

Neonatal Decortication and Adult Female Sexual Behavior

C. SUE CARTER¹ AND DIANE M. WITT

*University of Illinois, Departments of Psychology and Ecology
Ethology and Evolution and Program in Neural and Behavioral Biology, Champaign, IL 61820*

AND

BRYAN KOLB AND IAN Q. WHISHAW

University of Lethbridge, Department of Psychology, Lethbridge, Alberta, Canada

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CARTER, C. S., D. M. WITT, B. KOLB AND I. Q. WHISHAW. *Neonatal decortication and adult female sexual behavior*. *PHYSIOL. BEHAV.* 29(4) 763-766, 1982.—Neonatal lesions of the cerebral cortex in female rats did not eliminate female sexual behavior as measured by lordosis. However, lordosis in response to prolonged low levels of estradiol benzoate (1.0 $\mu\text{g}/\text{day}$ for 6 days) was attenuated in lesioned females. Following estradiol benzoate plus progesterone (0.5 mg) treatment the probability of lordosis increased markedly in the decorticate females, but still remained below control levels. Decorticate females were mounted by the male at least as often as control females. Hopping and darting and rejection behaviors on the part of the female were virtually eliminated in the decorticate group. However, these females continued to direct sniffing behavior toward the male at levels above those of the controls.

Neonatal decortication Female sexual behavior Estrogen Progesterone Rat

IT has been known since the 1930's that massive damage to the cerebral cortex does not eliminate female sexual receptivity, as measured by lordosis. In fact, Beach [1] observed in estrogen and progesterone treated rats that after adult decortication the lordosis posture in some female rats was enhanced or exaggerated. We have also observed prolonged lordosis responses (4-5 sec) following male dismount, in female rats after adult decortication (Kolb and Whishaw, unpublished observations). Beach [1] interpreted these changes in behavioral patterns in terms of a reduced neural inhibition or "disinhibition." As noted by Clemens [4], other explanations for these effects of decortication, including the possibility of posttreatment changes in estrogen sensitivity, have not been thoroughly explored.

One difficulty in studying totally decorticate rats is that they are difficult to maintain in healthy conditions for the first few weeks following surgery because of the severe behavioral effects of the decortication. One solution to this problem is to decorticate rats in infancy as the animals appear to suckle normally and develop into healthy adult rats [6]. Although the neonatal decortication provides a far healthier subject to study, there is no evidence of a significant behavioral difference between adult and neonatally decorticate rats when both are studied on a wide range of tests of species typical and cognitive behavior in adulthood [6]. However, there are at present no published studies of the effects of neonatal decortication on female reproductive behaviors.

The current study investigates the effects of neonatal lesions of the cerebral cortex on sexual and social behaviors in female rats. To explore the possibility that estrogen sensitivity might vary as a function of these lesions, adult behavior was recorded repeatedly during treatment with a prolonged (7 day) but relatively low (1 $\mu\text{g}/\text{day}$) dose of estradiol benzoate. These same females were also tested after exposure to a sequential estradiol benzoate and progesterone treatment. The latter protocol typically elicits maximal sexual receptivity in normal female rats.

In Experiment 1, females were tested in a relatively large arena (1 sq m) in which the female was allowed to interact freely with a sexually experienced male. In Experiment 2, the male was restrained and the female was permitted to choose to either spend time in a chamber containing the male or to be alone.

METHOD

Female rats of the Long-Evans strain were reared under standard laboratory procedures in a 12:12 light-dark cycle. Neonatal cerebral cortex lesions or sham operations conducted on day 4 postpartum, involved an aspiration procedure and cryogenic anesthesia (described in detail elsewhere [6]) in which all of the neocortex and cingulate cortex was removed.

Experiment 1

At approximately 7 to 9 months of age decorticate (N=10)

¹Please send reprint requests to Dr. C. Sue Carter, 725 Psychology Building, 603 E. Daniel St., University of Illinois, Champaign, IL 61820.

TABLE 1
BEHAVIORAL DEFINITIONS

Lordosis	A concave arching of the back in which the female extends her hind legs and elevates the genitalia.
Holding	An immobile female posture, with back flat and occurring in response to male contact.
Hop/Dart	Female moves abruptly then halts.
Kick-back	Female pushes male away, typically by extension of hind leg.
Vocalization	Female calling or squealing.
Grooming	Female self licking.
Sniffing	Female investigates male, frequently with naso-nasal or naso-genital contact.
Mount	Male places forelegs on female's hind quarters, oriented in a direction that would permit copulation.

and sham-operated control (N=11) females were ovariectomized under sodium pentobarbital anesthesia (60 mg/kg) and allowed to recover for 2 to 3 weeks. At this time each female was pretested and then received daily injections of estradiol benzoate (EB, 1.0 μ g/day) for 7 consecutive days. Each female was tested on day 1 (24 hrs after the first injection), day 2, day 4 and day 6 of EB and on day 7 of EB received progesterone (0.5 mg) and was again tested 4–6 hrs following progesterone treatment (for a total of 6 tests). All hormones were suspended in sesame oil and injected subcutaneously in a volume of 0.1 ml.

Behavioral tests were conducted by placing the female in a 1 m square wire cage. Each female was allowed to adapt for about 5 min, a male was then introduced and the behaviors described in Table 1 were recorded for 10 min using a keyboard and Esterline Angus event recorder. Males were screened just prior to use by allowing them one intromission with a receptive stimulus female. If at least 5 mounts were not recorded during this 10 min test, then a second and if necessary a third 10 min test was given to each female on each of the test days.

For statistical purposes the first 10 min test was analyzed for each of the 6 test sessions. Most animals responded on the first test or not at all, so subsequent tests were not analyzed. Analysis of variance was applied to each of the behavioral measures using a group (decorticate or control) by test (day 0, 1, 2, 4, 6 and 7) repeated measures design.

Experiment 2

Approximately 3 weeks after the last session in Experiment 1 each female was tested again before receiving three daily injections of EB (1 μ g/day) followed by progesterone (0.5 mg). On the third day, 4–6 hours after progesterone injection each female was retested.

For testing, each female was placed in a 77×40 cm solid walled box divided along its width into two approximately square chambers. The solid barrier between these chambers contained a small opening through which the (smaller) female, but not the male, could easily pass. Each female was initially placed either in the side containing a sexually vigorous male or on the other (empty) side. After a 6 min test the female was removed for approximately 2 min and then rein-



FIG. 1. Photograph of a representative neonatally decorticate rat.

roduced for a second 6 min test, which began on the opposite side of the chamber. The order of these two tests was counterbalanced and equalized within the groups.

This test procedure offered a possibility for observing the relative willingness of females to spend time in the chamber with the male (which could be termed a measure of "proceptivity" [3]). In addition, a rough index of female activity could be determined by counting the frequency of chamber crossings.

At the completion of behavioral testing the rats were deeply anesthetized and intracardially perfused with a solution of 0.9% NaCl and 10% Formalin. The brains were removed, weighed, photographed, embedded in celloidin, and cut at 26 μ m sections, which were mounted on glass slides and stained with cresyl violet.

RESULTS

Anatomical Results

The decortications were complete as they included virtually all of the neocortex as well as the cingulate cortex and variable amounts of the pyriform cortex below the rhinal fissure (Fig. 1). Analysis of brain weights showed the decortications reduced the total brain weight to 60% of control level as the mean weight of control and decorticate brains was 2.085 and 1.244 g, respectively (Mann Whitney $U=0$, $p<0.001$). The hippocampus sustained slight damage in many cases, but it was usually unilateral and restricted to the outer layers of CA1. The olfactory bulbs and other subcorti-

TABLE 2

BEHAVIORAL RESPONSES IN NEONATALLY DECORTICATED OR CONTROL FEMALE RATS AS A FUNCTION OF ADULT ESTRADIOL BENZOATE (EB, 1.0 $\mu\text{g/day}$) AND PROGESTERONE (P, 0.5 mg on day 7 of EB) TREATMENTS

Behavior*	Group		Decorticates (N=10)					Controls (N=11)					ANOVA	
	Test	Pretest	EB1	EB2	EB4	EB6	EB7+P	Pretest	EB1	EB2	EB4	EB6	EB7+P	F ratio, p^\dagger
Lordosis (f)		0	0	0.2	0.4	1.6	8.8	0	0	2.6	2.3	5.0	6.0	3.9, $p<0.005$
Lordosis Lat. (d)		600	600	513	511	466	181	600	600	394	316	175	191	3.2, $p<0.01$
Holding (f)		0.3	1.0	1.0	1.5	2.4	2.2	0	0	0.5	0.3	0.2	1.1	2.2, $p=0.06$ ns
Hop/Dart (f)		0	0	0	0	0	0	0	0	0.5	0.4	1.6	1.5	3.1, $p<0.05$
Kick back (f)		0	0.6	0	0.1	0	0	0.3	1.4	3.6	1.8	0.8	0	3.8, $p<0.005$
Vocalization (f)		0	0.6	0.1	0	0.1	0	0.3	0	0.5	0.2	1.0	0	1.3, $p=0.26$ ns
Grooming (d)		8	13	31	17	18	10	10	7	14	24	28	30	2.9, $p<0.02$
Sniffing (d)		141	175	214	233	235	217	188	208	162	180	158	166	4.4, $p<0.005$
Mount‡ (f)		4.7	5.8	5.9	7.5	8.6	13.2	4.6	5.0	8.0	6.8	6.7	7.4	2.1, $p=0.06$ ns
Number of 10-min tests§		1.5	1.5	1.7	1.4	1.2	1.0	1.4	1.5	1.3	1.0	1.1	1.1	0.7, $p=0.63$ ns

*Behaviors are reported for the first 10 min test as either mean frequency (f) or duration in sec (d).

†F ratios and p values for group by test interactions ($df=5/95$). ns=nonsignificant.

‡Mounting behavior is the only male response reported.

§Maximum of 3 tests. See Method section.

cal structures were not subject to direct damage in any cases, but there were severe retrograde changes in the basal ganglia and thalamus as described in detail elsewhere [6]. In comparison to the original work of Beach [1], the lesions in this study were larger and more complete, involving the cingulate cortex as well.

Behavioral Results

Lordosis quotients (LQ, Fig. 2, Top) and lordosis frequencies (Table 2) were lower than those recorded in control females from the second to sixth day of EB. Both groups responded to progesterone (P) treatment with increases in the LQ. The increase from the last EB-only test (Day 6) to the EB and P test (day 7) was particularly apparent in the decorticates, because 6 of the 10 decorticates showed their first lordosis response after EB plus P. In the first 10-min test after P, 7 of the 11 controls showed LQs of 100, while only 1 of the 10 decorticates had an LQ of 100. Failures to make postural adjustments appeared to account in part for the lower LQs of the decorticates. Holding still, in response to male attention but in the absence of a concave arching of the back, was more frequent in the decorticates than in control females (main effect for groups, $F(1,19)=4.9$, $p<0.05$, and increased across successive tests, $F(5,95)=5.5$, $p<0.001$).

Rejection behavior as indexed by kicking back. When normal females are unreceptive or partially receptive they may rebuff the male's advances by kicking at him [3]. As shown in the present experiment, kicking for control females was most common after females had been exposed to EB for only a few days, and almost disappeared when sexual receptivity was high (EB days 6 and 7, Fig. 2, Bottom; Table 2). Decorticates were much less likely to show this behavior. Both the frequency of kicking and the percentage of the females showing this response at least once during the tests (Fig. 2, Bottom) was generally lower in the decorticates than in control females.

Other sexual and social behaviors. Hopping and darting, sometimes termed "proceptive" behaviors in the rat [3]

were not observed in the decorticate females (Table 2). In the control females, this behavior increased in frequency with prolonged exposure to EB.

The decorticate females were at least as interested or more interested than controls in investigating the male; reflected by the time spent sniffing him (Table 2). Decorticates and controls also engaged in approximately the same amount of autogrooming, although the pattern of appearance of this behavior differed in the two groups. Normal females tend to self groom following copulation and this postcoital response was less apparent in the decorticates.

Experiment 2. Proceptivity as Measured by Willingness of the Female to Spend Time in Proximity to a Male

Both decorticate (100%) and control (86%) females tended to stay in a chamber with the male, rather than crossing a barrier to leave when they were originally placed with the male. This behavior was observed both before and after EB and P treatment. When females were placed in a chamber across a barrier from a male about one-half entered the male's chamber. The proportion crossing the barrier did not differ significantly between decorticates and controls and was not influenced by hormone treatment.

Beach [1] reported hyperactivity in some adult decorticates and felt that this probably interfered with normal copulatory patterns in his animals. Based on the frequency of barrier crossing and our other observations of these animals we have no indications that the present results were due to excessive activity on the part of our neonatally decorticated females.

DISCUSSION

It has been previously reported that the probability of female sexual behavior increases following acute adult suppression of cortical function [5]. Whether this represents a phenomenon related to neural "disinhibition" [2] or is due to secondary or stress-related hormonal changes, such as

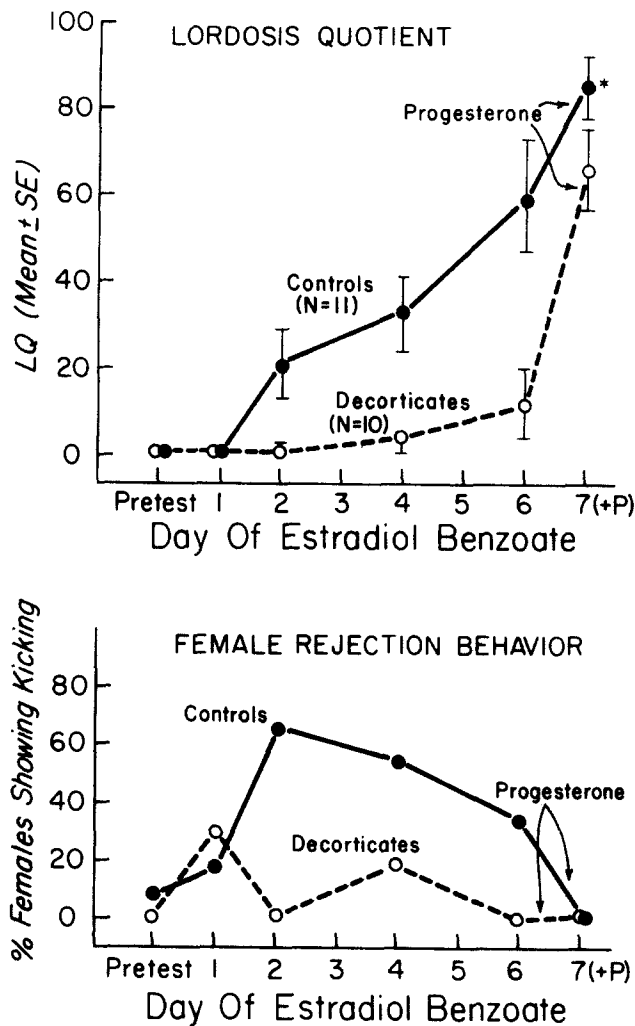


FIG. 2. Top: Lordosis quotients (LQ, mean \pm SE) are calculated for the first 10 min test by dividing lordosis frequency by mount frequency \times 100. *This point for the control group includes data for a second 10 min test for one female. This female was not mounted by the male in the first test. The LQ for her second test was 100. The mean \pm SE for this group calculated using her first test LQ of 0 is 86.6 ± 12.5 . Bottom: Percentage of females showing at least one kick-back toward the males during the first 10 min test.

progesterone release consequent from the procedure [8], remains open to question [4].

No enhancement of female sexual activity following neonatal cerebral cortex removal was observed in the present study, and in fact LQs were reduced, particularly in

females exposed to EB injections without the addition of exogenous P. This could represent a decline in the capacity to respond to estrogen [4]. The reliability of the group differences in LQ observed across several tests (Fig. 2, top) may support this interpretation. Alternatively the controls may have been more environmentally sensitive and thus produced more adrenal progesterone than the decorticates in response to the stress of our injection and test procedures [8]. It is also possible that the observed behavioral changes reflect effects on neurotransmitter systems or more generally might indicate some degree of motoric debilitation.

Although the decorticates were capable of showing LQs approaching those of controls after EB plus P treatments, they did not always show the well-timed lordosis posture characteristic of a normal female rat. In addition, hopping and darting were eliminated in the decorticates. These differences from normal animals tend to agree with the earlier observations of adult decorticates by Beach [1].

Beach [1] also reported that adult decorticates show exaggerated lordosis responses that were elicited by previously ineffective stimuli and which were held beyond the expected duration. After the described experiments were complete we attempted in several animals to elicit lordosis responses in EB plus P treated females by flank palpitation and vaginal probing (using a soft-tipped plunger from a 1 ml syringe), but were unsuccessful at producing a lordosis posture in either controls or decorticates using these procedures. The only measurable indications we have of increased responding on the part of our neonatally decorticate females comes from their willingness to hold a flat-backed immobile posture in response to male investigation and mount attempts. However, the sexual nature of this behavior is questionable. It is possible that the decorticates simply have attenuated sensory-motor feedback which reduces their awareness of or ability to respond to both appropriate and inappropriate male advances.

Investigations of the neural control of female sexual behavior have tended to emphasize the importance of subcortical structures [7]. The present findings and the earlier work by Beach [1] suggest that a number of components of female behavior, including those necessary for the expression and fine-tuning of lordosis, may be regulated by the integrity of the cerebral cortex. There are clear indications that neonatally decorticated females are less likely to respond with lordosis to estrogen-alone treatments. This could suggest a role for the cortex in estrogen sensitivity and/or adrenal production of progesterone (which in turn may facilitate lordosis).

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