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Induction of Maternal Behavior by Mouse Neonates: Influence of Dam Parity and Prenatal Oxazepam Exposure

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LAVIOLA, G., S. PETRUZZI, J. RANKIN AND E. ALLEVA. *Induction of maternal behavior by mouse neonates: Influence of dam parity and prenatal oxazepam exposure.* PHARMACOL BIOCHEM BEHAV **49**(4) 871-876, 1994. – The aim of the present report was to investigate the influence of pup stimulus properties and female parity on mouse maternal behavior. Outbred CD-1 mouse pups, prenatally exposed to either the vehicle (VEH) or oxazepam (OX, 15 mg/kg twice/day on pregnancy days 12-16) and fostered to untreated dams at birth, were offered as a stimulus on postnatal days 4, 6, and 8 to four groups of females that differed in maternal experience: virgin, experienced virgin females, primiparae, and biparae. Maternal behavior was observed during a 15-min session each day. Virgin females were less involved in crouching behavior than primiparae. Pups, age, and prenatal oxazepam showed interactive effects on maternal care, particularly by increasing licking and nest-building activities and decreasing still-out behavior. Moreover, dams receiving younger pups showed high levels of both locomotor activity and rearing. The present findings point to the need for a better understanding of mother-pup interactions in studies aimed at characterizing drug and toxicant effects on both animal and human development.

Maternal induction behavior Prenatal pup treatment Oxazepam Mouse

IN studies aimed at assessing the influence of prenatal exposure to drugs and toxicants, alterations mediated by direct effects on the fetus are necessarily confounded with prenatal and postnatal maternal effects. For these reasons, the usual procedure is to eliminate postnatal maternal effects by assigning at birth both treated and control litters to untreated, unhandled dams (1,22). In fact, it has been reported in mice that the fostering condition affects the dyadic mother-pup interaction (22).

Rodent maternal behavior depends upon dam experience and sensory information provided by the pups (19,31,36, 38,39). Concerning the first aspect, it has been reported that maternal responses in mice occur in a larger number of experienced virgin female than of naive control animals (25,26,28). The former are also more responsive to ineffective stimuli such as dead pups and spend more time in maternal activities during standard tests (29). Moreover, Cohen-Salmon and colleagues (11) found in inbred mice that multiparous females display a higher level of retrieval performance than primiparous ones. A further study also showed an improvement in retrieval behavior between first and second parturition, most probably due to both the internal state of the dams and to the previous experiences of cohabitation with other parturient females (10). In rats, long-term retrieval deficits and decreased litter weights were found, in primiparous but not multiparous females, after prepartum bulbectomy (5,35).

With respect to stimuli arising from the pups, it has been reported that olfactory signals released by the offspring play a key role in infant recognition for laboratory mice (8,15) and increase the quantity of specific items of maternal care such as licking and nest building (27). Moreover, vocalizations emitted by pups when in distress elicit retrieval behavior (12), and it is known that changes in pup stimuli related to litter gender composition can markedly affect the whole spectrum of maternal care (2,24).

Changes in the stimulus properties of pup cues can be pro-

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duced by prenatal treatment with drugs or toxicants (7). In a study using prenatal benzodiazepine (BDZ) exposure, Alleva and colleagues (3) found a dose-dependent retardation of postnatal body growth and of several developmental parameters in mice. These changes were accounted for by a direct effect of BDZ prenatal treatment on the pup CNS as confirmed by BDZ binding evaluation on 24-h-old pups (3). Moreover, Kurishingal and colleagues (21) reported that mouse pups prenatally exposed to chlordiazepoxide exhibit an overall increase in ultrasonic calling than corresponding prenatal controls. In light of these and other findings (22), it has been hypothesized that mildly affected pups might constitute a stronger stimulus for the elicitation of maternal responses (6). This possibility is considered in the present study, which aims at assessing the changes in the stimulus properties of BDZ-treated pups when offered to four types of females differing in maternal experience (virgin, experienced virgin females, primiparae and biparae).

METHOD

Animals Breeding and Fostering

Mice of an outbred albino Swiss-derived strain (CD-1) weighing 25–27 g were purchased from a commercial breeder (Charles River Italia, I-22050 Calco, Italy). Upon arrival at the laboratory the animals were housed in an air-conditioned room (temperature 21 ± 1°C, relative humidity 60 ± 10%) with a 12 : 12 reversed cycle (with lights on from 2130 to 0930 h). Males and nulliparous females were housed separately in groups of 8–10 in 42 × 27 × 15 cm Plexiglas boxes with sawdust as bedding and a metal top. Pellet food (enriched standard diet purchased from Piccioni, I-2500 Brescia, Italy) and water were continuously available. After 2–3 weeks breeding, pairs were formed and housed in 33 × 13 × 14 cm boxes. The females were inspected twice daily at 0900 and 2000 h for the presence of a vaginal plug (pregnancy day 0) and for delivery (postnatal day 1). The stud was removed 10 days after the finding of the plug. This procedure was adopted because in the mouse species the odor cues provided by the male are very important in preventing the block of female pregnancy, particularly during the first period after mating. An additional group of same-age females derived from a pool available in the laboratory was also used. It consisted of 10 virgin (nulliparous) females, 10 experienced virgin females that have been caged with pregnant females 48 h before these females gave birth and separated after 24 h following parturition (10), 10 primiparae that had reared only their first litter until the weaning period, and 10 biparae that had reared two subsequent litters until the weaning period. At the time of testing, they were not pregnant or in the lactating phase and had not received any treatment. The four groups were used as experimental subjects for tests on maternal behavior indicated in the following sections.

Prenatal Treatment

Oxazepam (purchased from Agrar, I-00195 Roma) was suspended in a 0.5% solution of sodium carboxymethylcellulose (Fluka AG, Switzerland) in water. Females were treated by orogastric infusion twice daily (between 0900 and 1000 h and between 1900 and 2000 h) on pregnancy days 12–16, with either oxazepam (OX, 15 mg/kg in each treatment in a volume of 0.01 ml per g body weight) or the vehicle (VEH). This treatment schedule has been used in several previous studies, and was originally adopted on the basis of a) pharmacodynamic considerations, b) preliminary behavioral assessments, and c) developmental data concerning both somatic and neurobehavioral end points from an initial multidose experiment that covered the 5–50 mg/kg range (3,6). All litters were reduced at birth to six pups (three males and three females) and fostered to unhandled dams that had given birth to healthy litters within the same 24 h.

Procedure of Maternal Behavior Induction

Tests were carried out in a laboratory room isolated from the animal colony and maintained under the same light/dark cycle and humidity and temperature conditions. Individual females (with the same number of virgin, primiparae, and biparae) were exposed to one VEH or OX (male or female) pup on postnatal days 4, 6, and 8. The order of pup presentation was alternated, with each individual female receiving two pups (VEH or OX) on each test day. All observation sessions of 15 min each were made under dim red light. At the beginning of the test, the female and the single pup subjects were placed at opposite ends of a test chamber (33 × 13 × 14 cm) and strips of paper towels were placed over the floor of the chamber. The session was video taped using a Sony VO-5360 apparatus equipped with CH-1400CE videocameras for red light. Recordings were scored by an observer blind to the pup treatment and to the assignment of females to different groups; general procedures and measures were as described elsewhere (2,8,23). The data were recorded using a keyboard event recorder system feeding to a computer for analysis (13,14), which enabled a record of the order of interactions, the duration, and frequency of behavioral events, and the sequence of events relative to the start of observation.

Behavioral Categories

The behaviors listed and defined below were monitored (pup-directed activities).

Retrieving. The female picks up the pup in her mouth and carries it to the nest.

Crouching. The female arches her back and assumes the nursing posture over the pup.

Licking. The female licks any part of the pup's body, usually concentrating on the ano-genital region.

Nest building. The female transports material towards the nest or manipulates the material already incorporated into the nest (e.g., pushing and pulling it).

The following were nonpup-directed behaviors.

Activity. The female moves up and down the test chamber but does not carry a pup or nesting material.

Rearing. The female rears on hind limbs to sniff the air and the cage.

Grooming. The female wipes, licks, combs, or scratches any part of its own body.

Still out. The female does not move at all (nor about the cage, neither transporting nesting material, or doing other pup-directed activities).

Design and Statistical Analysis

Factorial analyses of variance (ANOVAs 3 × 3 × 2 × 2) were performed for frequencies and durations of each behavioral response. These analyses considered the female's parity (virgin females, experienced virgin females, primiparae, or biparae) as the between-litter factor, the pup's prenatal treatment (VEH vs. OX) and gender as both within-litter and between-subject factors, and the pup's age as a repeated mea-

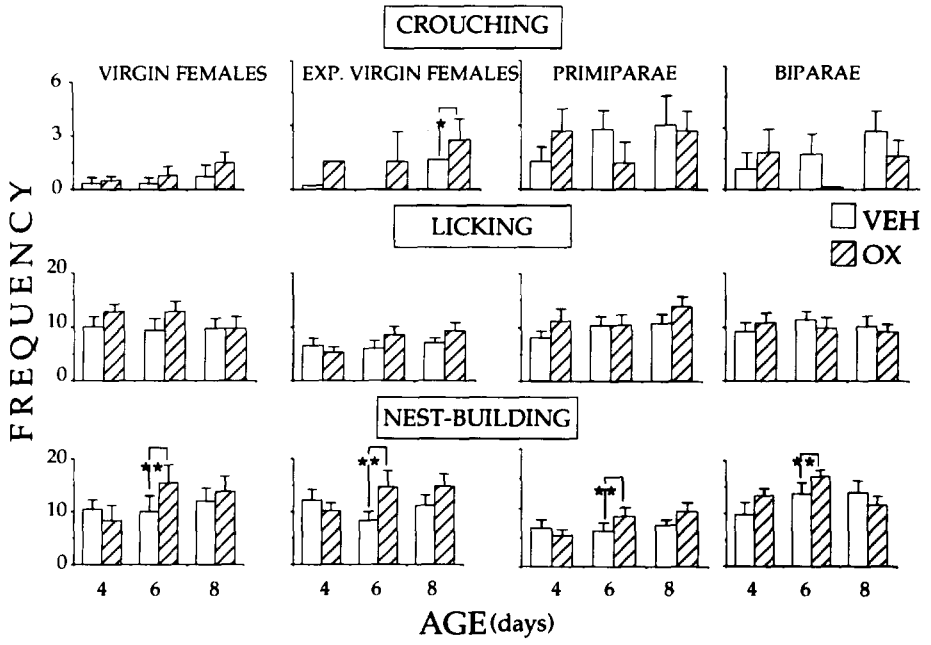

FIG. 1. Mean frequency (±SEM) of pup-directed activities (crouching, licking, and nest building) observed in virgin, experienced virgin females, primiparae, and biparae receiving either VEH or OX pups during a 15-min recording session on postnatal days 4, 6, and 8 (n = 10). *$p < 0.05$ **$p < 0.01$.

sures and as within-subject factor. Tukey's post hoc tests were performed on the appropriate ANOVA results. Because there were no significant main or interactive effects of gender, this variable was then excluded from the analysis.

RESULTS

Figure 1 summarizes the effect of dam parity and prenatal OX on pup-directed maternal activities. The data on retrieving are not reported in detail because no significant main effects or interactions of age, prenatal treatment, and parity were found for either frequency or duration scores.

Crouching

The frequency and duration of crouching increased as the pups grew older, and both measures were markedly affected by both female parity and prenatal pup treatment, $F(3, 36)$ = 2.9, 3.34, $p < 0.05$ or less, respectively. Specifically, virgin females showed lower levels of crouching than primiparae ($p < 0.05$). In addition, primiparae and biparae receiving VEH pups were more often involved in this behavior than experienced virgin females ($p < 0.05$). Conversely, the experienced virgin group exhibited a greater number of bouts of this behavior upon exposure to OX pups compared to VEH ($p < 0.01$), and they were also significantly higher than virgin females exposed to OX pups ($p < 0.05$). In general, the duration of this behavior followed the same trend as frequency.

Licking

Both the frequency and duration of licking were significantly affected by pup prenatal treatment, $F(1, 36)$ = 6.46, 9.23, $p < 0.05$ or less, respectively. With respect to duration, the ANOVA also yielded a significant main effect of pup age, $F(2, 72) = 9,47$, $p < 0.01$. In particular, dams receiving 4-day-old pups showed shorter durations of licking than those exposed to pups of 6 and 8 days ($p < 0.05$).

Nest Building

There was a significant interaction between prenatal treatment and pup age on both the frequency and duration of nest building, $F(2, 72)$ = 3.42, 3.96, $p < 0.05$, respectively. Specifically, on postnatal day 6 dams receiving OX pups were more often involved in this behavior than those exposed to VEH pups ($p < 0.01$). With respect to duration, dams receiving VEH pups were more involved in nest-building behavior on postnatal day 4 than during the later test days.

Activity

The frequency (Fig. 2) of this behavior was significantly affected by pup age, $F(2, 72) = 5.38$, $p < 0.01$. Dams exposed to 4-day-old pup showed higher levels of locomotor activity than those receiving pups of older ages ($p < 0.05$). The ANOVA yielded no significant main effects or interactions for duration.

Rearing

The frequency of rearing was significantly affected by pup age, $F(2, 72) = 5.97$, $p < 0.05$, and followed the same trend as locomotor activity. No significant main effects or interactions were found for duration.

Grooming

Both the frequency and the duration of this behavior were significantly affected by female parity, $F(3, 36)$ = 4.1, 4.17, $p < 0.05$, respectively. In particular, experienced virgin fe-

TABLE 1

MEAN DURATION (±) ON MATERNAL BEHAVIOR TOWARDS VEH OR OX PUPS BY VIRGIN, PRIMIPAROUS, OR BIPAROUS FEMALES*

	VEH				OX			
	VF	EVF	PR	BI	VF	EVF	PR	BI
Crouching	14.0 (6.7)	24.3 (10.2)	70.2 (22.8)	52.0 (23.0)	39.3 (20.0)	79.6 (22.5)	55.3 (14.3)	36.9 (23.4)
Licking	98.3 (25.0)	65.0 (12.8)	145.8 (24.4)	153.6 (32.7)	125.5 (26.3)	98.5 (19.7)	181.0 (28.1)	164.3 (42.1)
Nest building	203.2 (37.8)	165.0 (32.0)	164.5 (31.8)	194.2 (15.9)	182.5 (39.0)	152.9 (38.2)	185.3 (30.3)	245.4 (26.6)
Activity	199.4 (21.0)	214.2 (13.8)	167.9 (26.5)	188.6 (23.3)	202.7 (22.5)	192.3 (15.7)	153.2 (24.1)	174.2 (26.4)
Rearing	261.0 (44.9)	176.0 (58.7)	250.7 (40.5)	219.6 (33.4)	271.3 (58.7)	183.6 (19.5)	246.1 (48.5)	222.5 (34.4)
Grooming	46.5 (11.3)	102.0 (22.8)	50.4 (7.8)	57.0 (16.5)	43.6 (12.0)	94.7 (18.3)	57.4 (10.4)	43.0 (13.3)
Still out	48.8 (15.4)	144.7 (37.6)	43.6 (29.5)	22.9 (13.6)	24.3 (14.6)	89.6 (35.2)	12.0 (5.0)	13.5 (9.4)

*Data are pooled from observations carried out on postnatal days 4, 6, and 8. Animals are the same as Fig. 1 and 2 (n = 10).
VF = virgin females; EVF = experienced virgin females; PR = primiparae; BI = biparae.

males were higher than both biparous and virgin females ($p < 0.01$), the latter were also less often involved in grooming than primiparae ($p < 0.05$). In addition virgin females showed a shorter duration of this behavior than experienced virgin females ($p < 0.05$).

Still Out

Both the frequency and the duration of still out were significantly affected by pup prenatal treatment, $F(1, 36) = 5.0$, 4.83, $p < 0.05$, respectively. Specifically, dams exposed to

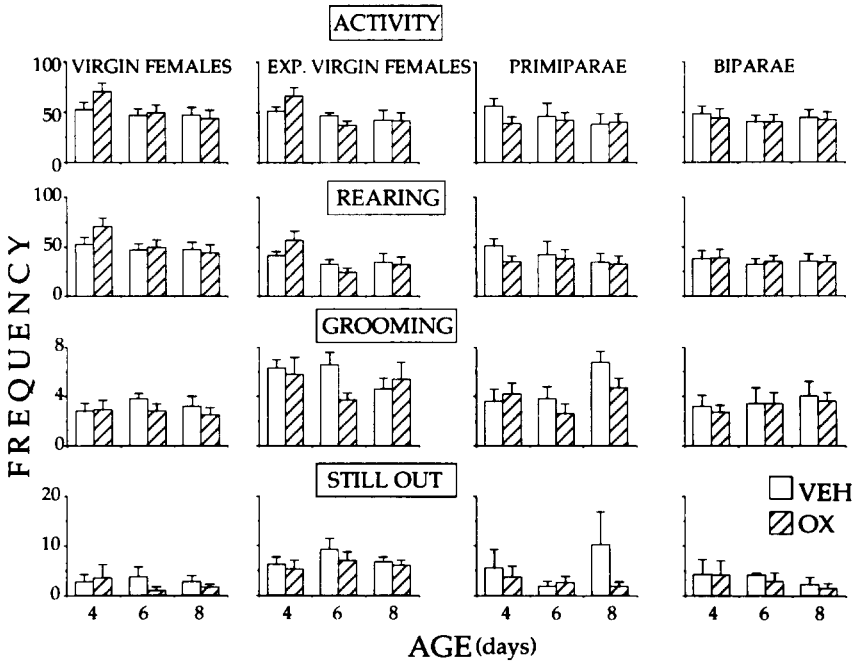

FIG. 2. Mean frequency (±SEM) of nonpup-directed activities (activity, rearing, grooming, and still out) observed in virgin, experienced virgin females, primiparae, and biparae receiving either VEH or OX pups on postnatal days 4, 6, and 8 during a 15-min session (n = 10). Animals are the same as Fig. 1 and Table 1.

VEH pups showed higher levels of this behavior than those receiving OX pups. With respect to duration, the ANOVA also yielded a significant main effect of dam parity, $F(3, 36) = 5.0$, $p < 0.01$. In particular, experienced virgin females were more involved in still out behavior than the other groups ($p < 0.05$ or less).

DISCUSSION

The present results confirm and extend previous observations showing that early mother–offspring interactions are influenced by both the female's experience of maternal care and pup stimulus properties. We found that mouse primiparous dams display a higher level of crouching behavior (a specific and important item of maternal care) than virgin females, and the latter were also less often involved in this behavior than the group of experienced virgin females. Interestingly, mouse biparous females showed lower levels of grooming than experienced virgin females. The expression of self-grooming occupied at least 7% of the female behavioral repertoire. This means that the amount of time spent performing this activity is substracted in the group of experienced virgin females more than in the group of biparous females from the time usually devoted to maternal care. These findings, in mice, allow a clear-cut separation between the group of more experienced dams and that of less experienced females, also confirming previous studies on rats showing that the latter are somehow less motivated to be good mothers than experienced ones (19,31). Noirot has extensively reported (29) that naive mice other than experienced or parturient females, when first encountering a newborn pup, tend to engage in varied ways, which often result in an approach–avoidance conflict. By contrast, naive rats show clear infanticidal tendencies towards both surgically and naturally delivered pups that are suppressed during the prepartum period (32).

Although generally in mice the period of sensitization is much shorter than in rats, it greatly varies among colonies (28).

In addition, virgin female rats appear more fearful and anxious when in the presence of newborn pups than experienced or lactating females (16,18,19,34). The low levels of fear and anxiety found in lactating animals (16,20) have been related to functional changes at the CNS level. More specifically, the cerebrospinal fluid concentration of GABA, which profoundly influences neuroendocrine and behavioral phenomena associated with lactation, is markedly increased by pup-related stimuli, reaching very high levels while the mother is nursing the pups, and decreasing after pup removal [(33), for literature and discussion see (22)]. Therefore, the speculative hypothesis can be formulated that a certain kind of neurochemical sensitization, resulting from previous maternal experience, exerts a residual influence on behavioral responses to pups shown by multiparous mouse females. As a result, experienced females, when observed in the presence of pups, should show a reduced level of anxiety, while exhibiting a strong tendency to maintain proximity to the newborn pups. Bauer (4) and Fleming (17) have reported that primiparous rat females are more attracted to the odor of the maternal nest than are virgin females. Although the neural basis of these experiential effects are not yet clear, much evidence suggests the inclusion of short- and long-term retention of maternal responsiveness into a sort of maternal memory (37).

Pup stimulus properties appear to be affected by prenatal treatment irrespectively of pup gender. In fact, our data clearly show that younger mouse pups belonging to the OX group were able to stimulate higher levels of both licking and nest-building behavior than corresponding controls. By contrast, the presence of OX pups caused a significant reduction of still out behavior, which is one item of mouse behavioral repertoire certainly not directed to pup survival or maintenance. Because it is known that maternal care in mice is more pronounced in the early postpartum days [see for literature (2,23)], the altered levels of maternal care reported herein, probably reflect specific changes in some aspects of the general set of cues caused by the prenatal pup treatment (3,22). We reported that prenatal oxazepam exposure causes a postnatal retardation of body weight gain and of several responses such as righting, bar holding, limb placing, and auditory startle mostly during the first two postnatal weeks (3), and Kurishingal and colleagues (21) found an overall increase in ultrasonic calling in newborn mice prenatally exposed to chlordiazepoxide. Moreover, acute benzodiazepine administration can cause hypothermia in adult animals (9), and it can be hypothesized that alterations in pup thermoregulatory mechanisms might result in an altered pattern of pup behavior. In fact, it is known that a low ambient temperature increases ultrasonic vocalization of newborn mice (30). Thus, the pattern of cues provided by a mildly affected pup, such as in the present study, might represent a stronger stimulus for the elicitation of maternal responses (6).

In summary, our findings stress the importance of a fine-grain analysis of dyadic mother–pup interactions, most notably the interaction between treated pups and mothers, in behavioral teratological studies aimed at characterizing drug and toxicant effects on animal and human development.

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