THE EFFECT OF STIMULI EMITTED BY SUCKLINGS ON THE COURSE OF THEIR FEEDING BY BITCHES

P. KORDA and J. BREWIŃSKA

Department of Neurophysiology, Nencki Institute of Experimental Biology
Warsaw, Poland

Abstract. A change in feeding behavior on the 15th and 16th day of the maternal cycle was observed in experimental bitches whose own litter was partly replaced, on the onset of the 15th day, by foster puppies 12–13 days younger. The number of feeding acts and the overall feeding time increased, as compared with the indices for 2 days preceding the exchange of puppies (the 13th and 14th day of the maternal cycle). In the control group, where puppies were not exchanged, no increase in the above behavioral indices was observed on the 15th and 16th day, and they remained at the level recorded on the 13th and 14th day of the cycle.

INTRODUCTION

Feeding of the sucklings by the mother must be regarded as a complex process involving her whole organism. Contrary to the some other manifestations of maternal care, it is known a priori that the aforementioned process is controlled both by relevant changes in the hormonal state and by the CNS which acquires a suitable level of selective reactivity during lactation. Thus, puppy feeding must be markedly affected by endogeneous factors and PCS (past cumulative stimuli) (see 7) on the one hand and CES (current exteroceptive stimuli) (see as above) on the other hand. Initiation of milk secretion, i.e., lactogenesis, as well as its maintenance, i.e., lactopoesis, during lactation depend above all on the appropriate secretion of the anterior lobe of the hypophysis (LTH, STH, ACTH), on adrenal cortex hormones and thyroxine. In turn, milk ex-
cretion and the related phenomenon, the so-called milkflow seem to remain under strong and predominant influence of the CNS, and hence on CES — despite the fact that efferent information descends to the periphery by means of oxytocin, i.e., the hormone of the posterior lobe of the pituitary gland.

This paper deals mainly with the CES' effect on bitches' maternal behavior. This is why we are interested in milk excretion (ejection) and not with milk secretion and lactation process themselves. We believe that the investigations into the maternal behavior closely related to feeding of the sucklings may be limited to the study of relevant behavioral manifestations disregarding milk secretion itself. For instance, one of the manifestations of maternal behavior registered in many experiments on laboratory rodents was merely the assumption by the female of the position specific for feeding the young, i.e., the so-called “crouching” (2, 3, 8).

This study refers to such manifestations of the bitches' behavior as are closely temporally (and in a sense causally) connected with the function of puppy feeding and milk ejection in the bitch or, to be more exact, with the function of sucking of the bitches’ nipples by the sucklings. Those manifestations point to the specific tolerance of mother to sucking by the young. It seemed that establishing the number of feeding acts and the time spent by the bitch at that function relatively to the effect of different stimuli emitted by pups who were in various stages of development would help to explain same mechanisms which control the maternal behavior in Canidae. Deeper studies of the above-mentioned parameters of behavior in the course of experimentally intact maternal cycle of the bitches might also supplement the very limited knowledge of the subject. Moreover, measuring the behavioral parameters on a natural undisturbed maternal cycle would enable to perform a proper analysis of behavior of the bitches whose own puppies were exchanged for younger ones.

MATERIAL AND METHODS

Nine randomly chosen bitches with their litters were used in the experiment. If the litters consisted of more than four puppies, their number was reduced on the day of delivery. Ten additional, randomly selected 1–4 days old pups from other litters were used consistently with the procedure described earlier (7). These animals served as replacements of the experimental bitches’ own puppies. Four of the nine bitches (bitches 1–4) made up the control group, and five (bitches 5–9) — the experimental group. The experimental procedure, duration of obser-
vation sessions, periods of observation of the tested behavioral manifesta-
tions in the bitches as well as moments of introducing the foster puppies
were the same as those described in the previous paper (7).

Two alien puppies 1–4 days of age were used as substitutes for the
experimental bitches' two own puppies. In each case this exchange
took place before the start of observation, on the 15th day of the maternal
cycle. In one of the bitches (bitch 9) only one puppy was exchanged.
When registering the duration and number of feeding acts it was as-
sumed that the feeding process takes place whenever at least one puppy
is holding the bitch's nipple in its mouth. We were not interested in
the lactation process, but in the quantitative determination of the bitch's
"tolerance" to the sucking of her nipples. Pauses in feeding lasting less
than 1 min were not recorded.

The data obtained from all the tested bitches, both experimental
and control ones, can be used for evaluating the course of experimentally
undisturbed phasic changes in the bitches' behavior until the 14th
day of the maternal cycle inclusive. This was motivated in the previous
paper (7).

The behavior of each experimental bitch on the 13th and 14th day
of the cycle may, to a certain degree, serve as a basis for comparisons
and evaluations of changes in their behavior following the puppies ex-
change, i.e., on the 15th and 16th day (see our former work (7)).

RESULTS

Number of feeding acts

The number of feeding acts performed by every bitch on tested days
of the maternal cycle is shown in diagram in Fig. 1 (control group) and
Fig. 2 (experimental group).

The data collected during daily sessions of 14 h duration are present-
ed in the form of blocks, each covering a 2-day period. Block I shows
the results of the 2nd and 3rd day of the cycle, block II — of the 13th
and 14th day, block III — of the 15th and 16th day. Each block contains
observations collected on two consecutive days in two sessions, each
lasting 14 h. Results of the 14th day are not included in the blocks and
are presented to supplement the description of maternal behavior in the
early stage of motherhood. In order to evaluate the results on the basis
of the diagrams it is necessary to compare:

1. Individual indices computed for the experimental bitches (Fig. 2,
bitches 5–9) on the 15th and 16th day with the relevant data for the
13th and 14th day as well as for the 2nd, 3rd and 4th day of the cycle
in these same bitches;
Fig. 1. Total number of suckle-acts recorded during 14-h sessions on selected days of maternal cycle in control animals. Overall data for the 2nd and 3rd day of the maternal cycle are presented in block I (diagonal lines), for the 13th and 14th day in block II (vertical lines) and for the 15th and 16th day in block III (crossed lines). The data of the 4th day of the maternal cycle (plain bars) are presented additionaly to describe fully the maternal activity during the first days after delivery. The last diagram presents mean data. Immediately below the abscissae the relative values are expressed in per cent. The total mean results for all bitches in the group on the 2nd and 3rd day were taken as 100%. 
Fig. 2. Total number of suckle-acts during 14-h sessions on selected days of maternal cycle in experimental animals (shown in the same way as in Fig. 1). Numerals in circles show the number of puppies exchanged prior to observation on the 15th day of the cycle, marked with a thick vertical line.
2. All individual indices obtained in the experimental bitches (Fig. 2, bitches 5-9) with the relevant indices in the control animals (Fig. 1, bitches 1-4);

3. Mean results for the control group with those for the experimental one (Fig. 1 and 2). Special attention should be paid to the 15th and 16th day versus the days 13 and 14.

The last diagram in Fig. 1 shows that mean number of feeding acts in the control bitches amounted to 43 (ranging from 31 to 59) in block I, then dropped by half, i.e., to 20 acts (ranging from 14 to 27) in block II and continued on this low level also in block III. This decrease was similar in all bitches but one (bitch 1) in which some rise in number of feeding acts in block III was recorded.

In the experimental bitches both individual (26 to 54 acts) and mean (38 acts) data in block I were similar to corresponding results in the control group. Block II was also similar for the two groups of bitches (marked drop in the number of feeding acts). However, in block III, i.e., after the substitution of pups in the experimental group — contrary to the controls — the individual and mean number of feeding acts grew suddenly, exceeding considerably block II, and they became again as frequent as in the early phase of motherhood (see block I).

The mean data are also presented in per cents (Fig. 1 and 2). The data for block I served as a framework for each group and were taken as 100%. The difference noted in block III between the control and experimental group as well as differences and similarities observed in all 3 blocks within both groups can be seen easily when the data are expressed in relative values. In the control group mean indices for the second and third block were equal and amounted to 48%; in the experimental animals, they amounted to 60% in block II and increased to 97% in block III. In the experimental bitches the mean indices for the third block of days returned almost to the early post-delivery level (or even surpassed it, as in bitches 5 and 7) exceeding indices for block II by one third. No such increase in the block III was found in the control bitches, except in bitch 1. In the control bitches the difference in the number of feeding acts between block II and III, as analyzed by Student–Gosset t-test, was statistically considerably below the level of significance ($t = 0.59$; $P_{0.05} = 2.45$). In the experimental group these differences ($P_{0.05}$) were statistically significant.

**Total time of feeding**

Data representing the total time spent on puppy feeding by every bitch noted during 14 h daily sessions are shown in the form of diagrams in Fig. 3 (control bitches) and Fig. 4 (experimental bitches). The presenta-
tion of the results was made in the same way as described in the former section dealing with the number of feeding acts.

Figure 3 shows that in the control bitches the mean total feeding duration amounted to 16 h 57 min in block I. In block II it dropped

![Chart of Control Animals](chart)

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Fig. 3. Overall time of suckle-acts recorded in 14-h sessions on selected days of maternal cycle in control animals. Data are presented in the same way as in the previous Figures.
to 6 h 31 min, i.e., by about one third of the initial value. This low level (with slight tendency to decrease) was maintained over the last 2 days (see block III) except in bitch 4.

![Graphs showing suckle-acts in experimental animals](image)

**Fig. 4.** Overall time of suckle-acts in 14-h sessions on selected days of maternal cycle in experimental animals (shown in the same way as in Fig. 3). Numerals in the circles show the number of puppies exchanged prior to observation on the 15th day of the cycle, marked with a thick vertical line.
With mean indices for the first 2-day block of observations taken as 100% — the mean indices for block II fell to 38% and for block III to 35%. The trend of changes for individual control bitches resembles the one for mean results with the aforementioned exception of bitch 4 (considerable shortening of the measured time in block II, but a slight rise in block III).

In the experimental bitches both mean and individual data for the first two blocks of observations, i.e., till the end of the 14th day were close to the corresponding results in the control bitches. However, in block III the two groups of bitches differed markedly: in all five experimental bitches the total duration of feeding was considerably prolonged after the exchange of puppies. This prolongation was especially marked in three bitches (bitches 6–8), where feeding duration in block III was more than double of that in block II. In the remaining two bitches, one of whom (bitch 9) had only one puppy exchanged, the increase was less pronounced (about 25%). Mean data in per cents show that feeding duration in the second 2-day block was 31%, and after puppy substitution — in block III — 68% of the initial values (i.e., in block I). The tendency of feeding duration to be shorter in block II and markedly prolonged in block III was found in all five experimental bitches, despite their individual differences. In the control bitches the difference in the total time of feeding between blocks II and III, as analyzed by Student–Gosset t-test, was statistically considerably below the level of significance \( (t = 0.88; P_{0.05} = 2.45) \). In the experimental group all bitches (bitches 5–9) showed a clear tendency towards an increase of total feeding time in block III compared with values for block II. The mean increase was more than two times. This difference is, however, slightly below a statistical significance limit \( (t = 2.16; P_{0.05} = 2.31) \).

### Additional observations

Six out of nine bitches of both groups were observed to assume, at times, a sitting position during puppy feeding. This phenomenon has never been noted during the first days after delivery. Sitting down to feeding was seen, at the earliest, when the pups were 13 days old. Altogether 19 cases of puppy feeding in a sitting position were recorded in our observations. The relevant data irrespective whether the bitches belong to the control or experimental group are specified in Table I.

Moreover, during observation of the behavior of puppies, we recorded a second phase of milk excretion noticeable in the bitches after some length of sucking time. This is the so-called milkflow which we could identify only by typical changes in the sucking behavior of the pups.
Cases of puppy feeding by bitches assuming a sitting position

According to us the milkflow started when the puppies stopped to press ("massage") the mammary gland of the female, became motionless and began to emit a typical rhythmic sound of swallowing. This observation was carried out at random in three bitches in various phases of motherhood. In each case the duration of sucking up to the onset of milkflow was measured (see Table I).

**Table I**
Cases of puppy feeding by bitches assuming a sitting position

<table>
<thead>
<tr>
<th>Age of the puppy (in days)</th>
<th>Feeding in sitting position</th>
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<tbody>
<tr>
<td></td>
<td>Number of acts</td>
<td>Number of bitches assuming sitting position</td>
</tr>
<tr>
<td>13</td>
<td>2</td>
<td>2</td>
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<tr>
<td>14</td>
<td>5</td>
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<tr>
<td>15</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>16</td>
<td>6</td>
<td>4</td>
</tr>
</tbody>
</table>

According to us the milkflow started when the puppies stopped to press ("massage") the mammary gland of the female, became motionless and began to emit a typical rhythmic sound of swallowing. This observation was carried out at random in three bitches in various phases of motherhood. In each case the duration of sucking up to the onset of milkflow was measured (see Table II).

**Table II**
Second phase of milk excretion ("milkflow")

<table>
<thead>
<tr>
<th>Age of the puppies (in days)</th>
<th>Number of acts</th>
<th>Lapse of time from the beginning of sucking to the onset of &quot;milkflow&quot; (min)</th>
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<tbody>
<tr>
<td>4</td>
<td>3</td>
<td>5</td>
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Additional observations seem to support the idea that in the early post-delivery phase the sucking act is initiated and terminated mainly by the puppies; the situation is similar in the later phase of the maternal cycle in the bitches with substituted 2–4 days old pups. Thus, it is mainly the puppy that regulates the number of sucking acts and the duration of feeding. From the previous studies (7) it is known, that mother bitches which are directly exposed to stimuli emitted by 2–4 days old sucklings
remain in constant tactile contact with the puppies during nearly the entire sessions of observation. Hence, their nipples are almost ceaselessly accessible to the young, who avail themselves of that accessibility according to their needs. As we mentioned before, also the termination of the sucking act depends on the puppies at that stage of their development. Satiated pups simply release the nipples, but as long as they are holding them — the bitches almost never leave their nest. We also noted that after the 13th day of life of the puppies, the initiative of interrupting the sucking act was more and more frequently taken by the bitches. After some time of sucking (varying individually and periodically) the bitches get up and leave the nest, forcing their young to release the nipples. Rosenblatt (9) claims that in the cat the initiative to begin the sucking act belongs to the mother. However, as far as the bitches are concerned, we still lack the data supporting this notion. The bitches only provoke 2–4 days old pups to approach their body by licking them or touching with the nose. As a result the sucking act is frequently started by the puppies. Yet, especially in the first days of life, it happens that the pups lie down on the body of their mother only to get warm. In this they are helped by the bitches who assume a suitable position. It is known that the thermoregulatory mechanisms in the Carnivora are not definitely formed in the first days after birth.

DISCUSSION

The results permit to conclude that the changes observed in the course of maternal feeding behavior are very similar to the changes in the course of other manifestations of care-giving behavior described in our former paper (7). The very characteristic shift in the behavior of mother bitches after the substitution of some of their litter by younger puppies was also found in the related case: the presence of 2–4 days old foster sucklings evoked in the bitches a tendency to regress to the maternal behavior typical for initial days of the maternal cycle. In other words, on the 15th and 16th day the bitches behaved again as if the foster sucklings were their natural puppies. However, this tendency was somewhat less clear than in the earlier studied manifestations of maternal behavior (Korda and Brewińska, 1977). In three experimental bitches the puppy exchange strongly influenced the number of feeding acts that returned to, or even exceeded their level on the first days of maternity (in bitches 5–7). In the bitch 8 that index almost reached its initial level, and only
in bitch 9 the phenomenon was less visible. This might have been due to the fact that bitch 9 had only one puppy exchanged. As regards the overall puppy feeding duration, the effect of the substitution of puppies was evidently seen in four bitches (bitches 6–9), though only in one of them the observed index returned to its initial level. In bitch 5 the result was negligible.

In general, these data seem to point univocally to a great importance of the CES for the control of the bitches' behavior related to puppy feeding. However, the results concerning the total feeding duration indicate that other factors besides CES must have been present. It was impossible to identify these factors by the methods applied in this study. It seems right to assume that they represent PCS (see Introduction) like e.g., the stimuli related to past phases of the maternal cycle and the lapse of successive days since the onset of lactation. It could as well be the effect of habituation of the bitches to stimuli produced by the puppies or the endogeneous, mostly hormonal factors correlated to the current stage of maternity and lactation. Similarly, in the course of epimeletic vomits in female dogs (5, 6) the effects of the CES and of the endogeneous factors were both noted simultaneously. The occurrence of care-giving vomiting acts strictly depended on the presence and suitable behavior of the puppies. Nevertheless, the top frequency, of care-giving vomit acts occurred when lactation had already passed its peak.

Although in this study we dealt exclusively with behavior related to puppy feeding and not to the process of lactogenesis or milk excretion itself, it is very likely that both these processes somehow affected the observed behavior of the bitches. Therefore, it is plausible that the hormonal state of the bitches also strongly influenced that behavior. As known, the so-called second phase of milk excretion, i.e., the excretion of a large portion of milk that at the onset of sucking is still filling the lactogenic alveoli (before descending to the lactiferous sinus) is controlled by oxytocin, released into the blood. This milk excretion, alias "milkflow", is a complex neurohormonal reflex. Its afferent arm begins in the sense organs, while the efferent part is represented by a neurohormone carried over the organism via the humoral routes. During the first phase of sucking nervous impulses are generated in response to the tactile stimuli acting upon the lactiferous gland. These impulses together with other CES acting on various senses of the mother, are transferred to different structures of the CNS. The excitation reaches the nucleus supraopticus and nucleus paraventricularis in the hypothalamus and evokes the relase of oxytocin in the latter. Then oxytocin descends to the neurohypophysis from where it proceeds further into the blood and lymph. Oxytocin induces contraction of muscular elements in the lacti-
ferous alveoli, thereby pressing out milk which flows down to the lactiferous sinus. According to Baryshnikov (1) the efferent nerves, with fibers running mostly through the external spermatic nerve, also participate in milk-passing reflex.

On the basis of the above-cited unconditioned reflexes numerous conditioned connections are formed which subsequently take part in milk excretion. For instance, the odor, sight, vocalization or appropriate appetitive behavior of the sucklings, as well as other environmental cues that in the past accompanied the sucking act, jointly evoke milk excretion. Conditioned reflexes may also be responsible for the inhibition of milk excretion. It is a well-known fact that stimuli which cause anxiety in the animals can easily check the second phase of milk excretion (i.e., milkflow). In this phenomenon, frequently observed in dairy farms, the superior centers in the CNS and the CES seem to play an important role. Moreover, we found in our former study (7) that the cues (so-called key stimuli) emitted by the younger pups are stronger for the mother bitches than those produced by older puppies. When both groups of situations are taken into account it becomes obvious that the tolerance of the bitches to the tactile contact of the pups with their nipples (or just to sucking) markedly increased in result of the substitution of part of the litter with younger puppies. This was manifested both by the growing number of feeding acts and by the increase in the total feeding duration. For that reason the older pups (i.e., natural puppies of the experimental bitches — see 7) overate, taking advantage of the bitch's tolerance to sucking, which suddenly increased in the presence of foster sucklings. As for the 15 days old pups — her tolerance was supernormal.

The observed indices of the bitches' behavior could, have been influenced in a small degree by the fact that (see 10) newborn puppies learn to find the nipples and, to some extent, also the function of sucking itself. In a sense, it is evidenced also by Korda's earlier observations (4) on the sucklings of the fox.

Finally, it should be stressed that the total duration of feeding registered in this study did not exactly correspond to the actual overall time of effective sucking. That was the case mainly in the early phase of maternity. Sometimes the pups lay clasped to the mother's body — sleeping and just holding the nipple or occasionally making sucking movements. We are unable to say whether sucking in sleep was effective or represented one of the puppies' behaviors which satisfy other drives irrelevant to feeding. This tendency seems to exist also in human sucklings that are so eager to use soothers. A soother apparently helps the baby to fall asleep. An analogous phenomenon may as well exist in puppies.
To sum up, it has been found that the current exteroceptive stimuli (CES) play a very important role even in the control of behavior which seemed to be regulated mostly by interoceptive stimuli, like, e.g., the stimuli generated by filling up the udder.

This investigation was supported by Project 10.4.1.01 of the Polish Academy of Sciences. The excellent technical assistance of Mrs. Elżbieta Maciulewicz is greatly appreciated.

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Accepted 16 December 1976

Piotr KORDA and Janina BREWIŃSKA, Nencki Institute of Experimental Biology, Pasteura 3, 02-093 Warsaw, Poland.