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BRIEF COMMUNICATION

Maternal Behavior in Rats With Kainic Acid-Induced Lesions of the Hypothalamic Paraventricular Nucleus

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OLAZÁBAL, D. E. AND A. FERREIRA. *Maternal behavior in rats with kainic acid-induced lesions of the hypothalamic paraventricular nucleus.* PHYSIOL BEHAV **61**(5) 779–784, 1997.—The rat maternal behavior consists of different pup-caring activities, such as retrieving, licking, and crouching. Mothers also build a nest, consume more food, are more aggressive, and show less fear behavior than in other stages of the reproductive cycle. It has been reported that oxytocin (OT) and the milk-ejection pathway could be involved in modulating maternal behavior. The paraventricular nucleus (PVN) of the hypothalamus forms part of the milk-ejection pathway and is also the major source of OT release in the brain. Kainic acid (KA) lesions (0.5 μg/0.5 μl) in the PVN performed on day 2 after parturition, affected retrieving behavior in the mother rat and produced a decrease in pups' weight gain. Because KA destroys only cell bodies, the changes that we observed could be due to the local destruction of neurons, rather than that of the fibers of passage. No alteration was observed in other components of the pup-caring activities, food intake, aggressive behavior, and fear in the lesioned mothers. © 1997 Elsevier Science Inc.

Hypothalamus Kainic acid Maternal behavior Nervous system Neurotoxin PVN Rat

THE postparturient rat shows a set of behavioral patterns related to the pups' care, such as retrieving, cleaning, licking, and nursing of the pup (26). In addition, mother rats build nests (26), eat more food than during other periods of their lives (20), are more aggressive towards potentially hostile conspecifics (3) and react with less fear in response to sudden environmental changes (11).

It has been suggested that the milk-ejection pathways are involved in modulating some components of maternal behavior in rats (4,6,8,29). Oytocin (OT) is released in response to the suckling stimulus in several regions of the brain (13,15,16), and this neuropeptide would modulate maternal behavior (5,23,24,30). Immunocytochemical and electrophysiological studies have shown that the paraventricular nucleus (PVN) is the principal source of OT in the central nervous system (21). This nucleus projects to many limbic and hypothalamic areas in addition to its well-known pathway to the neurohypophysis and median eminence (15,16,21).

Insel et al. (12) found that electrolytic lesions of the PVN, performed on day 15 of gestation, disrupted the initiation of maternal behavior. However, PVN lesions performed on day 4 postpartum did not affect maternal behavior, although some components of this behavior did show nonsignificant changes (an increase in the retrieval latency and less pup weight gain). Accordingly, the investigators concluded that PVN and OT play a role at the onset, although not in the maintenance of this behavior in primiparous rats. These results agree with those obtained by Numan and Corodimas (18), who performed radiofrequency lesions of the PVN on day 4 postpartum and found no changes in maternal behavior, other than the interruption of lactation, loss in the pup's weight, and a decrease in nest-building behavior.

During the first days after parturition, there is a period in which the hormonal factors are more important than the exteroceptive stimuli of the pups in the control of maternal behavior (26). Therefore, we speculated that KA lesions of the PVN per-

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formed on day 2 (i.e., closer to delivery), would affect the mothers' behavior (pup-caring, food intake, aggression, and fear).

METHODS

Subjects

The present studies were approved by the Ethical Committee of Animal Care and Use of the Faculty of Veterinary. The animals employed in the experiment were 36 nulliparous female rats of the Wistar strain, weighing between 180 and 250 g, with ages of between 80 and 100 days. Rats were housed in groups of 2–4 in cages measuring 53 × 36 × 25 cm, with transparent Plexiglas walls, and with ad lib access to food and water. The food consisted of a balanced nutritional feed in the form of pellets (Molinos, San Jose, S.A.) mixed according to a formula approved by the Dirección de Laboratorios de Análisis del Ministerio de Agricultura y Pesca. The floor of the cage was covered with wood shavings. All females were maintained under a 14:10 h reversed dark:light cycle and a relatively constant environmental temperature of 21°C.

Behavioral estrus in these females was determined by placing them with a sexually active male and observing if receptive behavior (i.e., lordosis) was present. The receptive female was left with the male for 1 night and separated on the following day, which was considered as Day 1 of pregnancy.

One week before delivery, the rats were housed in individual cages. A water bottle and a feeder were mounted on the roof of the cage. Paper towels were provided as nesting material. Litter size was adjusted to 7 pups within 2 days after parturition. The parturition day was considered as Day 0. The surgical procedure (see below) was performed 48 h after parturition. All females and pups were weighed daily from the day of the operation until the end of the experimental period.

During the first 2 days after surgery, pups of additional mothers (donor mothers, not included in the experiment) were interchanged daily with the pups of the lesioned rats to prevent the pups weakness by possible alterations in nutrition. After this, the lesioned females were left with the last placed pups.

Behavioral Testing

Four behavioral tests were performed. In the first test, maternal behavior was examined. On postpartum Day 4, 5 h after darkness, the pups were removed. Immediately, 3 pups were placed in the cage diagonally opposite the nest site. During 5 min, the following behavioral responses were recorded: retrieving, nest building, crouching position, and licking. These parameters were defined as follows:

Retrieving: number of mothers that picked pups up in their mouths, transported 1, 2, or the 3 pups and placed them in the nest;
Crouching position: number of times the mothers hovered over the pups, remaining immobile except for occasional postural adjustments. Every 10 s, crouching was recorded if the female remained in this position;
Licking: number of times the female licked the pups. Every 5 s, a new score was recorded if the mothers continued this activity;
Nest building: nesting was considered when, before testing, pups were found inside a gathering of material (generally about 6 cm high).

In the second test, aggressive behavior was examined at 1700 h of Day 4 postpartum. A male rat (weighing 200–300 g) was placed in the female's home cage and, for 5 min, the following behavioral responses were recorded: attack and bite, lateral posture, boxing. The latency to the first aggressive act performed by the female was registered. The number of times the intruder adopted the upright subordinate posture was also recorded. Each male served only once to stimulate the mother rat's reaction. The behaviors recorded are defined as follows:

Attack and Bite: sudden approach of the female with the mouth open toward the male that generally leads to a fight that concludes with the typical male submission posture;
Lateral Posture: the female places herself with the lateral part of her body toward the male. Sometimes this behavior includes only contact but, generally, the female pushes the male in this position;
Boxing: the female stands on her hind legs, knocking with her fore legs on the male's face; the male frequently adopts the same posture;
Submissive Posture of the Intruder: the intruder remains immobile, sitting on its hind legs, with the fore legs lifted and showing a pronounced dorsal arch. On some occasions the animals can be observed in a supine position raising their 4 limbs in a protective manner.

A freezing test was used to examine fear behavior. Starting at 1900 h on Day 5 postpartum, the rats' reactions to a sudden auditory stimulus in a new environment were evaluated (11). Each animal was placed, along with 3 pups, in a circular Plexiglas arena (39 cm in diameter) and the floor was covered with paper. The cage, similar to the one designed by Hard & Hansen (11), had a glass window through which observations were made. The doorbell (100 dB) and the light bulb (25 W) that lit the area were placed on the roof of the cage. After a 5-min adaptation period to the new environment, the doorbell was turned on for 6 s. The duration of the freezing behavior was defined as the time elapsing from the cessation of the signal until the mother's first distinct head or leg movement. Eye blinks and respiratory or vibrissae movements were excluded. The number of defecations were recorded and the floor covering was changed before the next rat was tested.

The last test, carried out to determine the food intake, was recorded for the 2 h after a 20-h period of fasting. On Day 4 postpartum, at 1900 h, the rats were deprived of food: all pellets in the food hopper were removed and the wood shavings changed. The next day, at 1500 h, they were offered a preweighed amount of their usual food and allowed to eat for 2 h. Afterward, the remaining food was collected and weighed.

Surgical Lesion

Rats were anesthetized with pentobarbital IP (Mebumal™, 9 mg/200 g body weight) and placed in a Kopf stereotaxic apparatus for bilateral kainic acid (KA) lesions and sham surgery. KA (Sigma, St. Louis, USA), a glutamate agonist and a powerful excitotoxin that provokes neuronal destruction, was injected with a 1-μl Hamilton syringe (2). The stereotaxic coordinates relative to Bregma were 1.5 mm posterior, 0.5 mm lateral, and 7.8 mm below the dura (22), with the incisor bar positioned at −2 mm.

Lesioned animals received 0.5 μg/0.5 μl of KA in phosphate buffer, and the speed of infusion was 0.1 μl/min. Sham-operated animals were injected with 0.5 μl of phosphate buffer (0.1 M, ph 7.4). The needle (22 gauge) was kept in place for an additional 4 min after the completion of the infusion.

A total of 26 primigravid female animals were subjected to surgery on day 2 postpartum: 11 rats were PVN-lesioned and 15 were sham-operated. A Control Group of nonoperated animals was used (10 individuals) to determine if the operation interfered with maternal behavior.

Histology

Two weeks after surgery, all rats were deeply anesthetized with thiopental and perfused intracardially with 4% paraformaldehyde-1.25% glutaraldehyde in 0.1 M phosphate buffer. Brains were removed and stored in the same medium. Brains were embedded in paraffin and sections were cut at 8 mm using a microtome. All sections around PVN were saved, mounted on slides, and stained with thionine. By means of a microprojector, the extent of each lesion was drawn on appropriate copies of frontal plane diagrams taken from the Paxinos and Watson atlas of the rat brain (22). All histological material was examined (without reference to behavioral scores) for determination of the size and location of the lesion. Data from animals with lesions outside the PVN or asymmetrical lesions were not included in the analysis.

Data Analysis

The results are expressed as means ± SE. Behavioral data were statistically evaluated by the Kruskal–Wallis analysis of variance followed by the Mann–Whitney *U*-test. Frequencies were analyzed by the X^2 and Fisher tests (28).

RESULTS

In this study, the lesion was identified by means of gliotic reaction, which shows the phagocytic activity upon the degen-

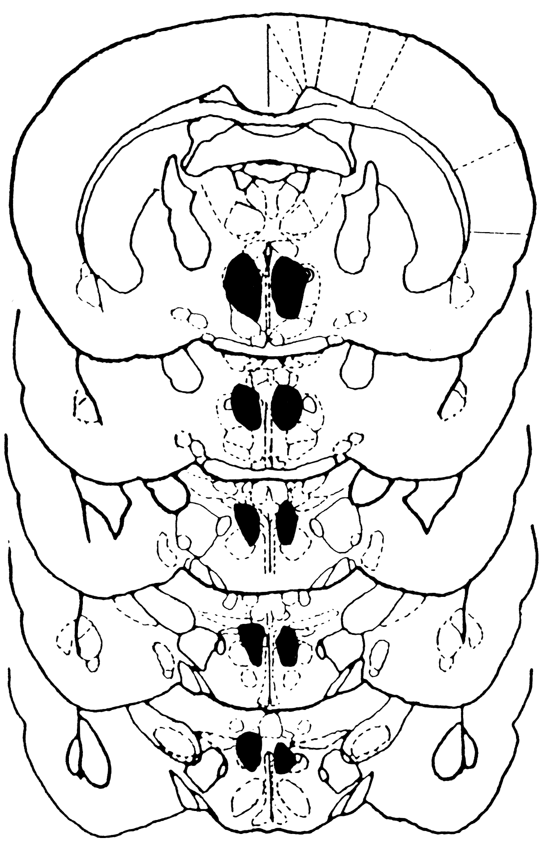

FIG. 1. Reconstructed diagram of representative thionin-stained sections of the most extensive damage sustained by PVN-LES Group.

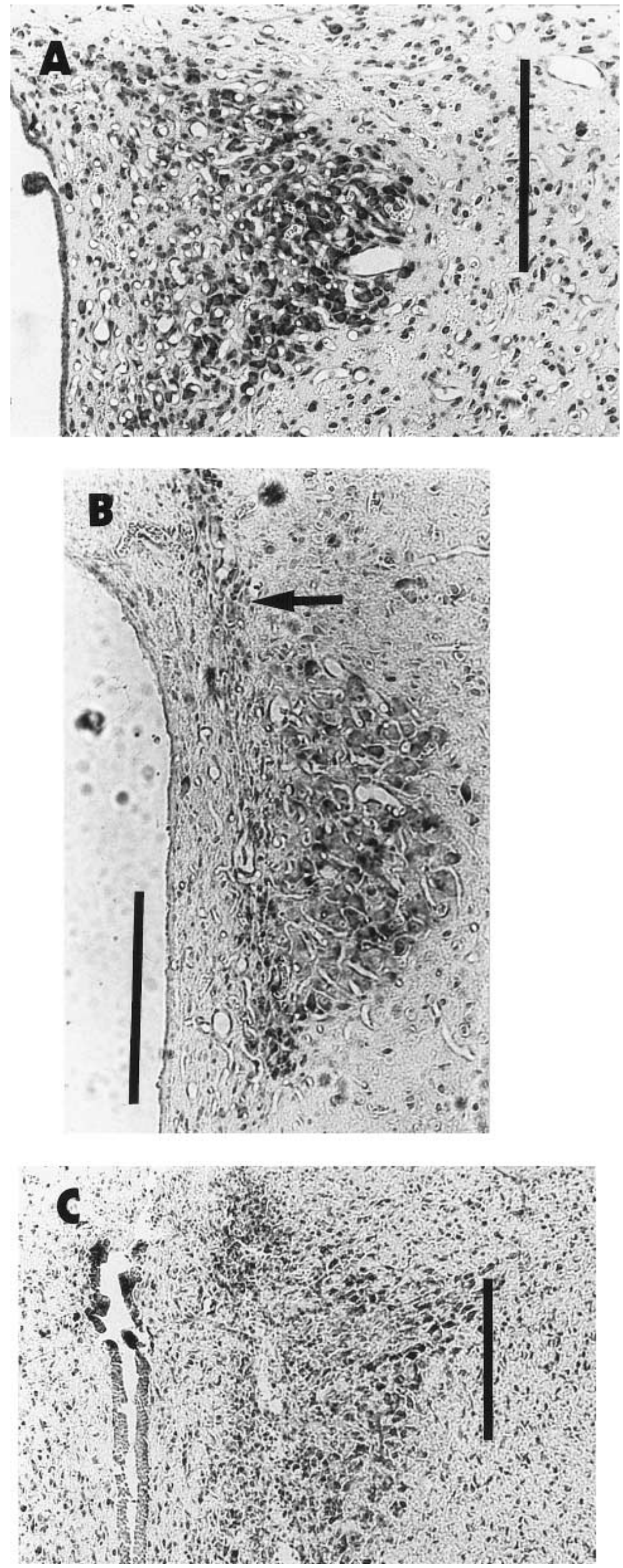

FIG. 2. Photomicrographs showing (A) the magnocellular region in the Control Group; (B) the magnocellular region after kainic acid infusion in the PVN, and (C) cell body degeneration and glial proliferation in the part anterior of the PVN after kainic acid infusion. See (B) traces of the injection needle (arrow). The vertical scale bars represent 0.2 mm in (A, B) and 0.3 mm in (C). Thionin stain.

erating neurons. The lesion damage was confined between the levels of −1,30 and −2,30 to bregma (see Fig. 1). The results of the lesions showed an incomplete loss of neurons in the PVN. The histological analysis show little vulnerability to the KA actions in the magnocellular region (see Fig. 2A, B, C). The lesions affected the parvicellular subdivisions of the PVN with minimal damage to stria terminalis and more caudal nucleus (dorsomedial nucleus and part posterior of the anterior hypothalamus). The medial preoptic area and ventromedial hypothalamic nucleus were not affected by the lesion. There was also an inevitable cell loss caused by the needles in the region of zona incerta and ventromedial thalamic nucleus, but it did not extend beyond that.

The behavioral tests showed a significant reduction in the number of females that displayed retrieving behavior on Day 4 postpartum in the Lesioned Group compared to the other 2 Groups ($p < 0.05$). Only 3 of the lesioned mothers retrieved all the pups during the test (3 of 11). In the remaining groups, all the animals retrieved the 3 pups (see Table 1 and Fig. 3). The number of females that built nests was less in the Lesioned Group in comparison with the Sham-Operated and the Control Groups, although the differences were not significant. In the test carried out on Day 4, no changes were observed in the number of crouching postures and licking (Table 1). Visual inspection of the pups' stomachs showed that 100% of the lesioned mothers' litters had not received food. No motor deficiencies were observed in the lesioned mothers, and all individuals were able to carry pellets similar to their pups in size and weight.

The pups' weight decreased significantly in the Lesioned Group ($p < 0.05$) in comparison with the other groups during the 4 days following surgery. Figure 4 shows the percentage of overweight changes in relation to the day before; these observations were made during the period between the day of surgery (Day 2) and the 4th day after the operation (Day 6).

No differences among the groups were observed in maternal body weight gain except on the day after surgery. In this case, significant loss of body weight in the operated groups was observed. The body weight percentages with respect to the day of surgery were: PVN-lesion 98.1 ± 1.3%; Sham 99.4 ± 1.9%; Control 101.2 ± 0.6% ($p < 0.05$). During the following week, mothers increased their body weight by 2.4 ± 1.1% Control, 1.7 ± 1.2% Sham, and 2.2 ± 1.1% PVN-lesion (mean ± SEM). Food intake was not modified by the PVN-lesion (PVN-lesion: 8.9 ± 0.9 g; Sham: 10.8 ± 0.8 g; Control: 10.2 ± 1.0 g, mean ± SEM).

Maternal aggression was not modified by the lesions in the PVN when compared with the Sham-Operated Group. The frequency of aggressive acts remained unchanged among the groups and the score of total aggressive reactions during a 5-min test was 3.8 ± 1.6 (PVN-lesion), 3.0 ± 0.8 (Sham) and 3.7 ± 1.0 (Control), mean ± SEM. Of these aggressive acts, an average

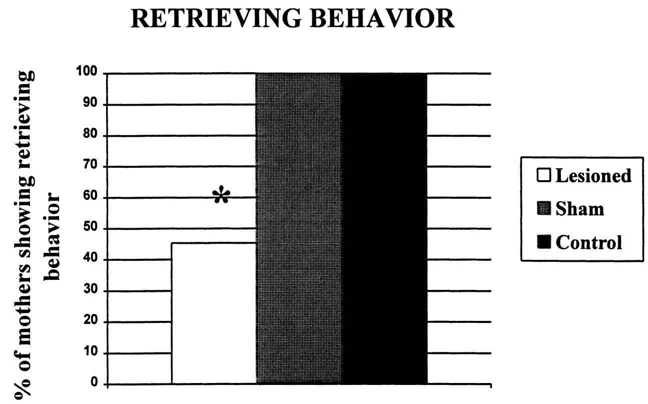

FIG 3. Percentage of mothers that showed retrieving behavior during the test (*$p < 0.01$).

of 1.9 ± 0.9 (PVN-lesion), 2.2 ± 0.6 (Sham) and 2.8 ± 0.9 (Control) were attacks and bites. No other recorded behavioral patterns were affected (data not shown).

There were no significant differences between groups in freezing time (PVN-lesion: 35.0 ± 17.0 s; Sham: 19.0 ± 7.0 s; Control: 17.0 ± 5.0 s, mean ± SEM). The Treated and Control Groups did not differ in number of defecations (PVN-Lesion: 4.6 ± 1.1; Sham: 7.4 ± 1.5; Control: 4.8 ± 0.9, mean ± SEM). Exploratory activities remained unchanged by the PVN kainic lesion. PVN-Lesioned mothers performed 16.8 ± 2.5 rearing and 2.6 ± 0.5 grooming before the auditory stimuli, Sham mothers performed 18.7 ± 2.7, 1.9 ± 0.7, and Controls 15.1 ± 3.8, 2.6 ± 0.6, respectively (mean ± SEM). No other recorded exploratory parameters were affected (data not shown).

DISCUSSION

The KA lesion of the PVN affected the retrieving behavior (the main component of pup-caring activities) (26) and decreased the pups' weight. Due to the neurotoxic properties of the KA, these effects were probably produced by the local destruction of neurons, rather than that of the fibers of passage.

The significant decrease in the retrieving behavior observed in the lesioned rats in this study was not observed by other authors when the lesions were performed on Day 4 postpartum (12,18). These differences could be due to the variation of days on which the lesions were performed (Day 2 in the present study and Day 4 postpartum in other studies), to different types of lesions performed (chemical, electrolytic, and radiofrequency), or to the cell groups affected by the lesions. The reduction of the pups' weight gain observed in the postpartum Lesioned Group accords with that reported

TABLE 1

MATERNAL BEHAVIOR OF LESIONED (PVN-LES), SHAM, AND CONTROL RATS

Group	*n*	Day	Crouching posture	Nest building	Licking	Number of mothers retrieving: 0 pups	1 pup	2 pups	3 pups
PVN-LES	11	4	2.4 ± 1.4	7 of 11	3.8 ± 1.8	6*	2	0	3*
Sham	15	4	3.6 ± 0.7	13 of 15	3.8 ± 0.8	0	0	0	15
Control	10	4	4.4 ± 1.1	10 of 10	4.1 ± 0.6	0	0	0	10

Number of Crouching postures and Licking are means ± SE. Nest-building scores are expressed as frequencies of females that built nests. Statistical analysis was obtained by means of the Kruskal–Wallis analysis of variance. Retrieving is the number of females that retrieved; statistical analysis was obtained by means of Fisher (*$p < .01$).

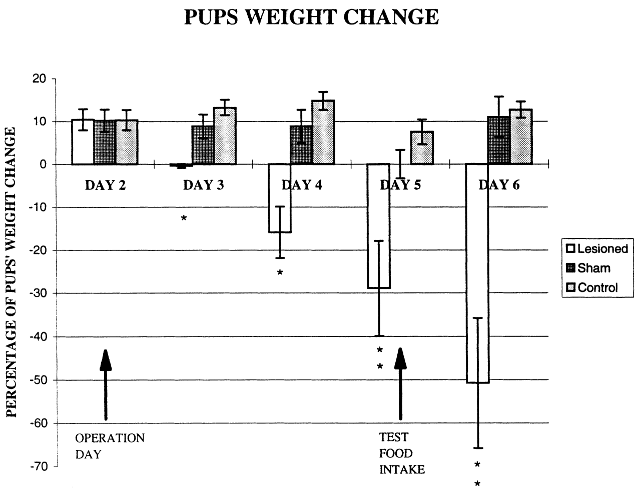

FIG 4. Daily percentage of pup weight gain (* $p < 0.05$; ** $p < 0.01$).

by Numan et al. (18) and is probably due to the interruption of the milk-ejection reflex. This interpretation is supported by the fact that the lesioned mothers' pups had no milk in their stomachs when visual inspection was performed.

Although PVN lesions in this study did not affect aggressive behavior, other authors (4,8) have observed decreased aggression when lesions were performed after parturition (Days 7 and 9) in the peripeduncularis nuclei (NPP, part of the milk-ejection pathway). However, the same lesions performed during the first postpartum days did not affect aggressive behavior (4).

The freezing time showed a tendency to increase (although nonsignificant) in the lesioned mothers. These results are supported by those observed in the open-field test by Insel et al. (12) in mother rats lesioned before parturition.

In accordance with several reports (12,18), we did not find any changes in food consumption or mothers' weights. Other studies performed on nonmaternal rats, reported that food intake increased after lesions in the PVN (1,14). This apparent contradiction may be due to the fact that the period in which the weight was recorded (1 week) may have been too short to detect differences. Indeed, Aravich and Sclafani (1) reported that the weight gain of females with PVN lesions was not evident until after the second postoperative week.

These results could be associated with a reduction of neural OT activity, considering that PVN is the major source of OT. There is evidence of an OT release in the PVN and in other areas of the brain (limbic and hypothalamic) in association with the suckling stimulus (13,16,25). Thus, it appears as an attractive proposal that, due to this stimulation, OT could be released (from PVN) to different brain areas regulating, in a selective way, some patterns of pup-caring activities. In addition, several studies have related OT to maternal behavior and nourishing activities (23–25,30).

Nevertheless, such behavioral changes could be mediated by the remaining neurotransmitters in the PVN, such as dopamine (DA). Particularly interesting are the recent reports ascribing a role in motivation (27) and pup-caring activities (7,9,10) to the DA system. In addition, PVN would be the more important source of oxytocinergic axons in the VTA region (19,24) and the reduction of DA in the ventral tegmental area (VTA) by means of 6-OHDA infusion, increases the pup's retrieval latency (9). An interaction between DA and OT during the postpartum period has recently been suggested (25). According to these results, the delay observed in the retrieving behavior could reflect changes in the motivation and sensitivity of the mothers' response to the pup's stimuli (27).

The results obtained could also be due to changes in the different neural circuits in which the PVN participates, for example, the MPOA, which projects to the PVN and is one of the most important areas of brain related to the regulation of maternal behavior (17,18). As mentioned above, the postpartum PVN lesions significantly affected only the pup-retrieval behavior, leaving the other behavioral patterns unchanged. Consequently, it seems plausible that other neural areas would have a more important role in the modulation of the other components of maternal behavior during this period. However, the possibility that the neurons of the PVN that were not affected by the KA participate in the control of these behavioral patterns should not be eliminated. New studies may contribute to the understanding of neurotransmitter interactions in the different areas of the brain that modulate maternal behavior in the rat.

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REFERENCES

1. Aravich, P. F.; Sclafani, A. Paraventricular hypothalamic lesions and medial hypothalamic knife cuts produce similar hyperphagia syndromes. Behav. Neurosci. 97:839–843; 1983.
2. Coyle, J. T.; Schwarcz, R. The use of excitatory amino acids as selective neurotoxins. In: A. Björklund, T. Hökfelt, eds. Handbook of chemical neuroanatomy: Methods in chemical neuroanatomy. Vol. 1. 1983:508–524.
3. Erskine, M. S.; Barfield, R. J.; Goldman, B. D. Intraspecific fighting during late pregnancy and lactation in rats and effects of litter removal. Behav. Biol. 23:206–218; 1978.
4. Factor, E. M.; Mayer, A. D.; Rosenblatt, J. S. Peripeduncular nucleus lesions in the rat. 1. Effects on maternal aggression, lactation, and maternal behavior during prepartum and postpartum periods. Behav. Neurosci. 107:166–185; 1993.
5. Fahrbach, S. E.; Morrell, J. I.; Pfaff, D. W. Possible role for endogenous oxytocin in estrogen-facilited maternal behavior in rats. Neuroendocrinology 40:526–532; 1985.
6. Gandelman, R.; Simon, N. G. Postpartum fighting in the rat: Nipple development and the presence of young. Behav. Neural Biol. 28:350–360; 1980.
7. Giordano, A. L.; Johnson, A. E.; Rosenblatt, J. S. Haloperidol-induced disruption of retrieval behavior and reversal with apomorphine in lactating rats. Physiol. Behav. 48:211–214; 1990.
8. Hansen, S.; Ferreira, A. Food intake, aggression and fear behavior in mother rats: Control by neural systems concerned with milk ejection and maternal behavior. Behav. Neurosci. 100:67–70; 1986.
9. Hansen, S.; Harthon, Ch.; Wallin, E.; Lofberg, L.; Svensson, K. Mesotelencephalic dopamine system and reproductive behavior in the female rat: Effects of ventral tegmental 6-hydroxydopamine lesions on maternal and sexual responsiveness. Behav. Neurosci. 105:588–598; 1991.
10. Hansen, S.; Harthon, C.; Wallin, E.; Lofberg, L; Svensson, K. The effects of 6-OHDA-induced dopamine depletions in the ventral or dorsal striatum on maternal and sexual behavior in the female rat. Pharmacol. Biochem. Behav. 39:71–77; 1991.

11. Hard, E. G.; Hansen, S. Reduced fearfulnes in the lactating rat. Physiol. Behav. 35:641–643; 1985.
12. Insel, T. R.; Harbaugh, C. R. Lesions of the hypothalamic paraventricular nucleus disrupt the initiation of maternal behavior. Physiol. Behav. 85:1033–1041; 1989.
13. Kendrick, K. M.; Keverne, E. B.; Chapman, C.; Baldwin, B. A. Intracranial dialysis measurement of oxytocin, monoamine and uric acid release from the olfactory bulb and substantia nigra of sheep during parturition, suckling, separation from lambs and eating. Brain Res. 439:1–10; 1988.
14. Leibowitz, S. F.; Hammer, N. F.; Chang, K. Hypothalamic paraventricular nucleus lesions produce overeating and obesity in the rat. Physiol. Behav. 27:1031–1041; 1981.
15. Neumann, I.; Russell, J. A.; Landgraf, R. Oxytocin and vasopressin release within the supraoptic and paraventricular nuclei of pregnant, parturient and lactating rats — A microdialysis study. Neuroscience 53:65–75; 1993.
16. Neumann, I.; Landgraf, R. Septal and hippocampal release of oxytocin, but not vasopressin, in the conscious lactating rat during suckling. J. Neuroendocr. 1:305–308; 1989.
17. Numan, M. Medial preoptic area and maternal behavior in the female rat. J. Comp. Physiol. Psychol. 87:746–759; 1974.
18. Numan, M.; Corodimas, K. P. The effects of paraventricular hypothalamic lesions on maternal behavior in rats. Physiol. Behav. 35:417–425; 1985.
19. Numan, M. Neural control of maternal behavior. In: Knobil, B.; Neill, J., eds. Maternal behavior. The physiology of reproduction. New York: Raven Press; 1988:1608–1627.
20. Ota, K.; Yokoyama, A. Body weight and food consumption of lactating rats: Effects of ovariectomy and of arrest and resumption of suckling. J. Endocr. 38:251–261; 1967.
21. Page, R. B. The anatomy of the hypothalamo-hipophyseal complex. In: Knobil, E.; Neill, J., et al., eds. The physiology of reproduction. New York: Raven Press; 1988:1161–1234.
22. Paxinos, G.; Watson, C. The rat brain in stereotaxic coordinates. Orlando, FL: Academic; 1986.
23. Pedersen, C. A.; Caldwell, J. D.; Fort, S. A.; Prange, A. J., Jr. Oxytocin antiserum delays onset of ovarian esteroid-induced maternal behavior. Neuropeptides. 6:175–182; 1985.
24. Pedersen, C. A.; Caldwell, J. D.; Walker, C.; Ayers, G.; Mason, G. A. Oxytocin activates the postpartum onset of rat maternal behavior in the ventral tegmental and medial preoptic areas. Behav. Neurosci. 108:1163–1171; 1994.
25. Richard, P.; Moos, F.; Freund-Mercier, M-J. Central effects of oxytocin. Physiol. Rev. 71:331–370; 1991.
26. Rosenblatt, J. S. Prepartum and postpartum regulation of maternal behaviour in the rat. Parent-infant interaction Ciba Foundation Symposium 33 (New Series). Amsterdam: Associated Scientific Publishers, Elsevier; 1975.
27. Salamone, J. D. Dopaminergic involvement in activational aspects of motivation: Effects of haloperidol on schedule-induced activity, feeding, and foraging in rats. Psychobiology 16:196–206; 1988.
28. Siegel, S. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill; 1956.
29. Stern, J. M.; Dix, L.; Bellomo, C.; Thramann, C. Ventral trunk somatosensory determinants of nursing behavior in Norway rats: 2. Role of nipple and surrounding sensations. Psychobiology 20:71–80; 1992.
30. van Leengoed, E.; Kerber, E.; Swanson, H. H. Inhibition of postpartum maternal behavior in the rat by injecting an oxytocin antagonist into the cerebral ventricles. J. Endocr. 112:275–282; 1987.