrissae, the female begins a 180° hop and turn (frames 80–92), which leave her facing away from the male. At the completion of this sequence of movements the relative positions of the two animals are what they were when the sequence began. The sequence begins again as the male turns to again approach the female (frame 80).

The pattern of movements described in Figs 2 and 3 were performed again and again as the two rats interacted, such that the animals appeared to perform a 'dance' which always began and ended

makes an approach from one side and behind the female she remains in the same location but raises her head as he places his paws on her back (47–53). The male passes over the female, dragging the trailing rear leg in a characteristic manner, as if marking the female's back (61–70). As the male's head approaches the forepart of the female, it turns quickly away, leaving both animals in the initial topographical relation with respect to each other (109). See text for further details.

FRAMES	1	2	6	13	14	15	35	36	50	54	61	79	80	92
TOPOGRAPHIC	4						4	4P	4P	4T	6S	6H		4P
PAIR-WISE	2						0							7
FEMALE														
NECK														
FRONT														
MALE														
WEIGHT														
FRONT														
FOREPAWS														

Fig 3 Notation for the behaviour illustrated in Fig 2, showing the sequence of movements displayed by a male decorticate rat and a primed female rat. Numbers refer to clockwise 45° points in which 0 is at the female's nose. For the topographic relation, numbers refer to a hypothetical horizontal sphere surrounding the female, thus the male is initially located at 4 directly behind her, crosses her body to one side (6) and finally is again located behind her. For the partner-wise relation, numbers refer to the location of the male as superimposed on this sphere, i.e., 2, his nose pointing to her left, 0, his nose pointing along her forward axis, 7, his nose pointing to her right. Letters in the topographic column represent points of contact: P, pelvis; T, trunk; S, shoulder; H, head. Other symbols include ||, end of movement; ∪, ∩, counterclockwise and clockwise movements; →, direction of movement. The important feature of this sequence of movements is that the female moves in response to certain movements of the male, i.e., an approach directly from the rear, and remains stationary in response to other movements, i.e., approaching from an oblique rear angle.

with each in the same pairwise and topographical relationship. Within this dance there were many variations in the actual movements that might occur. The following are a few which we were able to identify. If the male approached head down so that he contacted the base of the female's tail, he sometimes sniffed her rump or sniffed beneath her tail. These contacts did not induce movements on the part of the female except that she sometimes elevated her rear and tail. If the male approached the female's head, from the front or side, or even if he approached her shoulder, she hopped or turned away immediately. If the male approached from directly behind the female, she usually hopped forward and kicked. When the male reared up and placed his paws on the female's back she usually remained relatively motionless unless he passed over her, moved his paws caudally down her rump, or moved his paws laterally down her

body on the side towards which he faced. All of these movements invariably resulted in the female hopping away.

Copulatory interactions

Examination of the video recordings of copulatory acts showed that the same general patterns of behaviour, as described above, occurred between the male and female, except that copulation was the end point of the males' behaviour rather than genital sniffing, treading, or passing over. Fig 4 shows a drawing of a typical copulatory sequence taken from a video recording of a male decorticate rat and a primed female. The notation for this sequence is shown in Fig. 6. The sequence begins with the male positioned just behind the female, facing away from her. The male turns towards the female, and by frame 1 is walking directly towards her right rear side. In response to his approach the female raises her head slightly (frame 1). The male continues his forward motion and rears lifting his left forepaw across the female's back in the first act to initiate clasping. When the male clasps the female with his forepaws, his forward motion, which to this point has been propelled from a fulcrum of control from his rear legs, is arrested. The fulcrum of control is shifted to the male's forelimbs, and the rat's rear is swung rapidly to the left (frame 23) so that it is appropriately positioned for thrusting. As the male begins to clasp, the female continues to raise her head, she raises her left forepaw against the chamber wall, she arches her back, thus elevating her rump, and by frame 22 she has completely adopted the lordosis posture. The male engages in pelvic thrusting from frame 23 to 46 and then releases the female by making a quick lateral movement of his forepaws, while at the same time rearing back to a standing position (frame 46). The female then returns to a normal position (frames 46–51). The male lowers his head to begin genital grooming and the female hops to the left so that the pair is left in a topographical relation approximating their initial starting positions.

In light of the observation that hand movements could trigger copulation on the part of decorticate male rats, we also examined whether movement on the part of the female was necessary

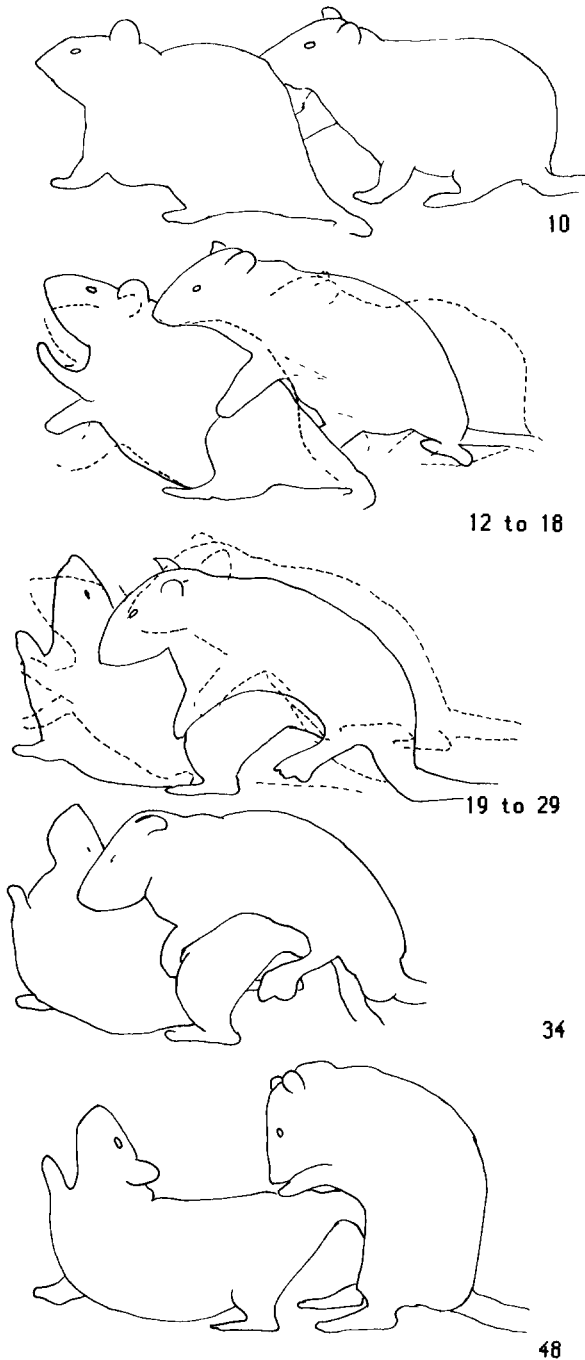


Fig 4 Tracing from a videotaped sequence (30 frames/s) in which a male decorticate rat mounts a primed female rat. Dotted outlines illustrate initial frame position and bold lines illustrate terminal frame position. Note the angle of approach and the rapid side movement of the rear of the male after clamping is initiated.

FRAMES	1	10	18	22	23	27	46	47	48	51
TOPOGRAPHIC PAIR-WISE	4	2P	4T	6S				4T	4P	4
	7					0	0			
FEMALE										
NECK	($\frac{1}{2}$)	↑		($\frac{1}{2}$)				↓		($\frac{2}{3}$)
TRUNK		[4]X					X[0]			
WEIGHT										
MALE										
FOREPAWS				C			P			
WEIGHT	($\frac{2}{3}$)				[THRUSTING] 4					
FRONT				(1)						

Fig 5 Notation for the behaviour illustrated in Fig 4, showing the sequence of movements displayed by a male decorticate rat mounting a primed female rat. X, ventral or dorsal movements of the back, other symbols as in Fig 3.

in eliciting approach by the male. Many copulatory sequences made by the decorticate rats seemed to be triggered by a movement on the female's part. There were, however, instances in which it was quite clear that the male decorticate rat initiated an approach towards the female before she moved. Two other observations supported this conclusion. In one experiment a female was given an injection of 2 mg/kg of haloperidol. This treatment effectively immobilized her and left her standing in a posture of lordosis, after copulation. The decorticate male that had been paired with her did return to her and mate in the absence of any movement on her part to initiate his approach. In a second test a female and male decorticate were placed in a large open enclosure (200 x 200 cm). In this situation the decorticate male was able to complete a copulatory sequence to ejaculation even though, for many mounts, it was necessary for him to locate the female who was otherwise sitting immobile a considerable distance away.

Comparisons between normal and decorticate rats

Comparisons of the movements made by normal and decorticate male rats revealed that their patterns of approach and most of the details of their copulatory acts were indistinguishable from those of the normal males. A difference difficult to quantify was that the normal males seemed more precise and efficient in their approaches. Most

noticeably, some of the normal males simply pivoted on their rear legs, from their position of genital grooming, to grasp the female and initiate another copulatory act. The decorticate rats in-

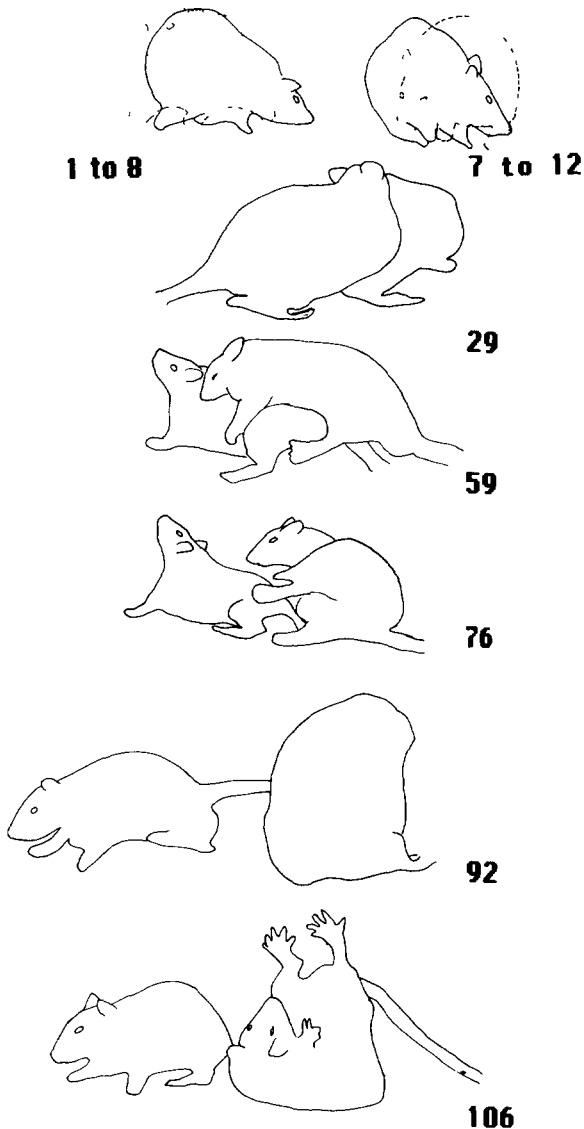


Fig 6 Tracing from a videotaped sequence (30 frames/s) illustrating some movement abnormalities displayed by a male decorticate rat. Dotted outlines illustrate initial frame position and solid lines illustrate terminal frame position. In the sequence the male initiates the sequence by approaching the female's head (1-8). The female turns to face away from the male (7-12). The male mounts, clasps, and makes an intromission (59). Upon dismounting the male falls to the side (76) and then, as it sits back to genital groom, propels itself onto its back and engages in genital grooming from this position (92-106).

variably walked around to find the female. Their inefficiency is also reflected in the greater number of non-copulatory contacts (see Table II) that they made with the females once copulation had begun, that is, these contacts may in large part reflect failures in clasping, and in their longer intermount intervals (Fig 1), which may reflect inefficiencies in locating and approaching the females.

The most notable abnormalities of the decorticate rats were the many exaggerated movements that they made when dismounting after intromission or ejaculation. They frequently fell to one side, reared back too far so that they landed on their backs, or reared back so that they completed a backward somersault. Fig 6 illustrates some of these abnormal movements. Here the male initiates the approach by turning towards the female's head (frames 1-8). This could be considered an error in approach, but it is corrected by the female who turns away (frames 7-12). After intromission the male falls completely over onto his right side while dismounting (frame 76). He then rights on his rear legs only to flip completely over onto his back (frame 106). The animal remained on its back while it engaged in genital grooming.

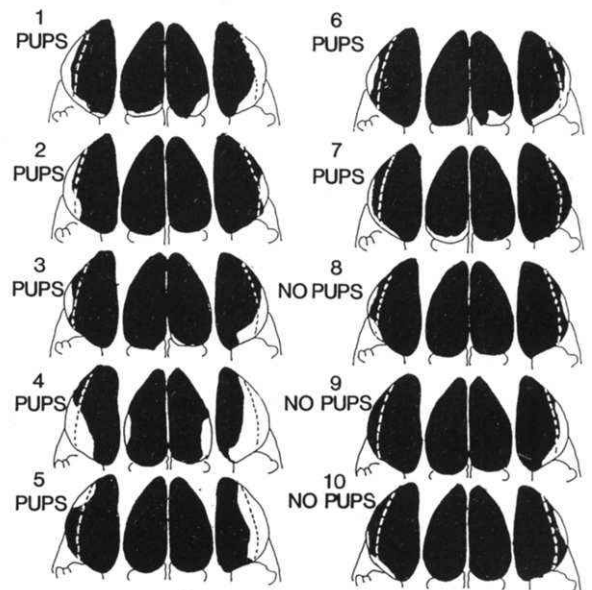


Fig 7 Cortical reconstruction of 10 decorticate rats used in the experiments. Rats 1-7 sired pups in the cohabitation test and rats 8-10 did not.

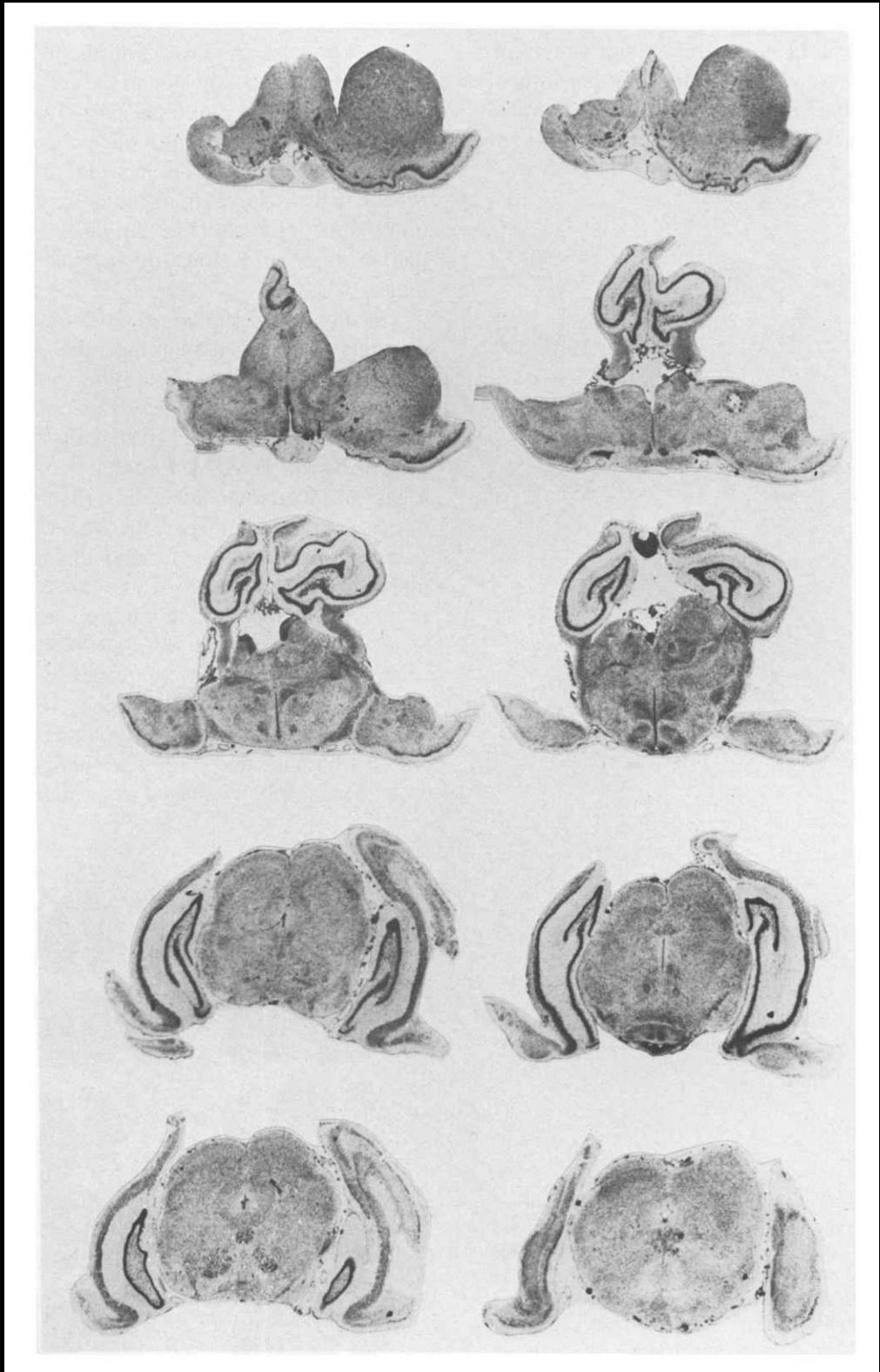


Fig 8 Photomicrograph of cresyl violet-stained coronal section of a decorticated rat that sired pups

Occasionally, normal males leant over to one side after intromission or ejaculation, but the frequency and amplitude of the abnormal movements made by the decorticate rats were simply not characteristic of the normal male rats

Histological results

Surface reconstructions of the brains of the 10 decorticate rats are shown in Fig 8 and coronal sections from a representative rat are shown in Fig 9. There was very little difference in the extent of the lesions in the 7 males that sired pups and those males that did not sire pups. The lesions removed most of the neocortex and cingulate cortex, sparing only small strips of tissue adjacent to the rhinal fissure²³. For some animals the lesions invaded tissue below the rhinal fissure. Measures of residual cortex in 20 representative sections from each rat showed more than 97% of neocortex and 100% of the cingulate cortex was removed in all of the rats. Measures of the residual neocortex were complicated by the observation that the residual cortex that appeared to lie above the rhinal fissure, particularly in the caudal sections, did not have the histological features of neocortex. This cortex has the appearance of archicortex of the entorhinal area and may very well represent an abnormal extension or growth of entorhinal cortex. There was little direct damage to subcortical structures such as the basal ganglia, thalamus or hippocampus. The greatest amount of subcortical damage seen was an extensive unilateral invasion of the caudate of one rat, which is shown in Fig 8.

DISCUSSION

The results confirm previous reports that male rats with cortical ablations can mate^{2,11,24,37}. They also confirm that complete cortical removal delays but does not abolish mating^{19,37}. The interrelations between the male and female rats, revealed by notating their interactions, also provides novel information about the regulation of sexual activity. The findings are relevant to at least 3 separate issues. First, they show that the relation between the male and female is importantly controlled by the movements of the female

It may even be the case that it is the female that ultimately ensures copulatory success of the decorticate males. Second, they provide support for Beach's²⁻⁵ initial observations, by demonstrating that the decorticate rats do have deficits in initiating mating. Third, they are relevant to general notions of the function of the cortex in the control of complex behaviour. Decorticate rats are able to execute complex sequences of actions but they do display deficits in timing and executing certain movements. These issues will be discussed in turn.

Sources of control of male-female interactions

Female rats engage in a variety of behaviours during mating that contribute to the success of the engagement. These include soliciting, darting, hopping, and ear wiggling, etc.^{11,12,14,27} Tactile stimulation to the rump and genital area of the female also inhibits her locomotion and facilitates the adoption of the lordosis posture so that the male can mount³¹. Here we report that the locomotion and other movements by the female constrain the male to only certain kinds of approaches.

Prior to copulation the normal male rat makes a brief general inspection of the female and then restricts its behaviour to a number of more stereotyped movements, prominent among which are genital sniffing, treading on the female's sides or back with the front paws, and passing over the female. The full significance of each movement is not clear but it is possible to speculate about some aspects of their function. Genital sniffing no doubt provides information about the identity of the female and her sexual condition. The treading movements may be ideally suited to induce the female to remain motionless, particularly when it is focused on the rump area, to which such appropriately applied contact induces immobility and facilitates the appearance of lordosis³¹. In turn, immobility by the female permits easier execution of genital sniffing, passing over, and eventually clasping. Passing over may serve at least two functions. First, during a pass the male lifts and drags its trailing rear leg so that its genital area is dragged across the female's rump. Since male rats engage in urine marking during sexual

encounters²⁷, it is likely that the male is marking the rump of the female. This could serve as a signal to other males, were the encounter to take place in a colony environment²⁷. It also could serve as a signal to the marking male, directing its subsequent attention to the rump of the female. A second function of passing over might be to adapt the female to contact and thus facilitate subsequent copulation.

Although the male engages in these different behaviours with non-primed females, the present analysis shows that the behaviour of the primed female restricts and focuses the movements. The male can execute the behaviours only if he approaches the female from the rear at an angle of about 45°. The female achieves this modification of the male's approach in a number of ways. If the male approaches from the front or approaches her head, she hops in a circle to face away from him. Both the visual stimulus of the approaching male as well as the contacts that he makes with the forepart of her body seem potent stimuli for eliciting these movements. Direct approaches from the rear also induce her to move. Here the eliciting stimuli appear more tactile than visual. The female usually moves after the male has touched her tail or her rear legs. Not only does a rear approach cause the female to hop away, after a hop, she frequently makes one or two rapid back-kicks to hit the male or propel sawdust at its head. The kicks deflect the male's approach and make it raise its head. Therefore, the male's next approach will be from a different angle, head up, thus facilitating mounting.

The behaviour of the female raises two questions. The first concerns the mechanisms through which hormonal influences modify her sensorimotor behaviour and the second concerns the utility for the male of making an oblique rear approach.

A discussion of how hormones influence the behaviour of the female lies beyond the scope of the present report. But, it seems worthwhile noting that with respect to the behaviours described above, that non-primed females do not behave like primed females. Usually non-primed females orient with their head toward the male. This dis-

courages sexually-related encounters and it promotes other interactions, including mutual sniffing, boxing, or wrestling, etc. Although there is a substantial literature on the sensorimotor behaviour of the rat, it has focused on describing orienting, immobility, or avoidance of potentially noxious stimuli (see ref. 41). Thus the present report describes a new pattern of behaviour that is a reversal of the usual rostral-caudal gradient of orienting and one which might be usefully examined in further studies. With respect to females in oestrous, neglect or avoidance of stimuli presented to the forepart of the body may not signify neglect or aversion per se, but rather orienting that involves presenting the rear of the body to the male.

In hindsight, it seems that an oblique rear approach on the part of the male has utility. First, it ensures that the first contact that the male makes with the female will permit clasping, were the male to approach from the rear or front it would have to clamber across the female to initiate clasping. Second, it keeps the male's body clear of the female's rump, so it can be raised for lordosis, before the male completes the mount. Third, given that the male swings its rear laterally in a rather quick movement after clasping, it permits the male's movements to carry the female's tail to one side, thus facilitating intromission.

The degree to which the decorticate male owes copulatory success to the behaviour of the female cannot be fully determined, but given that normal males will not attempt copulation with a passive female and thus are in part dependent upon her behaviour²⁶, so too must be the decorticate male. And, the decorticate male may have an even greater dependence. It seems to us that had the female not controlled the decorticate male's approaches, it may have made many errors, i.e., head or side mounts, etc., even to the point of having difficulty in initiating or executing an appropriate copulatory sequence. Thus, the female's behaviour helps us understand that many aspects of decorticate males' seemingly normal orienting and approach is not the product of its residual subcortical neural systems, but is rather attributable to the normal behaviour of the female.

Role of the cortex in initiating copulation

In a review of the copulatory behaviour in the male rat, Sachs and Barfield³³ point out that Beach's dual-factor theory of sexual behaviour still has utility in explaining some features of male sexual behaviour, particularly those features related to why the male starts copulating when it does. On the basis of his work with decorticated rats, Beach² had suggested that the cortex is essential for arousal but unnecessary for the actual execution of copulatory movements. Subsequently, a study by Larsson²⁴, showing that male rats with motor cortex lesions could copulate but that their initiation latencies were increased, seemingly supported Beach's hypothesis. The results of the present study, as well as the results of our previous work³⁷, confirm that the cortex is not necessary for the actual execution of copulatory movements. Furthermore, since completely decorticate rats will initiate copulation, the cortex does not appear essential for arousal. The present finding that the male's latency to initiate copulation is dramatically increased by decortication does demonstrate, however, that the cortex is in some way important for rapid initiating of the copulatory sequence. Features of the animals' behaviour also provide some clues for understanding what mechanisms are involved in the successful initiation of copulation. The following considerations are relevant. First, decorticate rats were socially interactive with female rats and the degree of their interaction and the extent to which they made precopulatory relevant movements increased when they were paired with primed females. Thus, the delay in initiating copulation was not due to lack of social interaction. It may be the case that the precopulatory movements provide some essential information to the normal male that in the absence of the cortex is not readily registered, and which in turn leads the rats to repeat the movement. Second, in passing over the female rat, a movement that the decorticate rats made repeatedly, all of the appropriate precopulatory movements occurred, except clasping. So delayed copulation was not due to inappropriate approaches, but due to a failure in clasping. Thus, we feel that a critical behaviour that may be central to triggering the copulatory sequence is the

first clasp. This conclusion seems supported in part by our observations of the only decorticate rat that spontaneously initiated copulation. The rat had made numerous passes over the female over a period of nearly an hour when one pass carried it directly into the wall of the chamber. As it fell back, it landed on the female with its forepaws straddling her back. It immediately clasped and then began pelvic thrusting. This one accidentally initiated clasp seemed to trigger the entire subsequent mating encounter. There is a precedent for the suggestion that a single experience is sufficient to maintain subsequent behaviour in decorticate rats. We have previously reported that decorticate rats that do not spontaneously drink after surgery will do so after a brief experience of drinking after presentation of a water spout to their mouth⁴⁴.

Anatomical and behavioural studies have demonstrated that corticofugal and brainstem-spinal cord pathways are involved in controlling limb movement^{9,25,43}, and that brainstem control is insufficient to maintain normality. Limb abnormalities that occur following cortical damage may delay clasping for two reasons. First, it is possible that there is a release of forelimb treading responses, which would help the male maintain balance as it reared up on the female with a consequent increase in the threshold for activating clasping, a movement which would cause the animal, at least initially, to give up limb support of the forepart of its body. Second, a difficulty in initiating clasping could be advanced as the sole explanation of the long latency to initiate copulation, however, our observation that activating stimulation contributes to the initiation of copulation in turn suggests that the matter is more complex. We have no clear understanding of how 'activation' might facilitate clasping, but stimulation did seem to produce an arrest reaction on the part of the animal. So it might reduce tendencies to walk, which are involved in passes over the female, and increased tendencies to 'freeze', which might ordinarily occur in response to a female's movements in adopting lordosis, and thus make the animal's behaviour more compatible for clasping. This suggestion is consistent with a previous suggestion that the cortex is importantly involved in

controlling voluntary movements³⁶ and also with the finding that appropriate changes in stimulus conditions can facilitate more normally appearing behaviour from decorticate rats⁴². At any rate, given that activating stimulation promotes the initiation of copulation, and given that activating stimulation promotes copulation in normal rats as well^{4,6}, it is possible to conclude that the cortex facilitates the appearance of, while still not being essential for, adaptive, or at least situationally appropriate, responses.

Cortical contributions to the control of copulation

The male decorticate rats displayed all of the components of mating behaviour, and furthermore, the incidence of mounts, intromissions, and ejaculations approximated normal¹⁰. Measures of the durations of mounts and pelvic thrusting during intromission and ejaculation showed they were normal. The decorticate rats did seem to display longer durations of immobility after ejaculation, both with clasping and following release, but the pattern of successively longer periods of immobility following successive ejaculations, has been described in normal rats²⁹. It has been reported that mount bouts, a series of mounts interrupted by some non-sexually directed behaviour, such as resting, exploring, eating, etc., form a unit of the male rats' sexual behaviour³². Decorticate rats had significantly longer mount bouts, characterized by significantly fewer mounts, than did the control rats. This was in part because they displayed longer intermount latencies than did the control rats. The decorticate rats also made more non-copulatory contacts with the females and were often inexact in their approaches. These errors also delayed mounts, increased the duration of mount bouts, and reduced the number of mounts per mount bout.

The surprising preservation of copulatory movements following decortication is consistent with previous studies that have shown that the cortex is not essential for most of the motor patterns displayed by the rat^{19,36-44}. The results also demonstrate that rather complex sequences of behaviour, such as is characteristic of the species-typical behaviour of male rat copulation, is not dependent upon the integrity of the cortex.

This result is consistent with previous work showing that the complex sequence of grooming behaviour of the rat survives decortication^{36,43}. The results, however, do not support the conclusion that social behaviour is essentially abolished by decortication³⁶, since by most definitions copulation, and the non-copulatory interactions of genital sniffing, treading and passing-over, etc., would be considered social behaviours. Other observations from preliminary studies (Whishaw and Kolb, unpublished observations) showing that decorticate male rats will engage in pup killing, hovering over pups, and will defend a territory, and that female decorticate rats will raise pups, and that male and female decorticate rats will engage in play behaviour also confirm that decorticate rats will engage in considerable social behaviour. Different findings with respect to the incidence of social behaviour in decorticate rats is likely attributable to the test situation, for as we have pointed out⁴³, more normal behaviours can only be expected from decorticated rats in optimal test situations. It must be noted, however, that decortication may have differential effects on different types of species-typical behaviours, for there are currently no demonstrations that behaviours such as nest building and food hoarding survive decortication^{19,36}. Finally, the results suggest that some species-typical behaviours, which involve sequencing a number of different movements within a temporal dimension, must have a different neural basis from praxis behaviours as they are described in humans²⁰⁻²². Although decorticate rats can acquire quite complex instrumental responses (see ref 28 for a review), they cannot perform tasks requiring the appreciation of place³⁹, and it is unlikely that they could master tasks requiring timing or sequencing a number of different acquired responses^{21,28}.

The present results do not mean that the cortex plays no role in the control of male sexual behaviour. It has been suggested that the role of the cortex, or its non-specific afferents, is to facilitate the acquisition of new motor responses²¹, to regulate type I movements (walking, rearing, turning, etc.) so that each occurs in an appropriate context³⁶, to extend the range of environmental conditions in which normal behaviour can occur⁴³,

and to facilitate the analysis of and responses to the relational properties of distal stimuli³⁹ Since the laboratory test situation used here was relatively confined and simple, and since the female rats regulated much of the approach behaviour of the male rats, it is understandable that male copulation might appear surprisingly normal. Were the tests conducted in a more natural setting, however, it is possible that the male rats' abnormalities would be more pronounced and the contributions of the cortex more obvious. Nevertheless, our general impression of the male decorticate rats, as well as results showing abnormalities in mount bouts and intermount intervals, was that they lacked the precision and speed of normal rats in their approaches to the female rats. This must indicate that even in the simple laboratory test situation they are unable to respond to ambient events in the way that intact rats do.

An aspect of the decorticate male rats' behaviour that was characteristic were the exaggerated falls and tumbles made when dismounting the female. After intromissions they often fell to one side or reared excessively to land on their backs. Abnormalities in limb and body posture are a feature of decorticate rats^{36,43,44}. Their cause might be due to an exaggeration of certain reflexes. At the end of an intromission the rat makes a rapid kick with one rear limb. An exaggeration of this kick may cause the rats to be thrown to one side. Dismounts from intromission are characterized by a rapid rear, exaggeration of this act may throw the rat onto its back. The long periods of immobility, with clasping and following release, after ejaculation, may have also been due to an exaggeration of a reflexive response. The presence of these abnormalities does demonstrate that the cortex is essential for the more normal execution of many motor responses.

Finally, it is interesting to note that social deprivation has been reported to disrupt male sexual behaviour¹⁶. Since it might be thought that deprivation produces its consequences through inappropriate cortical development¹³, it is surprising that our neonatally decorticated rats copulated. Although we took no special care to control social experience during development, experience could be a factor influencing copulatory success, which

might provide evidence that experience can also influence behaviour by modifying subcortical development.

In summary, although decorticate male rats do display long latencies to initiate copulation, have mount bouts that are long and contain few mounts, and display exaggerations in some movements, many aspects of their behaviour are remarkably normal. Two implications of these results are striking. The first is the surprising degree of control that subcortical structures can exert in producing and executing the complex sequence of behaviour involved in male rat mating. The second is the degree of control that the female rat, through her various movements, exerts on the behaviour of the male. It is unlikely that the contribution of the female would have been noticed had only normal male rats been observed, since in initiating mating so rapidly, they gave the appearance of regulating their approaches. It was only after observing and notating the repeated interactions between the decorticate males and the females, which did not result in copulation, that it became evident that the movements of the female were controlling the approaches of the male, and thereby enhancing the probability of successful mating.

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