12-1989

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Recommended Citation

Rushen, J., & Fraser, D. (1989). Nutritive and nonnutritive sucking and the temporal organization of the sucking behavior of domestic piglets. Developmental psychobiology, 22(8), 789-801.

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ABSTRACT

Detailed video recordings of the suckling behavior of one piglet from each of four litters were analyzed to determine how the components of piglet suckling behavior are organized in relation to the time of milk ejection and the temporal pattern of grunting by the sow. Early in the suckling episode, most piglets massaged the udder with their snouts, and then changed gradually to sucking the teats with slow mouth movements (1-2/sec). The piglets then had a distinct phase of sucking with rapid mouth movements (4-5/sec) which began suddenly and lasted about 5 to 15 sec. The weight gains of piglets removed at different times, showed that piglets consumed milk during the fast sucking but not during the preceding slow sucking, regardless of how much slow sucking had occurred. Three of the four sows showed a characteristic increase in rate of grunting about 20 to 25 sec before fast sucking began. The piglets' change from massaging to slow sucking often coincided with the increase in grunt rate, but the timing of the transition varied greatly. This suggests that the change in grunting is one but not the only cue used by the piglets to time their suckling behavior. During the slow, nonnutritive sucking, mouth movements were highly variable in duration, with occasional short bursts of rapid mouth movements. This contrasted with the more uniform duration of fast sucking movements. Evidently, in piglets, nutritive and nonnutritive sucking differ in both rate and temporal patterning.

Suckling behavior provides one example of how the behavior of young can be an age-specific adaptation to their unique requirements and to the maternal environment, rather than a simple precursor of more complex adult behavior (Hall & Williams, 1983). The suckling behavior of swine is especially interesting since it has some notable characteristics (Fraser, 1980) which are adaptations of the young to the peculiarities of the lactational physiology of sows (reviewed by Bissett, 1974; Ellendorf, Forsling, & Poulain, 1982; Hartmann, McCauley, Gooneratne & Witely, 1984).

The sequence of behavioral and physiological events culminating in milk ingestion by piglets has had considerable research (reviewed by Fraser, 1980, with more recent work by Ellendorff et al., 1982; Algers & Jensen, 1985; lllmann & Herbst, 1986; Algers, 1989), but several controversial points have arisen.

First, it is not clear how the piglets know when to switch from the preliminary massaging of the udder to actual sucking. Because the sow's mammary glands lack an anatomical cistern (Turner, 1939), the piglets ingest milk only during milk ejection, which represent only about 10-20 sec of each 2- to 3-min nursing episode (Barber, Braude, & Mitchell, 1955). The sow requires a great deal of mechanical stimulation of the udder before oxytocin is released and milk subsequently ejected (Fraser, 1975: Ellendorff et al., 1982; Algers, Rojanasthier, & Uvnäs-Moberg, in press). Consequently, most of the piglets' time on the udder is spent in vigorous massage of the teats rather than in sucking (Barber et al., 1955; Gill & Thomson, 1956). Piglets must stop massaging soon after oxytocin has been released so as not to miss the brief milk ejection. The rhythmic grunting of sows during nursing is unique in the sharp increase in rate that occurs (Fraser, 1973; Whittemore & Fraser, 1974). Since this increase in grunt rate appears to accompany the release of oxytocin (Ellendorff et al., 1982; Algers et al., in press), it might serve as an appropriate signal for the piglets to switch from massaging to sucking (Fraser, 1980). Data reported by Alger and Jensen (1985) tend to support this idea. Observations on our own herd, however, make us question how closely the rate of grunting controls the piglets' behavior.

Second, observations by Barber et al. (1955), Whittemore and Fraser (1974), and others led to the conclusion that piglets have two distinct modes of sucking: (a) sucking with slow, large-amplitude mouth movements, when milk is not being ingested, and (b) sucking with rapid, uniform mouth movements, during the period of milk ingestion. This interpretation runs contrary to the view of Wolff (1968, 1973, 1986) who claims that only human infants have two distinct modes of sucking that are used depending on whether milk is being obtained. According to Wolff, "differences between human and other mammals in the temporal organization of sucking behavior may represent a qualitative change in central nervous system control over the sucking reflex" (Wolff. 1968, p. 363), and the difference "qualitatively differentiates humans from other mammals" (Wolff, 1973, p. 256). This view has gained considerable acceptance (Crook, 1976: Herring, 1985: Daniels, Devlieger, Casaer, Callens, & Eggermont, 1986), but it will obviously require revision if the pig does, indeed have distinct modes of sucking.

Third, the occurrence of two phases of sucking has caused some confusion over the timing of milk ingestion by the piglets. Whittemore and Fraser (1974), supporting earlier observations by Barber et al. (1955), described a "quiet" phase of sucking with slow mouth movements between the phase of massaging the udder and the beginning of the milk ejection, which was apparent in a sudden change to rapid sucking. However, Gill and Thornton (1956) and Ellendorff et al. (1982) report only one phase of sucking, beginning immediately after the initial massage of the udder and, in the latter study, coinciding with the increase in intramammary pressure. On this basis, Ellendorff et al. (1982) and Ellendorff and Poulain (1984) contended that milk is ingested in the "quiet" phase, contrary to the conclusions of Barber et al. (1955) and Whittemore and Fraser (1974).

As Algers and Jensen (1985) have pointed out, many of the problems with the description of the suckling behavior of piglets lie in the crudity of the recording techniques used. Generally, the observers have made broad judgments about the behavior of the entire litter and have "averaged" records from many litters. We obtained detailed recordings of the suckling behavior of individual piglets and measured their actual milk consumption for the following purposes:

1. to clarify whether pigs do indeed have two distinct modes of sucking;
2. to clarify whether milk is obtained during the period of fast sucking but not during the preceding period of low sucking;
3. to consider how the piglets accomplish the transition from massaging to sucking so as not to miss any part of the brief milk ejection.

Methods

The normal pattern of synchronized suckling associated with the distinctive grunting of the sow develops gradually over the first 12 hr and is well established by the 2nd day (Algers, 1989; de Passillé and Rushen, 1989), with only quantitative changes occurring until the piglets are weaned (Jensen, 1988). For domestic pigs in seminatural conditions, weaning is a gradual process that is completed sometime between 8 and 20 weeks of age (Newberry and Wood-Gush, 1985; Jensen, 1986, 1988), although in commercial conditions, sudden artificial weaning at 4 weeks is most common. We observed piglets that were 2 to 4 weeks old, so that the normal pattern of nursing was well established.

To quantify the behavioral changes that occur during a nursing, we videotaped several nursing episodes of one piglet chosen from each of four sows and analyzed the tapes on a second-by-second basis. Recording were made at 60 fields/sec, each with the time of the recording shown with 1-sec precision.

Animals and Housing

Four Yorkshire sows of third to eighth parity from the herd of the Animal Research Centre were individually housed in a pen that allowed the piglets unimpeded access to the udder. The pen was in a quiet room in which there were no other sows present. The sow and litter were moved into the pen within 3 days after parturition, and the piglets were observed when they were 9 to 15 days old. From each litter, one "target piglet", chosen because it could be followed easily by the camera, was selected for detailed observations.

Method of Recording

A video camera was mounted on a tripod at the front or rear of the pen, less than 1 m from the sow. The camera was fitted with a 50-rnm ten and positioned so that the head of the target piglet filled the screen. The resulting video recordings allowed the opening and closing of the piglet's mouth to be followed in detail and timed to an accuracy of one video field ($^1/_{60}$ sec). For each recording, the experimenter remained in the room until a nursing seemed about to begin. He then positioned a microphone (leading to the video recorder) within 20 cm of the sow's head turned on the video recorder, and operated the camera to keep the piglet's head within the field of view. The recording was continued until the piglet left its teat after milk ejection or unlit it became clear that no milk ejection would occur: generally the recordings were 3-5 min long. Sufficient recordings were obtained over days 2 through 7 to ensure that about 10 usable recordings for each piglet were available for analysis. Of the 85 recordings obtained, we rejected those in which the record of grunt was not audible, those in which no milk ejection was observed (23% of all nursings), those in which the piglet could not be observed continuously for at least 40 sec before or at least 15 sec after the start of fast sucking, and those in which the piglet fought over a teat.

Analysis of the Recordings

The observer viewed the tapes several times at $^1/_6$ or $^1/_{12}$ normal speed and recorded three features of piglet behavior during each 1-sec interval. Massaging the udder was scored if the piglet pushed its snout into the udder and lifted the snout upwards at least once in the 1-sec interval. Small movements of the head, for example when the piglet took the teat deeper into its mouth, were ignored. Attachment to the teat was scored if the piglet had the teat in its mouth without simultaneously massaging at any time in the 1-sec interval. Each behavior was scored simply as absent or present in each second (one-zero scores: Martin & Bateson, 1986). lf the piglet had the teal in its mouth throughout the entire 1-sec interval, then the frequency of sucking was recorded. This was defined as the number of cycles of the mouth opening and closing on the teat, disregarding the amplitude of the movements and the degree of closure of the

mouth. In addition, the number of grunts by the sow in each 1-sec interval of the nursings was recorded. Three observers were used, but each record was analyzed by only one person and the consistency of the observers was checked.

The records for each piglet were aligned by the 1-sec interval during which fast sucking began. This was defined as the 1-sec interval in which the piglet's rate of mouth movements increased abruptly to 3-5 movements/sec with this rate sustained for at least 5 sec thereafter. For each piglet, we calculated the mean frequency of sucking in each 1-sec interval before and during fast sucking. We then grouped the 1-sec interval into 5-sec periods, and calculated the mean frequency of grunts and the proportion of 1-sec intervals in which the piglet massaged or was attached to the teat.

Recording of three suckling episode (chosen on the basis of good picture quality) per piglet were analyzed field by field to determine the duration of sucking movement for the 10 sec before and the 5 sec after the beginning of rapid sucking. The duration of a sucking movement was defined as the number of fields elapsed between successive closures of the mouth (i.e., the maximum closure that was reached before the mouth began to open again), with each field representing $^1/_{60}$ sec.

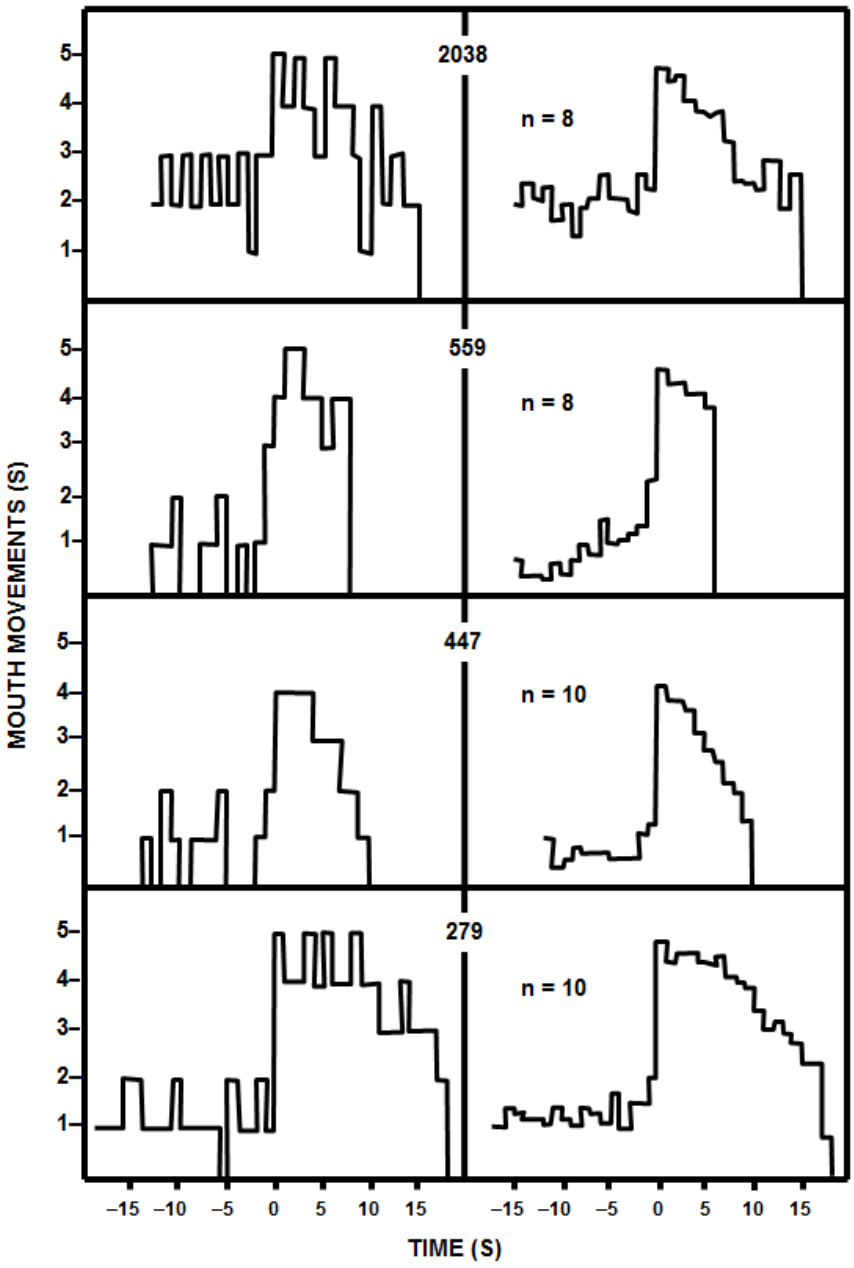
To determine how massaging and time attached to the teat changed in relation to the pattern of grunts we realigned the record for the individual piglets according to the 1-sec interval in which fast grunting began. We grouped the 1-sec intervals into 10-sec periods, three before the start of fast grunting and two after. For each 10-sec period, we calculated the mean (over piglets) proportion of 1-sec interval in which the piglet massaged or was on the teat, and used analysis of variance with Tukey's paired comparison test to see if these measures changed over time. The identity of the piglet was included as a factor. Since both measures were skewed, we used a logarithmic transformation of the data. Unfortunately, one sow (sow 279 in Figure 4) had an unusually low frequency of grunting and so was excluded from this last analysis.

Milk Intake Studies

The litters were studied for a further six nursing at 18 to 25 days of age to establish whether milk is obtained only during fast sucking. No substantial changes in the nature of the suckling behavior had occurred since our first observations. For three of the nursings, all the piglets were allowed to suckle until fast sucking ended and the nursing was over. For the other three nursings, the target piglets were removed from the home pen about 15 sec after rapid grunting had begun, a few seconds before fast sucking was expected to begin. Apart from a few mistakes, these two conditions were alternated. In both conditions, the remaining piglets in the litter were allowed to suckle until the nursings were over. For one sow that did not have a clear increase in the rate of grunting 20-25 sec before rapid sucking, a subtle change in the tonal properties of the grunts occurred at the corresponding time and was used to time the removal of the target piglet.

Before the first nursing and after each subsequent nursing, all of the piglets in the litter were removed from the home pen and placed together in a mall box bedded with sawdust for 60 min and then returned to the home pen. With this procedure, nursing reliably occurred soon after the piglets were returned. Before being returned, the target piglet and three haphazardly chosen litter/mates were weighed within an accuracy of 2-3 g on a Mettler PE-24 balance. These piglets were watched carefully during nursing to ensure that they did not urinate or defecate, and they were reweighed immediately on removal: the difference in weight was assumed to indicate the amount of milk consumed. The piglets were videotaped during each nursing. ln analyzing the tapes, we counted the number of seconds that the piglet sucked with slow mouth movements before it began fast sucking or was removed.

Fig. 1. The number of sucking movements per second, before and after the onset of fast sucking. At the left, the record of one representative suckling episode for the piglet filmed in each of the 4 litters. At the right, average values based on 8-10 episodes per piglet.



Results

Figure 1 shows, for each piglet, the rate of sucking in each second before and after fast sucking was first observed. The figure shows both a single record for each piglet and the average values based on the full 8 to 10 record available. Two phases of sucking are apparent. Initially, the piglets suck at a rate of 1-2 (or occasionally 3) mouth movements/sec. The rate suddenly increases to 4-5/sec and decreases gradually over the next 5-15 sec. These values are similar to those previously reported by Whittemore and Fraser (1974).

Fig. 2. The time of successive sucking movements (each vertical line indicates closure of the mouth) by the target piglet of litter 2038 during approximately 5 sec before and 5 sec after the beginning of fast sucking. The upper record (before the fast sucking phase) includes a burst of 3 relatively rapid mouth closures at the end of the first and third seconds, with longer and more variable intervals, during the rest of the period.

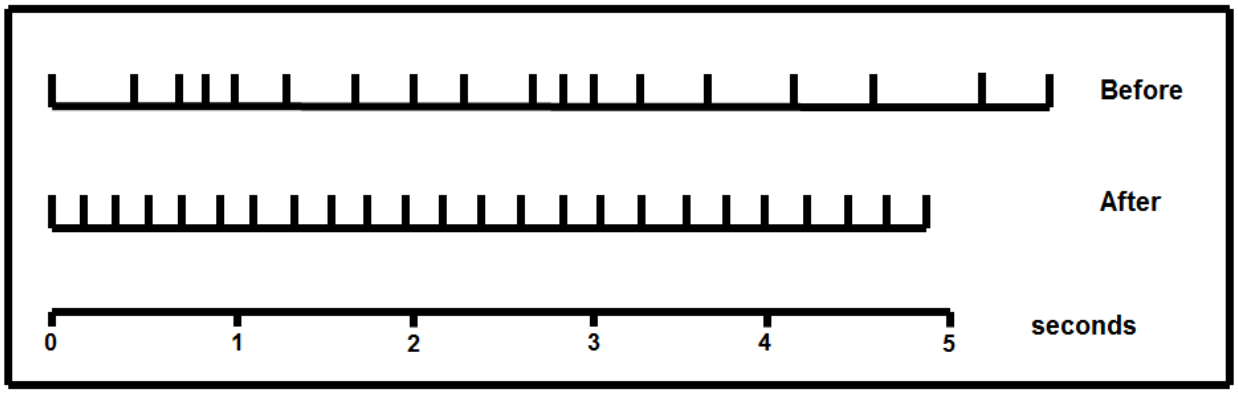
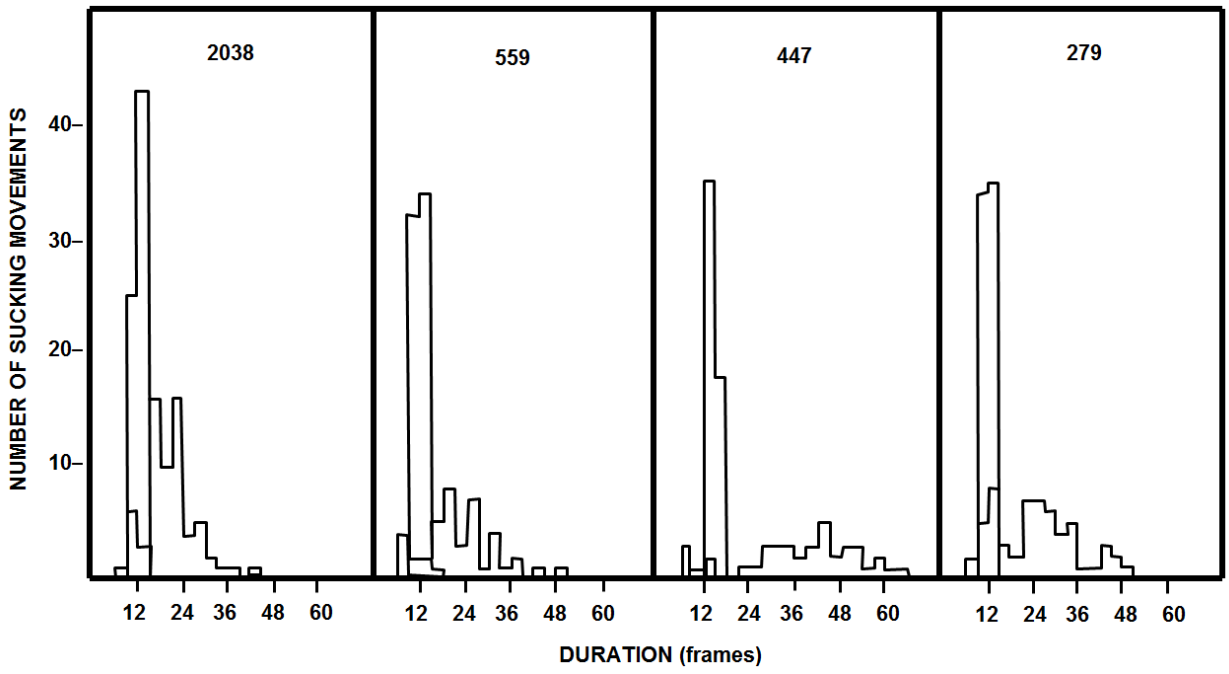


Fig. 3. Frequency distribution of the number of sucking movements of various durations during the 10 sec before (open bars) and the 5 sec after (shaded bars) the onset of fast sucking. The duration of a sucking movement was defined as the number of video fields elapsed between successive closures of the mouth, filmed at 60 fields\sec. Results are shown for 1 piglet in each of the 4 litters and are based on 3 suckling episodes for each piglet.



Two other differences between the phases of slow and fast sucking were apparent. First, the duration of sucking movements was highly variable during slow sucking but much more uniform during fast sucking. Figure 2 shows a typical record. Figure 3 summarizes the duration of sucking movements for the 4 piglets. During the 10 sec before fast sucking began, successive mouth closures occurred at intervals of 7-74 fields (0.12-1.23 sec), often with bursts of 2 or 3 rapid sucking movements separated by several longer movements of variable duration. During the first 5 sec of fast sucking, most sucking movements

lasted 12-16 fields, with extreme values of 10 and 18 fields (0.17-0.30 sec). Second, mouth movements were generally of large amplitude (with the tongue visible and wrapped around the teal) during slow sucking, but of smaller amplitude during fast sucking.

Fig. 4. Mean number of grunts (top section), mean proportion of seconds that involved attachment to the teat (center section), and mean proportion of seconds that involved massaging the udder (bottom section) per 5-sec interval before and after the beginning of the apparent milk ejection, shown by the dashed vertical line. Each quarter of the figure shows results from 1 piglet, each from a different litter, averaged over 8-10 suckling episodes.

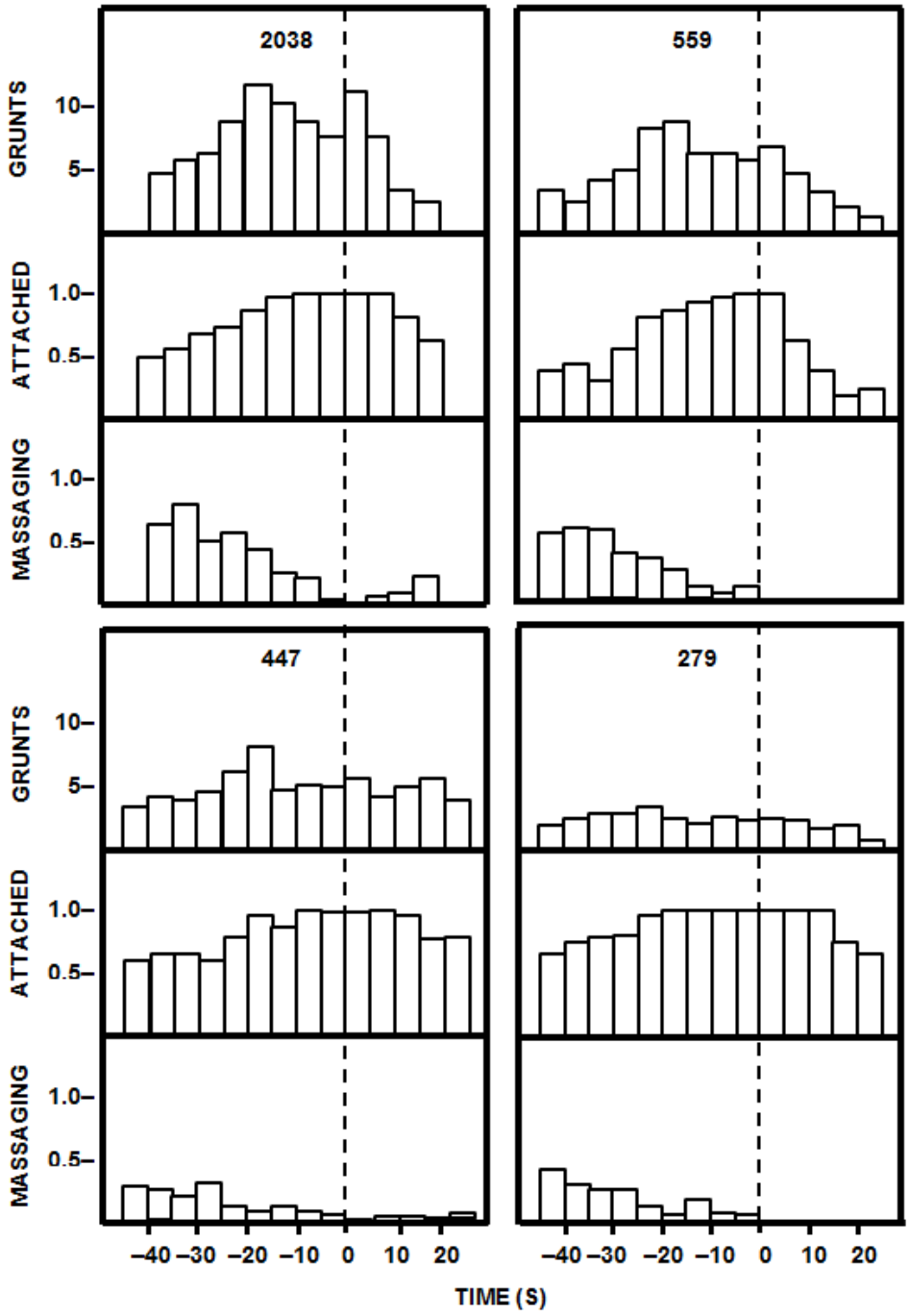
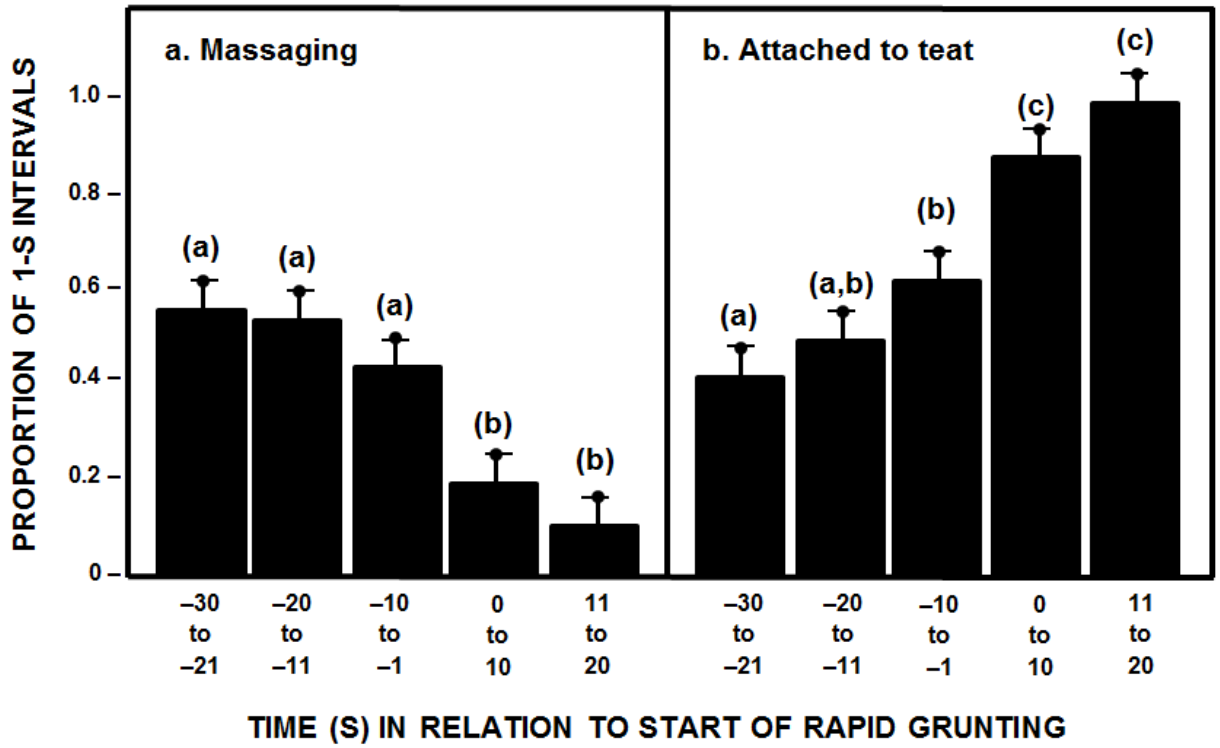


Figure 4 shows the rate of grunting by the sow, the proportion of time that the piglet was on the teal, and the proportion of time that the piglet was massaging the udder. Three sows (number 2038, *559.* and 447), showed a definite peak in their rate of grunting about 20 sec before the start of fast sucking by the piglet: for two of these sows, there was a second peak in the 5 sec following the start of fast sucking. For the piglets of these three sows, there was a decrease in the time spent massaging and a gradual increase in the time spent attached to the teal as nursing progressed. The rate of grunting by the fourth sow (number 279) was very low and changed little. The piglet of this sow massaged infrequently and was attached to the teat much of the time.

For the sows that did show a peak in grunt rate, we measured the interval between the increase in grunt rate and the start of fast sucking for each individual record. The values for each piglet were as follows: sow 2038, mean = 21.6 sec, CV = 11.0%, range 7 sec; sow 559, mean = 23.0 sec, CV = 11.9%, range 8 sec; sow 447, mean = 22.2 sec, CV = 10.6%, range 8 sec.

Fig. 5. Mean (+SE) proportion of 1-sec intervals in which piglet, (a) massaged or (b) were attached to a teat, at various times relative to the increase in grunt rate (time 0). Means with same letter do not differ significantly (p > .05).



The transition from massaging the udder to attachment to the teat was relatively gradual (Figure 4), with no sudden change coinciding with the increase in rate of grunting. In part, this could be due to averaging several nursings with different intervals between the change in grunt rate and the tart of fast sucking. Figure 5 avoids this problem by showing the time spent massaging and the time spent attached to the teat in each 10-sec period when the individual records were realigned by the 1-sec interval during which fast grunting began. There were significant overall differences between the periods in both the time spent massaging, F (4,96) = 18.20, $p < .001$, and the time spent attached to the teat, F (4,96) = 16.76, $p < .001$. The largest and the only statistically significant difference in massaging was between the periods before and the period after the increase in grunt rate. Nevertheless, there was a non-significant trend for

a decrease in massaging before the grunt rate increased (Figure 5a). The largest difference in the time spent attached to the teat was also between the period before and the periods after the increase in grunt rate. However, there was a statistically significant increase before the grunt rate changed (Figure 5b).

Milk Intake in Relation to Suckling Behavior

When the target piglets were removed just before the beginning of fast sucking, they had negligible weight change during the nursing (mean ± SD of –1.6 ± 2.9 g; see Table 1). When removed after the phase of fast sucking, weight change averaged 57.8 ± 26.9 g. The amount of low sucking differed only slightly between these two conditions and bore no relation to the piglet weight change (Table 1). Weighing of three other piglets in the litter confirmed that milk ejection had occurred in each of the nursings studied, with weight gains of the other littermates averaging 40.8 ± 19.8 g.

Discussion

Two Modes of Sucking?

Our results show (a) that piglet have a well-defined period of fast sucking which begins with a sharp increase in the rate of sucking movements, (b) that milk daily milk intake. Consequently, being on the teat and sucking throughout the milk ejection should be a higher priority behavior than massaging. We suggest that piglets do not need to be stimulated to suck by hearing rapid grunting. Rather, sucking on a teat is the ''fall back'' behavior that piglets revert to when uncertain about the likelihood of a milk ejection. Continued slow grunting may indicate a “safe period"' during which a milk ejection is unlikely and massaging can safely proceed. This is supported by the increased time spent sucking and the decreased amount of massaging when the piglet is unable to hear the peak in grunting (Figure 4, Sow 279; Algers & Jensen, 1985).

The increase in grunt rate is sometimes inaudible, can he masked by noise, and is often indistinct in primiparous sows (Whittemore & Fraser, 1974). Given the importance of making an optimal switch, it seems unlikely that piglets would depend on such an unreliable signal as the sole source of information about the likelihood of a milk ejection.

Notes

This is Animal Research Centre contribution No 1576. J. Rushen (Present address: Dept. of Animal Science, University of Alberta, Edmonton, Ala. T6G 2P5. Canada) had a Visiting Fellowship awarded by the Natural Sciences and Engineering Research Council of Canada when the research was carried out, and a Research Fellowship from the Alexander von Humboldt Foundation when the paper was written. We thank Greg Appleyard and R A Arcand for excellent technical assistance and Bo Algers for his useful comments.

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