ABSTRACT

Successful lactation in sows involves a complex, coordinated interplay between the behaviour and physiology of the sow and that of her pigs. The nature of this interplay is constantly changing and evolving from the birth of the first pig through to the removal of the litter at weaning. This overview of lactation in swine addresses this sow-litter interplay at two levels, including the shifting relationship between the sow and her litter, and the coordinated physiology that occurs between an individual pig and the mammary gland it suckles.

STAGES OF LACTATION

Getting going

At the time when the pregnant gilt or sow enters the farrowing barn several days prior to the expected farrowing date, her mammary gland is in the late stages of a rapid period of growth. The increase in mass of the mammary gland occurs most rapidly in the last third of pregnancy (Ji et al., 2006), and is regulated by several mammogenic hormones, especially estrogen from the placenta, progesterone and relaxin from the ovary, and prolactin and growth hormone from the pituitary. All of her mammary glands are stimulated to grow; however, typically the middle glands achieve the greatest mass prior to farrowing and the posterior glands are the smallest.

In the period immediately prior to farrowing the gland starts producing the antibody-rich colostrum. Attempts to remove colostrum from the glands usually are not successful until the time of farrowing when there is an increased release of oxytocin in association with the birthing process. As the milk ejection hormone, oxytocin plays an important role in the sow-pig interaction during lactation, as discussed below. After farrowing it again becomes difficult to manually “milk” a sow without exogenous oxytocin administration.

At the time of farrowing, the mammary gland undergoes the two-stage process of lactogenesis (initiation of lactation). The initial stage involves cellular development of the milk synthesis apparatus, expression of genes associated with synthesis of milk components (milk proteins, fat and lactose), and secretion of a limited amount of the milk components. In the sow, this initial stage of lactogenesis seems to only be occurring within a very few days prior to farrowing and coincides to some extent with the formation of colostrum (Kensinger et al., 1982). Copious milk secretion is the second stage of lactogenesis and involves a large-scale expression of all genes and cellular processes associated with milk synthesis and rapid secretion of large quantities of all milk components. In the sow, this second phase of lactogenesis is initiated shortly after farrowing.

The major hormone involved in regulating lactogenesis is prolactin from the pituitary. In the sow, the peripartum surge of prolactin secretion starts a couple of days prior to farrowing and continues for several days post-farrowing (Devillers et al., 2004), stimulating the gland to switch
from formation and accumulation of colostrum to synthesis and secretion of milk components. Anything that inhibits prolactin secretion around the time of farrowing can inhibit lactation.

**Assembly of the partners**

When the sow starts farrowing each of her mammary glands has developed structurally and functionally to the point of producing some colostrum. From that time forward, changes in the functioning of each gland will be determined by whether and how often it is suckled. Pigs can fairly quickly move around after birth, allowing them to act on their strong behavioural drive to suckle (Brooks and Burke, 1998). The synchrony of having mammary glands primed to lactate at the same time as the birth of pigs with a strong suckling drive is critical to getting the dynamic interplay of sow and pigs initiated.

For swine breeds most often used in the US swine industry, pigs establish a well-defined teat order or teat preference. Generally each pig will suckle from only one gland, although there are some pigs that are able to maintain some lactation function in two adjacent glands. Glands that are not suckled undergo regression. If a pig is removed from the litter, the gland that the pig suckled typically will not be adopted by another pig in the litter, but will undergo regression.

**Synchrony of the motion**

The process by which the pigs establish teat order continues for several hours post-farrowing. By approximately 11 to 12 hours post-farrowing the litter and sow have synchronized their respective behaviours and interact in a coordinated, repeatable manner. Teat order has been established so that the relationship among pigs is stabilized. The sow has started to let down her milk at fairly regular intervals, and the pigs have learned to pick up on the sow’s cues when she is going to let down her milk. At this point, the suckling interplay between the sow and her litter occurs at intervals ranging from about 45 to over 60 minutes. In addition, the sow’s mammary gland is refilling with milk between nursings, while the ingested milk in the pig’s gastrointestinal tract is slowly digesting, making room for the next feeding.

It is also important to consider the dynamic interplay of the pig and the gland it suckles. Each gland responds to stimuli carried in the blood, such as the lactogenic hormone, prolactin. Prolactin secretion from the pituitary is stimulated by the pigs nuzzling the mammary glands and by their suckling action on the teats (Algers et al., 1991). In addition, each gland responds to local inhibitory factors that are produced within the gland (Knight et al., 1998). The mammary epithelial cells secrete an inhibitory factor, referred to as feedback inhibitor of lactation, as part of the normal cellular mechanism of milk secretion. As the feedback inhibitor accumulates in the alveolar lumen, it has an inhibitory effect on further milk secretion by the cells. When the pig removes the milk during suckling the negative effect of the feedback inhibitor is also removed, allowing milk synthesis and secretion to be stimulated again by the suckling-induced elevated prolactin concentrations. Therefore, maintenance of lactation in each gland is determined by the repeated removal of the milk produced by that gland. Each pig is different in its demand for milk from its preferred gland and each gland is independent from the other glands in its responsiveness to the pig’s demands.

As a consequence of this synergy and coordination, the pig and the gland it suckles can be thought of as an interdependent, functionally linked unit. The more milk removed by the pig, the more the gland is stimulated to produce more milk and to grow, and the more the pig is stimulated to grow. The larger the pig, the more demanding it is for milk from the gland and perhaps the more effective it is at removing milk from the gland. This relationship results in a
positive and statistically significant correlation between growth rate of the pig and size of the mammary gland the pig is suckling. Pigs suckling heavier glands gain faster than pigs suckling lighter glands, although there is substantial variability among individual sows.

**Ejecting the product**

Milk ejection may be thought of as the climax of the sow-litter interplay. It is accompanied by an intricate and highly coordinated behavioural sequence involving activity of the sow and of the litter (Brooks and Burke, 1998). Typically the sow initiates a period of grunting that alerts the pigs. She lies on her side exposing the udder. While the sow continues her rhythmic grunting, the pigs assemble at the udder, nuzzling the glands and sucking on the teats. Release of oxytocin from the pituitary is stimulated by the extensive nuzzling of the udder by the pigs and occurs approximately at the point where the sow increases the rate of grunting. Milk ejection starts roughly 25-30 seconds later, however it only lasts for about 10-15 seconds. It is only during this short period of milk ejection that the pigs can remove milk from the gland. The end of milk ejection is evident when the pigs release the teat and start trying to suckle other teats. They will continue nuzzling the udder for several minutes after the nursing event. The nuzzling of the udder both before and after milk ejection also stimulates continued release of prolactin from the pituitary, which stimulates the refilling of the gland. Suckling during milk ejection not only removes the milk, but also removes the feedback inhibitory factor. After each suckling, synthesis of milk to refill the gland is nearly complete by about 35 minutes after emptying of the gland (Spinka et al., 1997).

**Factors affecting the results**

Total milk production by the sow and mammary growth during lactation are affected by many factors, including nutrition, environment, breed, stage of lactation, and parity (King, 2000; Hurley, 2001). Individual mammary glands also differ in their production ability according to teat location (Dyck et al., 1987). Suckling intensity is an important factor determining total milk production by the sow. Because of the strong teat order of the pigs, the larger the litter size, the more glands of the sow are maintained in a milk secreting state, and the more total milk will be produced by the sow (litter size is positively correlated with total milk production). This also means the larger the litter size the greater the total amount of mammary gland mass that develops on the sow during lactation. However, the increment of increase in total mammary mass or total milk production decreases with each additional pig in the litter. That is, the larger the litter size the lower the amount of milk received per pig.

Suckling intensity also is related to interval between sucklings, or how often the sow is suckled. Suckling intervals between 35 and 50 minutes, resulting in milk removal about 30 times per day, offers maximal daily production of milk. Sows that nurse every 45 minutes vs those that nurse every 60 minutes, will produce less milk per nursing, but more total milk in a day. Because the duration of milk ejection is very short and the process of milk ejection is negatively impacted by stress, some sucklings may be non-nutritive. The sow and litter go through the normal behavioural sequence of the nursing, but milk ejection does not occur.

**When it is all done**

When milk is not regularly removed from a gland the inhibitory factor gradually stops milk secretion in that gland. Lactation function is maintained only in those glands regularly suckled by the pigs. Those glands that are not suckled undergo involution. At the beginning of lactation, the milk secretion function of nonsuckled glands is irreversibly lost for that lactation cycle within
3 days of farrowing (Theil et al., 2005, 2006). At weaning, with the complete absence of suckling and milk removal, the mammary gland undergoes extensive regression and remodelling for about a week or more before reaching a regressed state that will be maintained until mammary development is initiated during the subsequent pregnancy (Ford et al., 2003).

SEVERAL IMPLICATIONS

Anything that disrupts the coordinated behaviours of the sow or litter will negatively impact the success of the pigs in receiving milk during the short milk ejection period. Pigs that are not able to participate in the suckling processes will miss a meal that may cause them to become weakened and unable to participate in further feedings. Stressors of any type in the farrowing barn may compromise the sow’s ability to let down her milk.

The lactation history of a gland seems to impact the functionality of that gland in a subsequent lactation. Glands that are suckled in a gilt’s first lactation will produce more milk and have a greater development in her second lactation than glands that were not suckled during the first lactation (Farmer et al., 2012). This indicates that there is a carry-over from the gland development that occurs in one lactation to the next.

Optimal success in cross-fostering a pig onto a non-suckled gland may be achieved on day 1 of lactation, with limited success on day 2, and no success by day 3. Even if a gland is not suckled during the first day after farrowing and subsequently a pig suckles that gland, the gland will not produce to the level it might have if regular suckling began sooner (Theil et al., 2005, 2006). If a pig dies during lactation, the gland it was suckling will undergo a regression similar to the involution process occurring at weaning. Efforts to successfully foster another pig onto that gland must be achieved rapidly before the regression process becomes established.

CONCLUSIONS

Successful lactation of a sow involves a highly coordinated interplay between the behaviour and physiology of the sow and her litter. This interplay occurs to a great extent at the point of physical interaction of the individual pigs and the mammary glands they suckle. The nature of this interplay is continually changing from the time of farrowing to weaning the litter. While there are many other factors that go into a successful lactation of a sow, ultimately it is the highly controlled milk ejection process of the sow, coordinated with the physical removal of milk from the gland by the pig, that determines whether and how much the pig grows, as well as how much the gland continues to produce milk. This coordinated interplay of the sow and her litter occurs many times daily in the farrowing barn. Careful observation of this sow-litter interplay may help us better understand those factors that would compromise their performance.

REFERENCES


