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A Review of the Behavioural Mechanism of Milk Ejection of the Domestic Pig

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ABSTRACT

The domestic pig has complex nursing and suckling behaviour, consisting of several distinct phases of suckling by the piglets and a characteristic pattern of grunting by the sow. A review of observations and experimental findings suggests cause-and-effect relationships between the different elements of sow and piglet behaviour, and the relationship of the behaviour to milk ejection. Characteristic features of pig nursing and suckling behaviour are interpreted as an adaptation promoting even distribution of milk among a number of precocious litter-mates.

INTRODUCTION

The nursing and suckling behaviour of the domestic pig has a number of characteristic features. At each nursing, the piglets progress through a sequence of several distinct phases of suckling behaviour which may last for a total of 2 or 3 min, while the actual flow of milk from the udder is commonly confined to a mere 10 or 20 s towards the end of the episode. The sow, when nursing, generally gives loud, rhythmic vocalizations related to the behaviour of the piglets and the time of milk flow. Under commercial conditions, sows often nurse 20 or more times per day for several weeks after parturition.

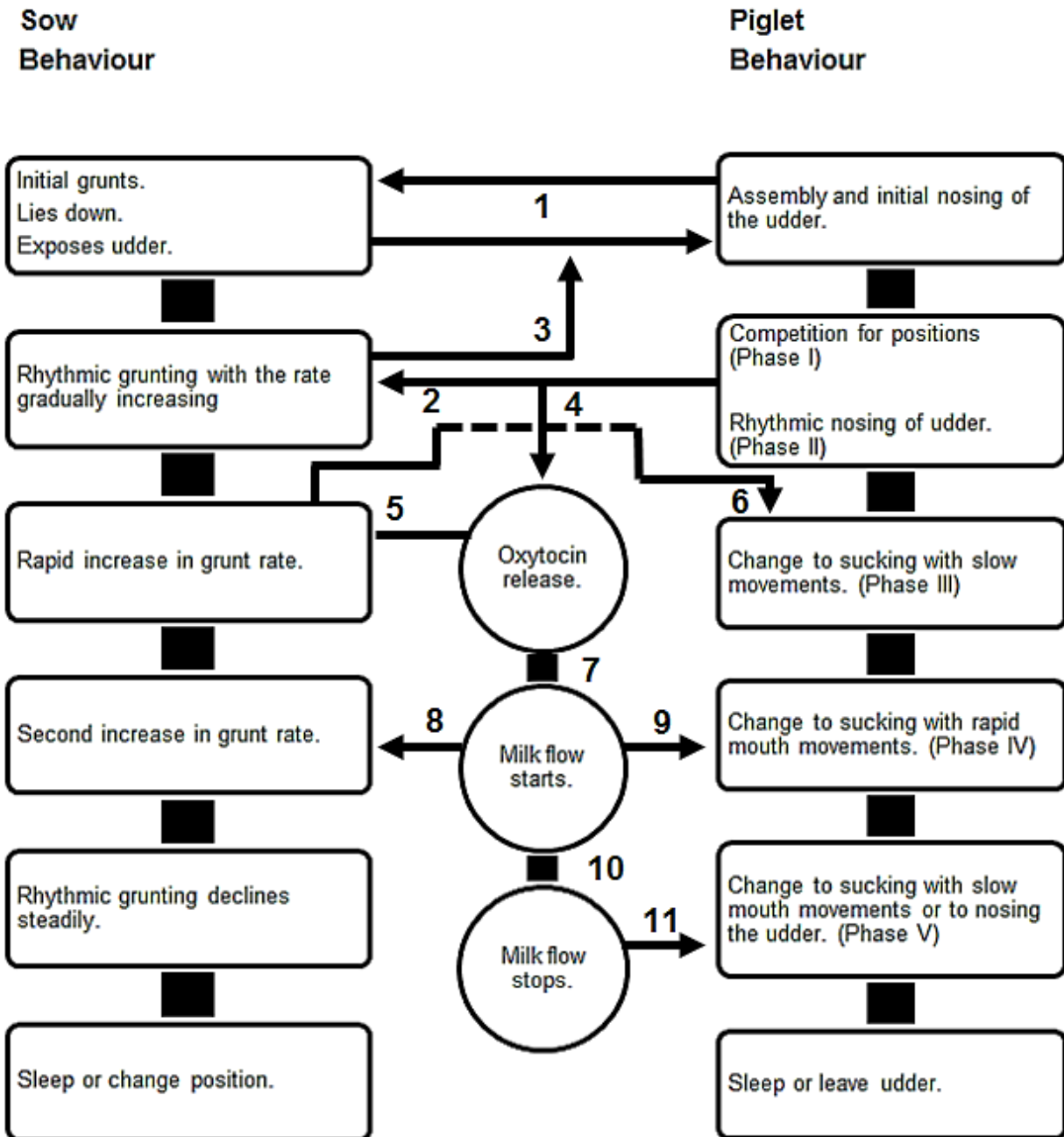
This behaviour is related in numerous ways to the health and productivity of the animals and has been the subject of considerable study. The present paper attempts to bring together a number of recent findings in developing an overall picture of the behavioural mechanism of milk ejection in the domestic pig. In so doing, the paper may serve to review, for ethological readers, a literature which has largely appeared in veterinary and agricultural periodicals.

SUCKLING BEHAVIOUR OF THE PIGLETS

The piglets' behaviour preliminary to suckling is highly variable. The animals generally assemble by the sow, sometimes grunting and squealing, frequently nosing at the udder and sucking on any exposed teats. This may be done in response to movement or grunting by the sow, or may be triggered by an external stimulus such as the sound of another litter suckling, or the behaviour may begin in an apparently spontaneous and contagious manner.

Once the piglets begin to assemble, five distinct phases of suckling behaviour can generally be distinguished, although they may be unclear with piglets less than one week of age or with a first parity sow. The following description is based on Whittemore and Fraser (1974), revised from the original observations of Barber et al. (1955), and is summarized in Fig. 1.

Fig. 1. Proposed behavioural mechanism of milk ejection and related activities of domestic pigs. (1) Reciprocal evoking of preliminary activities by sow and piglets. (2) Mechanical stimulation of the udder by the piglets elicits rhythmic grunting by the sow, which serves (3) to attract any remaining piglets to the udder. (4) The stimulation summates over time to trigger the milk ejection reflex, presumably by the release of oxytocin from the pituitary. This is accompanied (5) by a rapid increase in the sow's grunt rate which may (6, ?) be heard by the piglets and encourage them to begin sucking with slow mouth movements. (7) After a set interval, usually about 25 s, milk appears on the udder. This is often accompanied (8) by a second increase in grunt rate, usually less pronounced than the first. With the appearance of the milk, the piglets (9) begin ingesting it by sucking with rapid mouth movements. (10) Milk flow ends after a set interval, usually about 15 s, causing the piglets to return to sucking with slow mouth movements or nosing the udder (11).



In Phase I the piglets arrange themselves, usually one to each functional teat, in an order which is similar from one nursing to the next (McBride, 1963; Van Loen and Molenaar, 1967; Hemsworth et al., 1976). Some jostling for positions is common and may last for a few seconds or for several minutes.

As the animals settle into their positions they begin to massage the udder rhythmically with vigorous up-and-down movements of the snout (Phase II). This commonly lasts about one minute.

The change to Phase III can be gradual or abrupt. In this phase the piglets suck on the teats with slow mouth movements (about one per second) of large amplitude with the tongue generally visible and wrapped around the teat. These slow movements are frequently interspersed with brief bursts of several very rapid sucking movements. The head is usually held still, and the ears are often erect. Phase III typically lasts about 20 s.

Phase IV begins about the same time for all piglets. The animals begin sucking with uniform, rapid mouth movements (about three per second) often coupled with gentle movements of the head. The ears are frequently flattened and the piglets may draw back slightly from the udder extending the teats noticeably. This phase ends abruptly, typically after 10-20 s.

With the end of Phase IV the piglets frequently dart their mouths from teat to teat, and they may resume sucking with slow mouth movements or nosing the udder (Phase V). The final behaviour is as variable as the first: piglets may leave the udder promptly, or they may continue nosing the teats, falling asleep in position or moving away at any time.

Other classifications of the stages of suckling have been used. Donald (1937) noted only one phase of sucking on the teats between the initial and final nosing of the udder with the snout. Since the one sucking phase lasted 35-45 s on average, it may have represented a combination of Phases III and IV. Gill and Thomson (1956) noted only one sucking phase, lasting 14 s on average, between the initial and final massage of the udder. The short duration of this phase, coupled with the observation of "frequent trial sucks" in the latter part of the initial massage, suggests that this sucking phase corresponds to Phase IV, with Phases II and III both included in the initial massage.

The distinct third phase, coming between the initial massage and the rapid sucking, was first reported by Barber et al. (1955). Using first-parity females, they began to notice the phase only when the piglets were six weeks of age. With experienced sows, however, the third phase has been distinguished clearly from the end of the first week of lactation (Whittemore and Fraser, 1974).

THE TIME OF MILK FLOW

Milk appears to be available in quantity only during Phase IV, at which time the piglets gulp it down with their rapid sucking movements. C.T. Whittemore (personal communication, 1972) removed individual piglets at different times during sucklings, and found no change in weight unless Phase IV had begun. Donald (1937) concluded that piglets gain no measurable weight during prolonged final massage of the udder (Phase V), and piglets have been found to gain no measurable weight during abnormal sucklings which included Phase III but not Phase IV (Barber et al., 1955; Whittemore and Fraser, 1974).

If milk flow is confined to the brief Phase IV, then it, too, should have an average duration of only 10-20 s. Hand milking confirms this. When a single teat was milked by hand during otherwise normal nursings, milk flow was found to last 10.3 seconds on average (Whittemore and Fraser, 1974). Similar average durations of 10-14 s have been obtained by hand milking when the milk ejection reflex was elicited by manual stimulation of the udder or by the litter of piglets (Fraser, 1975a, b). The brief sucking phases observed by Barber et al. (1955), Gill and Thomson (1956), and Niwa et al. (1951) support this view. One

dissenting voice is Donald (1937) who, in not distinguishing between Phases III and IV, apparently assumed that milk was being obtained throughout the 40 s of sucking.

NURSING BEHAVIOUR OF THE SOW

Before starting to nurse, sows occasionally nudge their young, root in the bedding, and give a few soft grunts. They generally lie on one side with the udder rotated upwards exposing both rows of teats (see Fraser, 1976), although some sows nurse when standing (Gill and Thomson, 1956), perhaps in response to disruption among the litter. Once the piglets assemble on the udder, the sow gives characteristic, rhythmic grunts, typically at a rate of about one per second. The rate of grunting has a characteristic pattern (Fraser, 1973; Whittemore and Fraser, 1974). It stays fairly constant, or perhaps increases very gradually, for up to a minute or more. The rate then increases sharply (with experienced mothers at least), often doubling within a few seconds. At this time the calls may become louder, the pitch may drop, and several grunts may be run together in series. The grunt rate declines soon after, sometimes showing a second and usually less pronounced increase about 25 s after the first. Grunting then declines steadily and finally stops.

When the rhythmic grunting has ended, the sow may rise or change position within a few seconds, or it may continue to lie on its side for many minutes, especially during the first days of a lactation (Hafez and Signoret, 1969, p. 377).

The sow's pattern of grunting is related to the behaviour of the piglets and the time of milk flow (Fig. 1). The piglets' Phases I and II generally occur during the initial stage of constant grunting. The initial sharp increase in grunt rate coincides approximately with the beginning of Phase III, and the second increase, if present, with the beginning of Phase IV. The interval between the first increase in grunt rate and the beginning of Phase IV is about 25 s. The interval is quite consistent for any sow, although there are differences between animals. The interval may also increase during the first days of a lactation. When milk flow has been studied through squeezing a teat by hand, the interval between the increase in grunt rate and the first appearance of milk on the udder has also been found to be between 20 and 26 s on average (Whittemore and Fraser, 1974; Fraser, 1975a, b).

The rhythmic nursing grunts of the sow are easily elicited by simple mechanical stimulation of the udder, and the rate of grunting can be regulated by the type of stimulation provided. Stimulation of the anterior teats, either by hand or by the piglets, evokes much more grunting than similar stimulation of the posterior ones (Fraser, 1973, 1975b). Furthermore, a change from manual massage of the udder to squeezing and pulling on the nipples produces a sharp increase in the rate of grunting, at least among pregnant sows.

In view of this last observation, it was suggested that the first increase in the grunt rate might be caused by altered stimulation of the udder as the piglets change from Phase II to Phase III (Whittemore and Fraser, 1974). This view can now be discounted, since the sharp increase in grunt rate consistently occurs about 25 s before the beginning of milk flow even when milk ejection is elicited by uniform manual stimulation of the udder (Fraser, 1975a). It now appears that the first increase in grunting accompanies some aspect of the physiological triggering of milk ejection, probably the release of oxytocin from the pituitary or related events in the central nervous system. In experiments to test this, the relevant stimulation of the udder, either by hand or by piglets, has been terminated prematurely. If stimulation of the anterior teats ended before the first increase in grunt rate, milk ejection always failed to occur, but once the rapid grunting had begun, milk ejection of approximately normal duration invariably occurred about 25 s later, whether or not the stimulation of the udder continued (Fraser, 1975b).

If the rapid grunting coincides with the release of oxytocin, then the 25-s delay before milk appears on the udder should correspond approximately to the circulation time of the hormone. Evidence on this point is confounded by the fact that the circulation time has generally been measured using unphysiological doses of oxytocin administered to highly agitated animals which are restrained for hand milking. Under these conditions, circulation times of about 15 s are common (Whittlestone, 1953; unpublished findings, cf. Braude and Mitchell, 1950). In subsequent studies, however, Whittlestone (1954a, b) has observed longer intervals, closer to 25 s, which may be more typical.

Folley and Knaggs (1966) found that oxytocin was most commonly found in external jugular vein blood just before the sucking behaviour which they thought denoted milk ejection. Since they did not distinguish between Phases III and IV, however, the oxytocin may well have been released near the beginning of Phase III, which would agree with the other observations.

It is still unclear what causes the piglets to change from nosing the udder (Phase II) to sucking with slow mouth movements (Phase III) some 20 s before the main milk flow. Very small quantities of milk could become available at this time as a result of the direct mechanical stimulation of the udder (Barber et al., 1955) as occurs in some other species (Cross, 1954). Alternatively, the piglets might hear the dam's increase in grunt rate and begin sucking in anticipation of the milk flow. There appears to be ample opportunity for such a response to be learned: 1-week-old piglets have generally experienced well over 100 suckling episodes with the increase in grunt rate preceding milk flow by a relatively constant interval. This would help to explain why Barber et al. (1955), working with sows' first litters, did not notice Phase III until their litters were about 6 weeks of age; the increase in grunting is often indistinct during the early weeks of a female's first lactation (Whittemore and Fraser, 1974).

Presumably, it is the sudden availability of milk that makes the piglets begin rapid sucking (Phase IV), and the sudden end of milk flow that causes this behaviour to cease. Milk is ejected from the teats with considerable force during the main milk flow. The rapid sucking may be suited to speedy ingestion, as the piglets often gulp down 50 grams of milk in 15 s. The general appearance of the characteristic slow sucking, and its occurrence before and after the main flow, suggest that this behaviour may produce the more powerful suction suited to obtaining smaller amounts of milk when the main ejection begins and ends.

The second, and highly variable, increase in grunt rate may be caused in part by the initial sensation of the milk's being withdrawn from the teats, but it can be seen in the absence of any stimulation of the udder (Fraser, 1975b). A second oxytocin release, if it occurs, might possibly coincide with the second increase in grunting.

The proposed cause-and-effect mechanism linking the various behavioural components is summarized in Fig. 1.

POSSIBLE ORIGIN AND ADAPTIVENESS OF THE COMPONENTS

The nursing and suckling behaviour of domestic pigs has a number of characteristic features which require explanation in terms of their origin or adaptive significance.

First, it is difficult to elicit the milk ejection reflex of the sow as compared with some other ungulates. Milk ejection does not normally occur until the sow has received up to one minute or more of vigorous mechanical stimulation of the udder by the piglets or by hand, and even then it occurs only if an adequate interval has elapsed since the previous milk ejection. In addition, the reflex is readily inhibited by unexpected or unfamiliar stimuli, or by disorderly suckling by the piglets (Fraser, 1977). In fact, the sow's

discriminating requirements have evidently led to the mistaken view that in this species the milk ejection reflex cannot be triggered by human handlers (Braude, 1948; Cowie and Tindal, 1971, p. 190).

Second, the piglets' nosing of the udder is very highly developed. Some bunting of the udder is shown by most ungulates (Lent, 1974), but for piglets this preliminary stimulation generally lasts longer than the actual sucking. Interestingly, piglets which are weaned prematurely commonly develop the habit of nosing the bellies of their pen-mates (Fraser, 1974), whereas early-weaned lambs and calves are more likely to suck parts of the bodies of their pen-mates (Stephens and Baldwin, 1970).

Third, piglets display two distinct modes of sucking, and they change from one to the other presumably depending on whether they are obtaining milk in quantity. Such a shift in sucking pattern depending on the flow of milk is said to be rare in mammals (Wolff, 1973).

Fourth, the habitual attachments of individual piglets to particular teats or suckling positions is unlike some other polytocous species such as rats (Bonath, 1972) and mice (Bateman, 1957).

Fifth, and perhaps most conspicuous, is the loud vocalization of the sow throughout the nursing episode which forms a characteristic pattern linked to the time of milk ejection.

In most of these features, domestic pigs resemble wild *Sus scrofa* (Gundlach, 1968). However, in descriptions of wild pigs, as in early descriptions of domestic ones, only one sucking phase lasting 40-60 s has been noted.

Among the mammals, it is relatively uncommon for a polytocous species to have the young born in a highly precocious state. Much of the pig's nursing and suckling behaviour can be viewed as promoting even distribution of milk among numerous young which are capable, from the first days after birth, of approaching the mother independently to suckle.

Clearly it would be disadvantageous if individual piglets could elicit milk ejection when the other litter-mates were not prepared to accept the milk. The sow's frequency of milk ejection appears to be limited by the refractory period of the milk ejection reflex (Fraser, 1975a). Since the sow lacks a mammary cistern, milk is not available to piglets unless they are sucking during the actual few seconds of the milk flow. Accordingly, piglets which are absent from the udder will probably be unable to compensate for the missed feeding by subsequent sucking activity or by encouraging a second milk ejection soon after the first, and their failure to drain their teats will presumably contribute to mammary regression.

The sow's high requirement for vigorous stimulation of the udder helps to solve this problem, as individual piglets would not be likely to provide an adequate stimulus for milk ejection except under special conditions. In addition, the long preliminary phase of the nursing gives any stragglers a chance to reach the udder before milk flow begins, and the sow's vocalizations throughout this time apparently advertise to any absent piglets that a nursing is in progress.

While performing the vigorous massage of the udder, the piglets are poorly positioned to receive the milk when the brief main flow begins. It would appear beneficial, therefore, that the piglets stop nosing and begin their apparently non-nutritive sucking as soon as the vigorous stimulation has succeeded in triggering the milk ejection reflex.

A large litter of precocious young is capable of vigorous competition at the udder. This could be disadvantageous, not only to the combatants but also to the litter as a whole through the inhibition of milk ejection. The individual teat preferences that piglets develop are probably important in minimizing this type of disruptive competition.

Detailed study of feral domesticated pigs and wild Suidae might indicate to what extent the complex behaviour described above is brought about by domestication and the confinement which normally occurs under commercial conditions.

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