MATERNAL BEHAVIOUR IN THE RAT:
SOME PARAMETERS AFFECTING THE ACCEPTANCE
OF YOUNG DELIVERED BY CAESARIAN SECTION

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Summary. Rat offspring were delivered by Caesarian section at term
and fostered to lactating mothers which had had their own young
removed. The major variables studied were the presence or absence of
the placenta at the time of fostering, the rate of presentation of the
foster young to the mother, and the length of time a mother was without
any young. The percentage of animals surviving until weaning (21 days)
and the body weight of the survivors were recorded.

The presence of the placenta at fostering resulted in a decrement in
survival probability. The time that the foster mother was without pups
and the rate at which foster pups were presented to the mother had an
interactive effect: the highest survival rate was obtained when pups were
presented 5 min apart to mothers which had had their own young
removed 60 min before fostering.

INTRODUCTION

In a previous paper (Denenberg, Grota & Zarrow, 1963) we described an
approach to the analysis of maternal behaviour by means of a cross-fostering
procedure. Within 1 hr after birth, rat pups were fostered to mothers that had
been lactating for 1, 5 or 10 days. In addition, the young were fostered either
with the placenta still attached to the umbilicus, or after the natural mother
had eaten the placenta. Both of these variables significantly affected the per-
centage of young which survived through weaning as well as the weaning
weight of the survivors. These, as well as other studies (Denenberg, Ottinger &
establish that the behavioural and physical development of the young can be
used as sensitive end points for the analysis of maternal behaviour.

When young are born in the normal fashion, it is difficult, if not impossible,
to control certain aspects of the fostering situation which may be of importance.
One such variable is the duration of normal parturition; a second is the rate at
which the young are expelled through the birth canal. These variables can be

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controlled if the pups are delivered by Caesarian section. However, it is first necessary to determine under what conditions foster mothers will accept and care for Caesarian-delivered young. This paper reports the results of experiments investigating the effects of several variables upon the acceptance of Caesarian-delivered pups.

EXPERIMENTS

EFFECTS OF EATING THE PLACENTA AND LENGTH OF TIME WITHOUT YOUNG UPON CROSS-FOSTERING (EXPERIMENT I)

Previously we had found that a significantly higher percentage of normally delivered young survived through weaning if they were fostered with the placenta still attached (Denenberg et al., 1963). Although the pups were fostered within 1 hr after birth, no attempt had been made to control the amount of time the foster mother was without any young (i.e. the time between the removal of her own young and the presentation of the first foster pup). The purpose of the first study was to investigate the effects of the placenta and of the time without any young upon the acceptance and care of Caesarian-delivered pups.

Method

Nulliparous female Purdue–Wistar rats were maintained in groups of eight to ten. Each evening two males were placed into each cage. Vaginal smears were obtained the following morning. Spermatozoa in the vagina defined Day 1 of pregnancy.

Pregnant females were placed in individual 9×9×15 in. cages with wire mesh top and sides and a solid floor covered with shavings. The shavings were not changed after birth. Food and water were supplied ad libitum. Temperature and humidity were maintained at 22-2° C and 40 to 50%, respectively.

Those females which were used as foster mothers delivered their own young normally and maintained them for 12 to 36 hr before the young were removed. Either 30, 60 or 120 min after the removal of the foster mother’s own young, three or four pups, delivered by Caesarian section, were given to her. The young were fostered either with the placenta present or absent. When fostered with the placenta present, the foetus and the placenta were removed from the uterus intact and fostered to the new mother who then ate the placenta and cleaned the pup. When the pups were fostered without the placenta, only the foetus was removed from the uterus and given to the mother; she cleaned the pup to some extent.

The Caesarian operation was performed on the day of expected parturition (Day 22). The female was anaesthetized with ether, an abdominal incision made, and both horns of the uterus withdrawn to the outside of the female. An incision was made through the decidua parietalis along the entire length of the uterus. Each foetus was withdrawn from the uterus and care was taken to remove the amnion from the head area. When fostering was done without the placenta, the umbilicus of each foetus was occluded with a forceps and cut from the placenta. For the condition where the placenta was present, the placenta was removed from the uterus along with the pup. The pups were
covered with a damp towel and placed under a 100 W lamp until fostering. Each pup was carried to the foster mother's cage in a gloved hand and placed into the cage close to the female. The foster mother was observed until retrieving occurred. Young were presented one at a time 5 min apart.

All young were weighed at 10, 15 and 21 days of age when they were weaned. Only the 21-day weight data are reported.

**Results**

Survival ratios and body weights of the survivors at 21 days of age are presented in Table 1 for the six experimental groups. The presence of the placenta during fostering resulted in significantly fewer pups surviving than when the placenta was absent (52% as against 72%; $\chi^2 = 6.41$, $P<0.02$). In addition, removing a lactating mother's young 60 min before fostering results in a greater proportion of young surviving to weaning (76%) than fostering to

<table>
<thead>
<tr>
<th>Condition</th>
<th>Survival ratio by animal*</th>
<th>No. of litters in which:</th>
<th>Mean body weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>none died</td>
<td>some died</td>
</tr>
<tr>
<td>30 min without young</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Placenta present</td>
<td>11/28 (39%)</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Placenta absent</td>
<td>18/28 (64%)</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>60 min without young</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Placenta present</td>
<td>27/40 (68%)</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Placenta absent</td>
<td>34/40 (85%)</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>120 min without young</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Placenta present</td>
<td>9/23 (39%)</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Placenta absent</td>
<td>19/31 (61%)</td>
<td>3</td>
<td>4</td>
</tr>
</tbody>
</table>

* Numerator is the number of young alive at 21 days; denominator is the number of young fostered at birth.

mothers which have had their young removed either 30 min (52%) or 120 min (51%) before fostering ($\chi^2 = 12.03$, $P<0.01$).

The analysis of variance of the 21-day body weights used the mean of each litter as the basic unit of measurement. This failed to find significant differences between the time periods, the presence or absence of the placenta during fostering, and the Time x Placenta interaction.

**COMPARISON OF ANAESTHETIZATION WITH DECAPITATION OF THE MOTHER**

(experiment 2)

In the first study, the mothers were anaesthetized with ether before the Caesarian section. A more convenient procedure is to decapitate the mother, and then deliver the young. The purpose of this study was to compare the latter procedure with results obtained in the first study.
Method

The particular group from Experiment 1 chosen as the comparison group was the one in which foster mothers had their own young removed 30 min before receiving foster young. The pups still had the placenta attached and were presented to the foster mothers 5 min apart.

The Caesarian delivery was the same as in the first experiment except that the mothers were decapitated. Then an abdominal incision was made and both horns of the uterus excised. The placenta was removed from the uterus with the pup. The pup was carried to the foster mother's cage in a gloved hand and placed into the cage near the mother. Each mother was observed until retrieving occurred. The next pup was presented 5 min thereafter.

The young were weighed at 10, 15 and 21 days.

Results

The relevant statistics are presented in Table 2. When the mothers were decapitated before Caesarian section, 44% survived through weaning as compared to a 39% survival rate for mothers which were anaesthetized. This difference is not significant ($\chi^2 < 1$). The weaning weight of animals from the decapitation group was 49·31 g as compared to 53·54 g for the other group. This difference is not significant ($F < 1·0$)

**Table 2**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Survival ratio by animal*</th>
<th>No. of litters in which:</th>
<th>Mean body weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>none died</td>
<td>some died</td>
</tr>
<tr>
<td>Mother anaesthetized†</td>
<td>11/28 (39%)</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Mother decapitated</td>
<td>20/44 (44%)</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>

* Numerator is the number of young alive at 21 days; denominator is the number of young fostered at birth.
† Data taken from Experiment 1.

EFFECTS OF RATE OF PRESENTATION OF YOUNG TO MOTHER, IN COMBINATION WITH THE PLACENTAL EFFECT AND TIME WITHOUT YOUNG (EXPERIMENT 3)

Another variable which may have an effect upon maternal behaviour is the rate at which the young are delivered. Possibly, too rapid delivery may not allow the mother sufficient time to clean and care for the young. On the other hand, it may be that the rapid delivery of pups is a sufficient stimulus to elicit more appropriate maternal behaviour. The purpose of this experiment was to examine the effects of varying the rate of presentation of the young to foster mothers. In addition, this variable was studied in combination with the variables investigated in Experiment 1: foster mothers were without young for 30 or 60 min, and the pups were fostered with or without the placenta.
Method

Young, adult Purdue-Wistar female rats were housed, maintained and bred as described in Experiment 1. Those females which were used as foster mothers delivered their own young normally, ate the placentae, and maintained the young for 12 to 36 hr before the young were removed. Either 30 or 60 min after the removal of the foster mother’s own young, three or four pups, delivered by Caesarian section at term, were given to her. These foster young served as the subjects for the experiment.

The young were presented to the foster mother: (a) simultaneously, or (b) one every 10 min. These values encompass most of the range of delivery time for normally delivering females.

The Caesarian delivery was similar to the second experiment. The female

| Table 3 |
|--------|------------------|------------------|------------------|
| **Condition** | **Survival ratio by animal** | **No. of litters in which:** | **Mean body weight (g)** |
| | | **none died** | **some died** | **all died** |
| **30 min without young** | | | |
| Pups presented simultaneously | 27/38 (71%) | 6 | 2 | 2 | 48.84 |
| Placenta present | 15/31 (48%) | 2 | 3 | 3 | 52.73 |
| Placenta absent | | | | | |
| Pups presented 10 min apart | 13/33 (39%) | 3 | 1 | 5 | 53.26 |
| Placenta present | 28/34 (82%) | 4 | 5 | 0 | 50.30 |
| Placenta absent | | | | | |
| **60 min without young** | | | |
| Pups presented simultaneously | 13/20 (65%) | 2 | 2 | 1 | 47.66 |
| Placenta present | 16/24 (67%) | 3 | 2 | 2 | 49.12 |
| Placenta absent | | | | | |
| Pups presented 10 min apart | 17/29 (59%) | 2 | 4 | 2 | 49.30 |
| Placenta present | 21/27 (78%) | 4 | 2 | 1 | 58.64 |
| Placenta absent | | | | | |

* Numerator is the number of young alive at 21 days; denominator is the number of young fostered at birth.

was decapitated, an abdominal incision made, and both horns of the uterus excised. The placenta was either removed from the uterus with the pup or was removed from the umbilicus as described in the first experiment. The pup or pups were carried to the foster mother’s cage in a gloved hand and placed in the cage near the mother. Each mother was observed until retrieving occurred.

All pups were weighed at 10, 15 and 21 days of age when they were weaned.

Results

The survival ratios and body weights at 21 days are presented in Table 3. The amount of time that foster mothers were without pups (30 or 60 min) did not affect the survival rate (61% and 67%, respectively) in this experiment. The absence of the placenta enhanced survival probability when the pups were fostered 10 min apart ($\chi^2 = 11.25$, $P<0.01$), but acted to reduce the survival
probability somewhat when the young were fostered simultaneously (69% survived when the placenta was present; 56% survived when the placenta was absent). Text-fig. 1 presents the functional relationship between survival probability and the time interval between successive presentations of pups to the foster mothers. These results were obtained by combining the data of the first three experiments in which females had been presented with foster young either 30 min or 60 min after their own pups had been removed. The two curves are almost mirror images of each other. The longer the interval between presentations of the pups to the foster mother (between 0 and 10 min), the higher is the probability that the young will survive through weaning, if the placenta is absent when the young are fostered; the exact opposite effect is obtained if the placenta is present at fostering.

![Text-fig. 1. Survival probability as a function of time interval between presentations of pups to foster mothers and as a function of the presence (○) or absence (●) of the placenta.](image)

An analysis of variance of body weights, using the litter mean as the unit of measurement, found no significant differences.

**DISCUSSION**

The major finding of this series of experiments is that the presence of the placenta led to a decrease in survival probability for Caesarian-delivered young (52% survived). This is in marked contrast to the results of our previous study (Denenberg et al., 1963) in which the presence of the placenta yielded a higher rate of survival when normally-delivered young were fostered (94% survived). The two most likely reasons for this large difference in survival rate appears to be the method of delivery or some factor associated with the placenta.

We have evidence that the method of delivery is probably not implicated. In our first paper (Denenberg et al., 1963) we reported that 76% of normally-delivered young survived to weaning when they were fostered without the placenta to mothers which had been lactating for 1 day. In Experiment 1 of
this study we found that 72% of Caesarian-delivered young survived to weaning when they were fostered without the placenta to mothers which had been lactating for 1 day. In another paper (Grota, Denenberg & Zarrow, 1966) we directly compared normally-delivered and Caesarian-delivered survival percentages when all young were fostered without the placenta to mothers which had been lactating 1 day; 90.9% of normally-delivered young survived and 71.0% of the Caesarian young survived, a difference which approached significance at the 0.10 level. Therefore, with our particular procedures Caesarian delivery itself does not have any major effect upon survival probability. This conclusion should not be generalized too widely since mode of delivery is known to be an important factor in other species.

A more likely reason for the difference in survival percentage appears to be the placenta. The data strongly suggest that some factor or factors associated with the characteristics of the placenta under the two types of delivery are of major importance. It was noted that the placenta at the time of Caesarian section appeared a bright red; following normal delivery the placenta was dark and appeared necrotic. Since the placenta at birth has been deprived of its blood supply for a greater period of time than the placenta obtained by Caesarian section, it is possible that the placental constituents might have changed. The hormonal complement appears to be a likely possibility since we have previously shown (Denenberg et al., 1963) that the injection of 4 µg of oestrogen into the foster mother enhanced the survival rate of the young while a 10-µg injection resulted in a decrement in survival.

Wicsner & Sheard (1933) were the first to study the maternal behaviour of rats whose own young were delivered by Caesarian section. The present study may be considered to be an extension of their procedure in which Caesarian delivery is combined with cross fostering to study various parameters of maternal behaviour. This technique offers considerably more control over a number of relevant variables than does the procedure of using normally-delivered young.

ACKNOWLEDGMENT

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REFERENCES


