Low-frequency sound communication by mouse pups (*Mus musculus*): wriggling calls release maternal behaviour

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Abstract. Low-frequency calls (wriggling calls), emitted mainly between days 2 and 15 after birth by mouse pups while pushing for the teats during suckling by the mother, are studied with regard to their significance in intraspecific communication. Wriggling calls release maternal behaviour and 'attention' responses in the mother. Licking of the pups is the most prominent maternal response, followed by changes of suckling position and by nest building. One function of the wriggling calls is to keep these maternal behaviours at a high level: otherwise their spontaneous rates of occurrence would decrease rapidly after the birth of the pups. Maternal and attention responses can be released in females lying on paralysed pups by playbacks of wriggling calls. The behavioural contexts of the production of wriggling calls and pure ultrasounds are mutually exclusive and the perception and recognition of each type of pup call cannot be confused by the mother.

It is well known that pure ultrasounds of lost mouse pups release maternal behaviour in adults, such as approach and retrieval of the pups (e.g. Noirot 1972; Smith & Sales 1980; Haack et al. 1983). In addition, calls after birth and pain calls of mouse pups, which are both broad-band sounds with prominent bands of energy in the high ultrasonic range, contribute to prevent pups being accidentally bitten or eaten by adult mice (Ehret 1975; Bernecker 1983; Haack et al. 1983). Thus pure ultrasounds and pup calls with prominent ultrasonic components indicate a kind of discomfort, distress or pain which is terminated by an appropriate response from an adult.

Besides these calls with energy in the ultrasonic range, low-frequency calls, with the major energy below 10 kHz and a frequency range rarely exceeding 20 kHz, are regularly emitted by mouse pups when struggling in the nest, mainly when pushing for the teats during suckling by the mother (Ehret 1975). Figure 1 shows three typical 'wriggling calls' with only low-frequency energy. Haack et al. (1983) classified these calls as probably non-communicative since it was not clear whether they could have effects on the behaviour of the lactating female. From the point of view of energetics and ecology, production of wriggling calls might have disadvantages for the litter, because the pups use energy to produce the calls and the sound may be heard by potential predators such as cats, which have hearing with maximum sensitivity in the same frequency range as the major energy of the wriggling calls (between 2 and 10 kHz; Neff & Hind

1955). As a counterbalance for these potential disadvantages we can expect these calls to have some communicative significance. Since mouse pups are deaf, at least until day 9 after birth (Ehret 1976), littermates can certainly be excluded as receivers of these calls. Instead it seems reasonable to suggest that they may influence the maternal behaviour of adults.

Sounds produced by the young during close contact with the mother, especially during feeding and cleaning sessions, have already been described for other mammals (grasshopper mice: Hafner & Hafner 1979; guinea pigs: Eisenberg 1974; Berryman 1976; pigs: Kiley 1972; cats: Haskins 1979; squirrel monkeys: Jürgens 1979). Except for the calls of human babies, which trigger the release of the hormone oxytocin and thus milk ejection in their mothers (Vuorenkoski 1975), possible influences on maternal behaviour of close contact calls of young have not been investigated systematically. The present study was carried out in order to investigate what communicative significance, if any, low-frequency wriggling calls of mouse pups might have in infant–mother interactions in the nest.

MATERIALS AND METHODS

Animals

Primiparous females (white laboratory mice, *Mus musculus*, outbred strain NMRI, aged 2–3
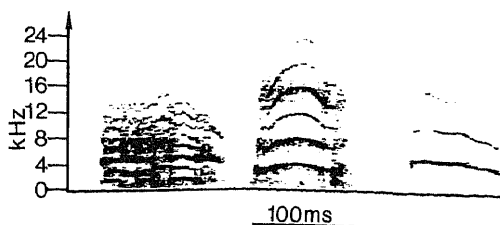
Figure 1. Sonagrams of three typical wriggling calls from mouse pups. No ultrasonic components are present and the major energy is below 10 kHz.

months) were kept in standard cages (26·5 × 20 × 14 cm) under a 12 h light–dark circle and at an average temperature of around 18°C in January, February and March and around 25°C in June, July and August (the months in which observations were made). After delivery, the litter sizes were standardized to seven randomly selected pups, either by taking pups away or by adding newborn pups from a different litter in which the mother received the same treatment (see below). The original litters contained 5–19 pups. All standardized litters were weighed every day from the day of birth (day 0) onwards.

General Procedure

Females and pups (from day of birth to day 18) were observed in their home cages, but with the grid-cover replaced by one without food pellets or a water bottle. Observations were made in a sound-proof and anechoic room between 0700–1300 hours. The animals were allowed at least 30 min to get accustomed to the conditions in the room before observations began. The following data were recorded on scoring sheets (by one or two observers) during a 30-min daily period while the mother was suckling at least part of the litter.

(1) The number of wriggling calls made by the pups. Calls could occur as separate events or, more often, in bouts with a repetition rate of about 3 calls/s. Bouts of several calls in a series were counted as one call.

(2) The number of wriggling calls that were followed within 2 s by a change in the behaviour of the mother. Pilot tests showed that this time window was the most appropriate one to separate call-induced behavioural changes from spontaneous maternal behaviour. Wriggling calls that occurred while a call-induced behaviour continued,

were not counted. Among call-induced behaviours, we discriminated the following maternal activities and an 'attention' response: (a) licking of pups; (b) changing suckling position by turning around or at least by lifting the trunk; (c) nest building (the mother starts digging in the chaff and/or removes faeces); and (d) 'attention' (the mother lifts and/or turns her head and starts sniffing around).

(3) The number of wriggling calls that were not immediately followed by a response by the mother as listed above (calls without response).

(4) The number of activities (2 a–d) without preceding wriggling calls (spontaneous maternal behaviour or spontaneous attention).

Experimental Groups and Treatments

In order to test what significance wriggling calls might have in communication between pups and mother, we formed four experimental groups.

(1) Bilaterally deafened (BLD) females (eight individuals). Under sodium pentobarbitone anaesthesia (Nembutal, 80 mg/kg intraperitoneally) the external meatus was incised and the tympanum, the middle ear and the oval window membrane were removed bilaterally.

(2) Unilaterally deafened (ULD) females (eight individuals). In this group the operation as described above was carried out on only one side. This group was necessary as a control for possible non-specific effects (besides being unable to hear) resulting from the surgery on the BLD females. If pups of BLD mothers show deficits in their developmental progress, pups of ULD mothers can help to decide whether this deficit is related to deafness or to other factors introduced by the surgery.

(3) Normal hearing females (eight individuals): in these animals a sham-operation, in which a small cut was made into the external meatus on both sides, was carried out under the same anaesthesia as described above.

(4) Normal hearing females with paralysed pups (eight individuals). These were subjected to playbacks of wriggling calls (NPB females). The rationale for including this group was that the hearing of wriggling calls could thus be decoupled from the sensation of other stimuli from the pups, which could possibly occur together with the calls. This decoupling could show whether wriggling calls alone are capable of releasing a certain response from the female and thus have a communicative significance, or whether they are just accompany-

ing some other activity of the pups which is the releasing stimulus for maternal behaviour. Observations were made only with females having 5- or 7-day-old pups.

Removal of the middle ear and oval window of the cochlea in experimental groups 1 and 2 is essential to ensure sufficient impairment of cochlear function. Earplugs were not sufficient to achieve the necessary sound attenuation in our study because they do not eliminate auditory sensitivity via bone conduction: this is only 20–50 dB less than that achieved by normal middle ear transfer (Tonndorf 1972).

All operations were carried out 1 week before pairing the females. The surgical procedure and the recovery of the animals was supervised by a veterinarian. No infection of the ears of experimental animals after surgery was observed. Successful pairing 1 week after surgery, delivery of normal litters and normal behaviour in general all indicate that our surgery had no obvious disturbing effects on the animals.

After the end of all measurements, hearing tests were conducted on the operated females. Evoked potentials (averaged over 256 tone bursts) were recorded from both inferior colliculi with stereotactically placed electrodes (see Stiebler & Ehret 1985). All unilaterally deafened animals had response thresholds of the inferior colliculus contralateral to the undestroyed middle ear similar to or maximally 25 dB higher than evoked potential thresholds of normal mice (Stiebler & Ehret 1985), which are comparable to the behavioural thresholds of this mouse strain (Ehret 1974) in the frequency range of interest (2–60 kHz). The inferior colliculus contralateral to the destroyed middle ear either did not respond to any sound with sound pressure levels up to 90 dB re 20 μPa, or showed responses at 10 and 15 kHz only, with thresholds at least 40 dB higher than those of the normal average. Four of the BLD females did not show any response. Four further BLD females responded at 10 and 15 kHz (in one or the other inferior colliculus) with thresholds again at least 40 dB above the normal means. These four animals thus had a severe bilateral hearing loss and were regarded as practically bilaterally deaf.

In experimental group 4 (females with paralysed pups), 5- or 7-day-old pups were anaesthesized with an initial dose of 60 mg/kg ketamine (Ketavet) intraperitoneally. Fifteen min after this injection, they received a dose of 3·5 mg/kg of the tranquil-

lizer chlorprothixene (Taractan). Thereafter, the pups remained motionless (except for the motions of breathing) for about 4 h. During this time they were totally unable to produce any sounds. Seven pups prepared in this way were put back into the home cage of the mother. The females were allowed at least 30 min to get accustomed to the new situation. Observations were started after the females had been lying for at least 5 min in a suckling position on the pups. Then 40–60 wriggling calls per 30 min total observation time (the same as the average number of calls produced by 5–7-day-old pups, see Results) were played back randomly at an average sound pressure level of 70 dB at the litter from a tape loop prepared on a Philips Analog 7 recorder (the frequency response range of the recording and playback equipment was flat within ±3 dB in the frequency range of interest; the recorded calls were filtered with a band-pass of 2–30 kHz). The loudspeaker was fixed 16 cm above the mother with her litter. The behavioural responses and activities of the female were noted in exactly the same way as when the calls were emitted by the pups themselves.

During the whole period of data collection, the observers did not know the identity of the experimental groups except for the last experiment with paralysed pups and playbacks of wriggling calls.

Controls for the Occurrence of Ultrasounds and Pain Calls

We used an extra three normal mothers with standardized normal litters to observe whether, in the situation in which wriggling calls were recorded, other calls by pups also occurred, e.g. pure ultrasounds (frequency range about 40–80 kHz) or pain calls (ultrasonic components up to about 80 kHz). An ultrasound detector (improved version of Andersen & Miller 1977) was used to detect any sounds made by the pups in a frequency band between 30 and 90 kHz. The microphone was mounted 12 cm above the litter. Observations were made for 30 min daily up to day 13.

Statistical Tests

The non-parametric U-test was used to compare means, the χ^2 and binomial tests were used to compare rates of occurrence of events.

RESULTS

Litter Weight

At birth, there were no significant differences in the weights of the standardized litters either between normal hearing and unilaterally deafened (ULD) mothers or between normal hearing and bilaterally deafened (BLD) mothers. Litters of ULD mothers were, however, significantly heavier ($P < 0.01$) than those of BLD mothers. Changes in weight after birth are shown in Fig. 2. Weight increased more slowly in litters of BLD mothers than of ULD and normal ones. From day 2 onwards for ULD mothers and day 7 onwards for normal mothers, litters were significantly heavier ($P < 0.05$) than those of BLD females. There were no significant differences between litters of normal females and those of ULD females on any day after birth. Similarly, the average day-to-day weight increase was larger for litters of normal and ULD females compared with those of BLD mothers ($P < 0.01$). Thus it is evident that pups raised by mothers with a severe binaural hearing loss are handicapped in their development while those raised by unilaterally deafened mothers are not.

Control Measurements

During the whole observation period we did not record a single pure ultrasound while mothers were suckling at least part of the litter. Pain calls with
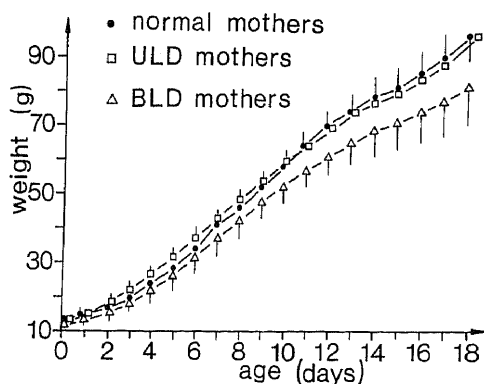

Figure 2. Average weight of the standardized litters (seven pups) of normal, unilaterally (ULD) and bilaterally (BLD) deafened females as a function of the age of the pups. Some typical standard deviations are also shown.

high ultrasonic components were recorded only three times. This shows that pups' sounds other than wriggling calls were practically absent in the behavioural context in which wriggling call production and responses by the female were quantified.

General Behavioural Observations

In the first 5 days after birth, females often remained continuously on the litter during the 30-min observation period. From day 6 onwards, breaks in feeding the pups occurred more and more often and the mothers left the pups for eating, drinking, grooming themselves or for dozing in another corner of the cage.

The pups emitted wriggling calls when the mother was in a suckling position on the litter. Wriggling call production was always associated with movements of the pups, mostly struggling with front and hind legs when they were pressing forward towards the teats. Pups older than 5 days also emitted calls when they pressed and crawled over each other in the nest while the mother was not on the litter.

Wriggling Call Production and Responses of the Mothers

There were no significant differences between mothers in different groups in the rates of wriggling calls produced by their litters. Figure 3 therefore shows the number of wriggling calls per 30 min of observation, averaged from all 24 litters and plotted against the age of the pups. The call production rate increased significantly from birth to a broad plateau ($P < 0.01$) which started at day 4 and continued to day 13. Then the call rate dropped significantly ($P < 0.01$) between days 13 and 16 and reached values comparable to those at birth.

Figure 4A shows the averages of all spontaneous maternal activities occurring in the 30-min observation period for normal, ULD and BLD females. Spontaneous levels were similar in all three groups except that a few days after birth BLD mothers showed significantly ($P < 0.05$) more spontaneous maternal behaviour than normal (days 2,6,8) and ULD mice (day 3). Overall, the rate of spontaneous maternal behaviour decreased significantly in the three groups from birth of the pups to day 5 ($P < 0.01$ in normal and ULD mice; $P < 0.05$ in BLD mice), and then stayed at a constant low level.
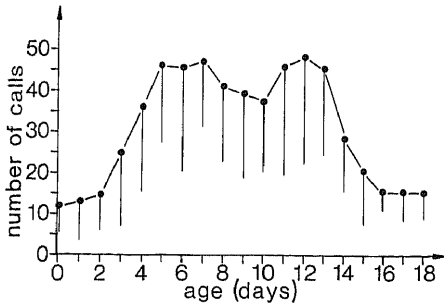
Figure 3. Average number of wriggling calls (with standard deviations) produced by mouse pups during a 30-min daily observation period while the mother was lying on at least part of the litter (average of 24 litters).

Figure 4B, C, D shows the numbers of the different maternal activities as a function of the age of the pups. It is equally evident from all three groups that licking was the most frequent spontaneous maternal behaviour. Spontaneous licking decreased after birth in all three groups ($P < 0.05$). Spontaneous nest building and changing suckling position were rather rare in normal and ULD females and somewhat more frequent in BLD mothers.

Figure 5 shows how spontaneous attention changed with the age of the pups. The average rate of occurrence of this activity was generally low and decreased in all three groups from day 1 to day 13 ($P < 0.05$ at least). There were no significant differences among the three groups of females on any day.

The average number of all maternal activities that followed wriggling calls is shown in Fig. 6A. In normal mothers, the rate of maternal behaviour following wriggling calls increased significantly between birth and day 5 ($P < 0.01$) and decreased thereafter (day 5 versus day 13: $P < 0.01$; day 13 versus day 18: $P < 0.02$). ULD mothers showed a significant increase (day 0 versus day 5: $P < 0.02$) and then a decrease from day 5 to day 10 ($P < 0.02$). If the average number of maternal responses to wriggling calls is compared among the three groups of females, normal mothers show significantly more maternal behaviour compared both with BLD mothers (on days 0, 1, 4–15: $P < 0.005$; on days 2, 3: $P < 0.02$) and with ULD mothers (on days 5, 9–12: $P < 0.05$ at least); ULD mothers also show more compared with BLD mothers (on days 3–7: $P < 0.01$; on days 1,2,8,9: $P < 0.05$). In general, unilaterally deafened females showed more maternal responses than bilaterally deafened ones and
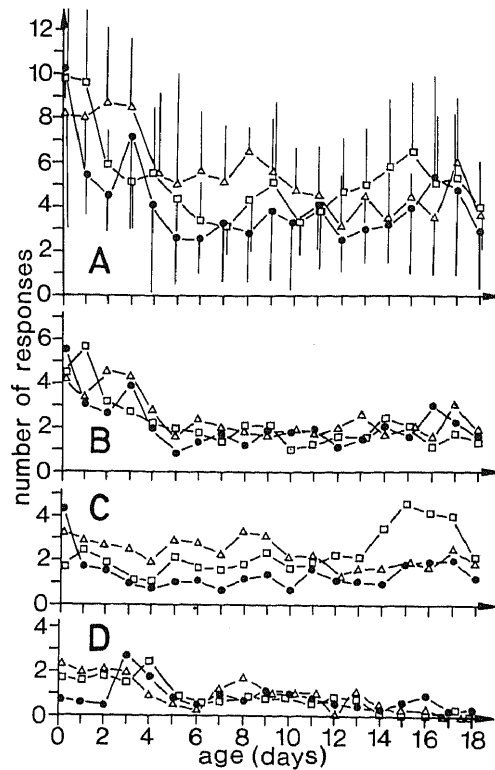

Figure 4. (A) Average numbers (with standard deviations) of all spontaneous maternal behaviours (sum of licking, changing position and nest building); (B) average numbers of spontaneous licking; (C) average numbers of changing suckling position; and (D) average numbers of nest building by normal, unilaterally (ULD) and bilaterally (BLD) deafened females as a function of the age of the pups. For key to symbols see Fig. 2.

normal mothers showed more than both the other groups. Since the rate of spontaneous activity was similar in all three groups (and if anything somewhat higher in BLD females), the increased maternal behaviour in normal and ULD mothers must be attributed to hearing wriggling calls. In BLD mice, the rate of apparent 'responses' after wriggling calls was almost equal to the predicted number of coincidences between maternal activity and preceding wriggling call production, calculated from the number of wriggling calls and the number of spontaneous maternal activities within the 30-min observation period. In ULD and normal females, the predicted number of coincidences was significantly smaller ($P < 0.005$) than the number of maternal responses that actually occurred after
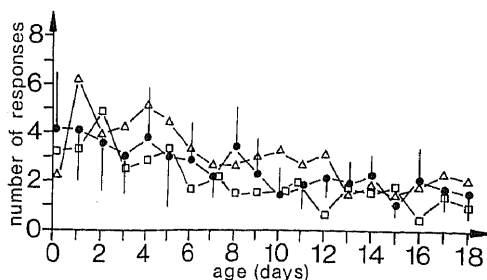
Figure 5. Average numbers of spontaneous attention responses by normal, ULD and BLD females as a function of the age of the pups. Standard deviations shown for normal mothers are also typical for the other groups. For key to symbols, see Fig. 2.

wriggling calls. This clearly confirms that wriggling calls are important elements of communication between mouse pups and their mothers.

Specificity of Responses to Wriggling Calls

Figure 6B, C, D shows the average numbers of the different maternal responses to wriggling calls as a function of the age of the pups. The values for BLD mothers (Fig. 6D) can be regarded as a result of coincidences between call production and spontaneous activity of the mother occurring merely by chance. Compared with these predictable 'pseudo-responses', normal and ULD females showed significantly more licking between days 0 and 15 and also more changing position and nest building during the first 7 days ($P < 0.005$ at least). It is obvious that licking was the most frequently shown maternal response to wriggling calls in ULD and normal mothers. Normal females showed more licking than nest building and changing position between days 1 and 15 ($P < 0.01$). Similarly, licking occurred more frequently in ULD mothers than changing position (days 0,1,3,4,5,7) and nest building (days 0, 3–9; $P < 0.02$). The high rate of the licking response between days 9 and 15 in normal females was absent in ULD females. In general, the rates of occurrence of the licking response increased from birth to days 5–7 and then decreased with increasing age of the pups.

Attention responses to wriggling calls are shown in Fig. 7. The values of BLD mice again represent the coincidence level between call production and spontaneous behaviour. Compared with these incidental pseudo-responses of BLD mothers, normal and ULD females showed more attention between days 2 and 15 (on days 4,6,7,8 and on day 14
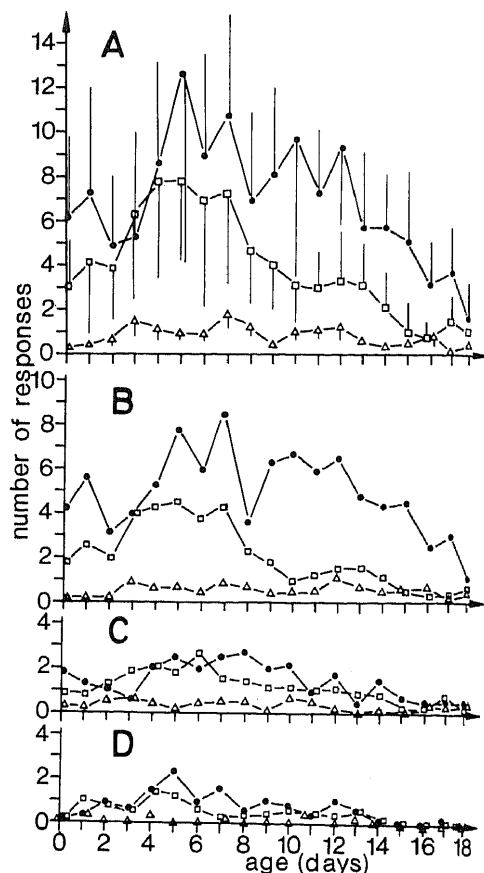

Figure 6. (A) Average numbers (with standard deviations) of all maternal responses to wriggling calls (sum of licking, changing position and nest building); (B) average numbers of licking; (C) average numbers of changing position; and (D) average numbers of nest building responses to wriggling calls by normal, unilaterally (ULD) and bilaterally (BLD) deafened females as a function of the age of the pups. For the key to symbols, see Fig. 2.

respectively; $P < 0.05$ at least). In normal females, attention responses, like maternal behaviour, first increased significantly ($P < 0.01$) after birth until day 7 and then decreased to very low values on day 16 ($P < 0.01$). An increase (between days 2 and 5) and a decrease (between days 5 and 16) are also statistically significant in ULD females ($P < 0.05$ at least).

Responses of Normal Females to Playbacks of Wriggling Calls

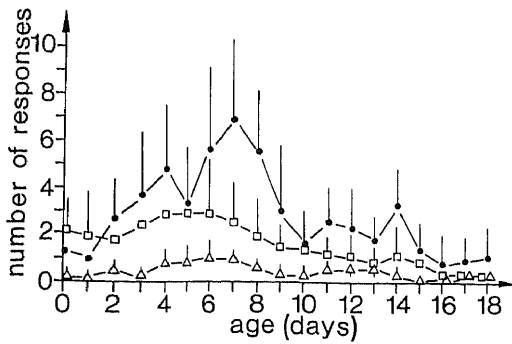Those females (NPB females) with paralysed

Figure 7. Average numbers (with standard deviations) of attention responses to wriggling calls by normal, ULD and BLD females as a function of the age of the pups. For key to symbols, see Fig. 2.

pups (5 or 7 days old) responded to playbacks of wriggling calls as shown in Fig. 8. The average numbers of licking, changing position, nest building and attention responses, the average total of maternal responses to wriggling calls and the average total of spontaneous maternal behaviours are presented. A comparison of these values from NPB mothers with those obtained from the other three groups demonstrates clearly that (a) NPB
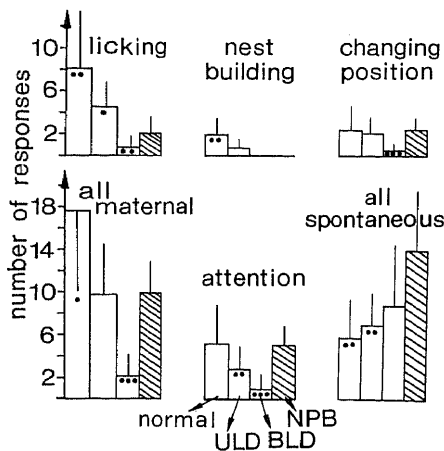

Figure 8. A comparison of wriggling-call-evoked responses and spontaneous activities of females of all four experimental groups. Averaged values with standard deviations from observations on days 5 and 7 after the birth of the pups are shown; normal: normal mothers; ULD: unilaterally deafened mothers; BLD: bilaterally deafened mothers; NPB: normal females with paralysed pups responding to playbacks of wriggling calls. The values of NPB mothers are compared statistically with those of the other groups. ●: $P < 0.02$; ●●: $P < 0.01$; ●●●: $P < 0.001$.

mothers responded significantly more often with maternal behaviour (licking and changing position) and with attention compared with BLD mothers; (b) NPB mothers showed significantly less call-induced licking and nest building compared with normal females; and (c) NPB mothers showed significantly more spontaneous maternal behaviour than normal and ULD mothers but there was no difference when compared with BLD females.

These results indicate that wriggling calls alone, without further activities on the part of the pups, are a significant stimulus for releasing maternal behaviour and attention in lactating females, while the presence of active pups is not an effective stimulus at all if wriggling calls are inaudible (BLD mothers). This is the final proof of the importance of wriggling calls as a releaser of maternal behaviour and of attention in lactating mice. It is also evident that wriggling calls in combination with active pups are more powerful in releasing licking behaviour than calls in combination with inactive pups.

DISCUSSION

The Behavioural Context of Wriggling Call Emission

Mouse pups typically produce wriggling calls when they are active in the nest and are pushing for the mother's teats. Pups older than 5 days also emitted these calls when they crawled over each other in the absence of the mother. We could not readily determine whether it was the pups pressing forward or those being pushed away that were the callers, although it often seemed that the more active pups emitted the calls. Thus, these observations of pup behaviour did not allow an unequivocal assessment of the motivational background of call emission. In view of the behavioural context of vocalization and of the maternal responses of the female, discussed below, we might hypothesize that wriggling calls signal a general search or need for maternal care when the mother is in the nest.

Functions of Wriggling Calls

The first function of wriggling calls is evident from Fig. 6: they release maternal behaviour. Licking of the pups was the most frequent response; rates of occurrence of changing suckling

position and of nest building were also increased, however, by wriggling calls. The need for an external stimulus to elicit these maternal activities is obvious from Fig. 4. From the birth of the pups to day 5, spontaneous licking, changing suckling position (at least in normal females) and nest building decreased rapidly. Such a decrease in the rate of maternal behaviour of lactating females during the first week, especially in the rate of licking pups, has also been reported by Noirot (1964), Priestnall (1983) and König (1985). After delivery, the mothers obviously lose maternal interest in their pups very rapidly (Scudder et al. 1967), and maternal behaviour is kept at a high level only by external stimuli from the pups, which may function as an indicator of the vitality of the young. Our present results show that wriggling calls are, in fact, typical of healthy and active pups and that they are a powerful stimulus in maintaining licking of the pups over the first 2 weeks of life. It is interesting that the calling rate showed a rapid increase between birth and day 5 (Fig. 3), which is the same period during which spontaneous maternal behaviour dropped markedly (Figs 6, 9). Thus the rate of wriggling call production counteracted the loss of maternal motivation in the females so that a high level of maternal care was guaranteed beyond the first few days after birth. Figure 9 indicates that the responsiveness of the females to wriggling calls decreased with the age of the pups from day 1 to day 10, by which time a fairly constant level was reached, with 20–25% of calls resulting in a response. Responsiveness to calls obviously decreased more slowly than spontaneous maternal behaviour and did not drop to zero during our observation period (Fig. 9). This is further evidence for the external control (with a significant contribution from wriggling calls) of maternal behaviour in lactating female mice.

We conclude that the production of wriggling calls by mouse pups has evolved as an effective strategy to keep maternal behaviour (mainly licking of pups) at a high level during the first 2 weeks of life where, otherwise, maternal activities would drop considerably. It has been shown (Hafez 1970; Coulon 1971) that licking of the trunk and of the anogenital region by the mother is important for stimulating digestion, urination and defaecation in the pups. Thus maternal behaviour in response to wriggling calls contributes significantly to the normal development of the pups and offers an explanation for the reduced weight of pups raised
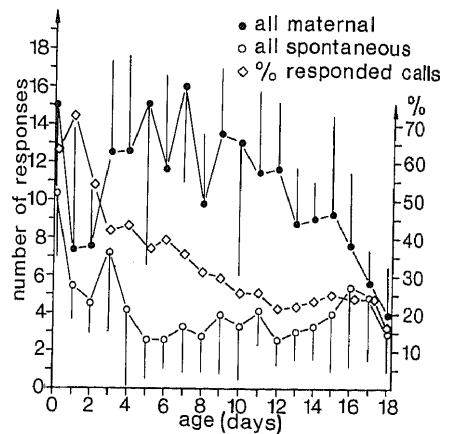

Figure 9. Left ordinate: average numbers (with standard deviations) of all maternal responses (sum of licking, changing position and nest building) compared with the average of all spontaneous maternal responses by normal females within the 30-min daily observation period as a function of the age of the pups. The difference between the two curves is the average number of responses to wriggling calls. Right ordinate: percentage of wriggling calls to which mothers showed a response (maternal and attention).

by binaurally deafened mothers compared with those raised by unilaterally deafened or normal hearing mothers (Fig. 2).

A second function of wriggling calls can be inferred from the increased rate of attention responses to the calls, mainly between days 2 and 9 after birth of the pups. Obviously, wriggling calls keep the mothers alert when they would otherwise tend to fall asleep while nursing their pups. Sleeping females do not show licking behaviour and other maternal activities like changing suckling position which would help unsuccessful pups to reach the teats. Keeping the mother alert by wriggling calls could, therefore, increase the probability of occurrence of maternal behaviour.

Whether or not wriggling calls have a third function, namely the induction of oxytocin release and milk ejection as in human mothers responding to baby calls (Vuorenkoski 1975), cannot be decided on the basis of the present data. Besides taking care of the pups, this would be the most direct maternal response to wriggling calls and would certainly be very adaptive in the behavioural context of call emission.

Differences in Responses among the Experimental Groups

Normal hearing females with normal pups

showed the highest responsiveness to wriggling calls and this call-evoked maternal care extended up to the 14–15th day after the birth of the pups. Unilaterally deafened females were less responsive to the calls, particularly to those of older pups (Figs 6, 7). This difference in response rate between normal and ULD mothers can be explained by the hearing deficit of ULD mothers. Since wriggling calls are, in general, of rather low intensity (mostly between 40 and 70 dB sound pressure level) and can be attenuated by pups covering each other, by the nest material, and by the female covering the pups, unilateral hearing loss could be expected to decrease the audibility of the calls and thus the probability of a response, especially if we assume a certain threshold intensity to be necessary for release of a response.

The pseudo-responses of bilaterally deafened females are very rare and are a result of coincidences between spontaneous maternal behaviour and call production. As if compensating somewhat for not responding to calls, BLD mothers showed a slight increase in spontaneous maternal activities and of spontaneous attention, mainly towards younger pups, compared with normal and ULD females (Figs 4, 5, 8).

The highest spontaneous rate of maternal behaviour was observed in females with paralysed pups. These females, however, were also quite nervous in the test situation (their pups did not move and calls were played back from above the nest) so that the increased level of spontaneous maternal activity could be attributed to the experimental situation. It is interesting, however, that these females licked their paralysed pups considerably less in response to wriggling calls compared to normal hearing mothers with active pups (Fig. 8), while changing position and attention occurred at the same rates. This is evidence for licking of pups being elicited, not only by wriggling calls alone, but to an even greater extent by wriggling calls supported by movements of the pups. On the other hand, movements alone had no effect. Thus, this seems to be a case of heterogeneous summation of external stimuli for the release of an instinctive behaviour (licking of pups).

Wriggling Calls and the Call Repertoire of Mouse Pups

With the present results it is clear that all three tonal calls of the mouse pup sound repertoire have

significance in intraspecific communication: (a) pure ultrasounds release mainly pup approach and retrieving in adults (e.g. Smith & Sales 1980; Ehret & Haack 1982, 1984); (b) broad-band pain calls inhibit biting and injuring by adults (Bernecker 1983; Haack et al. 1983); and (c) low-frequency wriggling calls release maternal behaviour, particularly licking of the pups (present study). Apparently, ultrasounds and wriggling calls elicit different patterns of maternal behaviour which are appropriate in the respective releasing situations (either leaving the nest and looking for a lost pup or staying in the nest and caring for the pups there). We showed that, in the situation when wriggling calls were produced, pure ultrasounds did not occur; on the other hand, wriggling sounds were never heard from lost pups that emitted ultrasounds (personal observations). Although the motivation of the pups while producing wriggling calls is not yet known, the behavioural contexts and motivational backgrounds associated with wriggling call and ultrasound production seem to be mutually exclusive. Similarly, the responses of lactating females to ultrasounds and wriggling calls seem to be stimulus specific and mutually exclusive: licking of the pups is not induced by ultrasounds (Noirot 1964; Hennessy et al. 1980; personal observations) and leaving the nest and pup searching is not stimulated by wriggling calls. This is evidence for two functionally different communication systems between mouse pups and their mothers. The mechanism of perception and recognition of ultrasounds by lactating female mice excludes confusion with the perception of wriggling calls (Ehret & Haack 1982).

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