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Factors Affecting Milk Ejection and Removal during Milking and Suckling of Dairy Cows: A Review

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Abstract: The release of oxytocin and milk ejection occurrence in response to teat stimulation is crucial for fast and complete milk removal during milking or suckling. The milk ejection reflex can be disturbed at central or peripheral level under different experimental and practical conditions. The important role in the pathophysiological regulation of the inhibited release of oxytocin is played by an opioid system. Endogenous opioids have suppressive effects on oxytocin release under the normal conditions of milk removal. However under the conditions of disturbed milk ejection their roles in dairy cows were not confirmed. Other possible mechanisms involved in the central inhibition of oxytocin release are discussed. In dairy cows as compared with rats the mechanisms involved in the regulation of oxytocin release at the central level remain unclear. The central inhibition of oxytocin release had often been observed in dairy practice during milking of primiparous cow after parturition, suckling by alien calf, calf removal before milking, milking of cowAs in the presence of her own calf, relocation and milking in an unknown milking place. When the released oxytocin cannot induce the transfer of milk from alveoli to cistern, peripheral mechanisms are involved. Peripheral mechanisms are related to the increased levels of catecholamine's and/or activation sympathetic nervous system at the udder level. In conclusion, the release of oxytocin and milk ejection efficiency can be suppressed very easily by many factors. The effect of milking conditions on regulation of milk ejection has to be considered. Thus the physiological requirements of dairy cows have to be respected.

Key words: Hormones · Milk Ejection · Milking · Suckling

INTRODUCTION

The payoff in the dairy farm is the harvesting of milk crop. Characteristic of good milking include: milking at regular intervals; fast, gentle and complete milking; use of sanitary procedures. A good milking process in dairy cows requires optimization of management, technological and physiological processes. For fast and complete milk removal, the active role of dairy cows must be considered [1]. The active role means that the milk ejection reflex must be induced to shift milk from the alveolar tissue to lower parts of the udder – cistern from which milk is available for mechanical removal. Before milk ejection occurs, only very small amounts of milk in cistern are available for removal. Complete milk ejection during each milk removal is necessary for the maintenance of high production level and udder health.

Although the basic elements of the milk ejection reflex have been known for more than 40 years, our understanding of this fascinating neuro-endocrine mechanism in dairy cows stems mainly from the results obtained in laboratory animals. Recent advances in farm animal research have demonstrated that the knowledge from laboratory animals is often specific to these species only [2]. It is clear from the animal science and dairy practice requirements that milk yield, time of milking and udder health are the most important parameters of good relationships between machine and cow. Thus the

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knowledge of the physiology of normal milk removal and pathophysiology of disturbed milk removal should be pointed out and taken into consideration as it was reviewed in dairy cows [3]. The knowledge is needed to create the optimal adaptation of the milking environment to the requirements of the cow.

Therefore, the objectives of this seminar was to show the effect of milking conditions on regulation of milk ejection and to present the importance of intrinsic mechanisms involved in milk ejection

Mammary Gland Anatomy: The mammary gland is a skin gland common to all mammals. Its function is to nourish and protect the neonate. The mammary gland is a milk producing gland in female mammals and present in a rudimentary and non-functional form in males of most species. The size and shape is species dependent. Several mammals have several pairof glands, while others have groups of one or two pair of glands that form the udder. Major components of the mammary gland are: a secretory system, a ductular system and teats [4]. The udder of the cow consists of four separate glands. It is located in the inguinal region and attached to ventral body wall of the cow. The udder is covered with hair, except for the teats. Supernumerary teats with or without a small orifices or with connections to one of the normal mammary glands could occur in some cows.

The intramammary groove divides the left and the right halves of the udder. Fore and rear quarters are disjoined by a thin connective tissue septa. Fore teats are usually longer than rear teats. The milk production in rear and fore quarters is approximately 60 and 40%, respectively. The teat length in Holstein cows is 4 to 7 cm with a diameter of 2.2 to 3.0 cm [5]. The teat canal is the only connection between the mammary gland and the outside environment. It is closed between milking to impede leakage and prevents exogenous pathogen from entering the udder. The length of the teat canal usually varies between 8 and 12 mm. It increases in length and diameter with proceeding lactation number [6]. It serves as a main barrier against infection. The teat canal is lined with keratin, a material derived from epidermal cells which consists of fatty acids which has bacteriostatic and bactericidal properties. The keratin closes the teat canal, except during milking time. Throughout milking, a substantial loss of keratin occurs by the sheer force induced during milk removal and by dissolving of the certain keratin components. The gland or udder cistern stores cisternal milk between milking. Usually large milk ducts are draining milk from the secretory tissue into the cisternal cavities. The udder suspensory system should be strong to keep up the proper attachment of the udder to the body of the cow. Both median and lateral suspensory ligaments provide the main support for the udder. The median suspensory ligaments are attached to the strong tendons of the abdominal muscles and to the pelvic bone. Theinterior of mammary gland is made up of connective (Fibrous and adipose tissue) and secretory glandular tissue. The lobes consist of groups of lobules which are surrounded by a connective tissue cove. The lobules are clusters of alveoli which are separated from other clusters by fibrous connective tissue.

Distribution of Milk Fraction: The epithelial cells secrete milk between milking, which is removed from the gland during milking. There are two milk fractions present in the udder before the start of milking: cisternal and alveolar. The cisternal milk fraction located in large mammary ducts and cisternal cavities is immediately available for milking. The alveolar milk fraction located in small milk ducts and alveoli is fixed by capillary forces and requires the milk ejection in order to be forcefully pumped into the cistern cavities to be available for milking [7].

Cisternal and alveolar milk partitioning mechanism in the cow is insiated by the slow increase ofcisternal milk fraction between 4 to 12 h after milking. Thereafter, it increases more rapidly to a plateau after 20 h while the increase of the alveolar fraction is more rapid reaching a plateau after 16 hour.The cisternal milk fraction is increasing with the number of lactations [8]. The largecisternal size of the cow is associated with low milk yield than cows with smallcisternal size during once daily milking. The reason could be an autocrine inhibitor of alveolar milk fraction which is active in milk stored in the secretory tissue and not in milk stored within the gland cistern. Therefore, large cisterned cows store their milk mainly in the cisternal area where the inhibitor is inactive. In contrast, cows with smaller cisternal size produce more milk when milked thrice daily [9].

Oxytocin and the Milk Ejection Reflex: Oxytocin (OT) is a nine amino acid peptide that is synthesized in hypothalamic neurons and transported down axons of the posterior pituitary for secretion into blood. It mediates three major effects in a female:stimulation of milk ejection, stimulation of uterine smoothmuscle contractionat birth and establishment of maternal behavior. OT is synthesized in the Supraoptic (SON) and parventricular nuclei(PVN) of the hypothalamus and secreted from the axon terminals of posterior pituitary gland [10].

The milk ejection reflex is an innate reflex that is not under conscious control of the animal andoccurs in response to tactile stimulation of the mammary gland. The neuroendocrine milk ejection reflex arc consists of a neural one and a hormonal one [10]. The neural component starts by the stimulation of the neural receptors primarily located in the tip of the teats [11]. The neural system carries the impulses from these receptors to the brain, especially to the supraoptic (SON) and paraventricular (PVN) nuclei of the hypothalamus [12]. These nuclei are clusters of the nerve cell bodies that are able to synthesize the nonapeptide hormone oxytocin, which moves, attached to a carrier protein (Neurophysin I), through the pituitary stalk via the nerve cell axons. Then oxytocin is stored in the neurosecretory terminals of the neurohypophysis [10]. The release of oxytocin into blood circulation represents the beginning of the endocrine way. After arriving via the systemic circulation, oxytocin binds at specific receptors in the mammary gland to influence the myoepithelial cell activity [13]. Myoepithelial cells are located between the basement membrane and the epithelial cells of the mammary alveoli and along the mammary duct system.

Due to the binding of oxytocin, the myoepithelial cells contract and the intraalveolarpressure increases, leading to the expulsion of milk from the alveoli through shortened ducts into the cisternal system [10]. Alveolar milk ejection causes a rapid increase of pressure within the cistern upto an individual maximum [14]. The release of oxytocin not only in response to prestimulation but also throughout whole milking is necessary for fast and complete milk removal [8].

Suckling and Machine Milking: Domestication of cattle has changed milk removal significantly. Due to the use of milk for human consumption suckling was replaced by hand or machine milking. This change probably influenced also the regulation of milk ejection in dairy cows as compared with less domesticated breeds. The two new kinds of milk removal are not natural and certain breeds do not release oxytocin in response to these stimuli and the milk ejection does not occur [15]. Although dairy cows are accustomed to hand and machine stimuli, it has been shown several times that different kinds of stimuli result in a different intensity of oxytocin release in high producing cows.

Both suckling and machine milking have a comparable stimulatory effect on oxytocin release [16]. When milking is performed in the presence of the calf, suckling induces higher oxytocin release than machine milking. A failure of oxytocin release was demonstrated in ewes during machine milking in a mixed system. Probably the release of oxytocin by milking in the presence of the calf is centrally suppressed and it is not related to the kind of stimulus.

The presence of the calf influences the regulatory mechanisms in the whole organism of cows, which was mainly studied in relation to reproductive functions. In literature there is also evidence that suckling evokes the release of oxytocin and milk ejection even in beef cows with de-enervated mammary glands causing interruption of the neural pathways from the udder to the brain. The mother young bonds also affect the release of oxytocin during suckling if the calf is her own or alien. It was pointed out that suckling induced stimulation traverses the lower brainstem through diffuse pathways in the reticular formation with many effects in the brain and cannot be ascribed to any compact somatosensory pathway related only to milk ejection as probably induced by milk The behavioural activity of calves and thus udder massage during suckling, is higher in beef than in dairy cows. The effect is induced by the available amount of milk in the mammary cistern in cows or rats. It has not been studied in dairy cows whether the mentioned factor intensity of suckling affects the oxytocin release. However, it cannot be excluded that there is an indirect influence on oxytocin release and milk ejection.

The reduction of the suckling stimulus by removing two or three pups from nipples produced a proportional fall in the magnitude of the burst of firing in rats [17]. The burst is known as one of the two different modes – burst and tonic, as thalamic cells respond to excitatory inputs.When compared the milk amount obtained by 3 times daily milking system with 3 times suckling (6 times daily milk removal) the amount of milk obtained by calf (Two calves per cow) represents 59% and 76% of the total milk yield in 2nd and 6th week lactation, respectively [18]. The calf presence also increased the residual milk volume [16]. It was supposed that higher volumes of residual milk might be due to reduced oxytocin release and milk ejection during milking of the nursed cows. Taking into consideration the threshold of oxytocin effect [8] reduced oxytocin is still significant to evoke milk ejection during milking in the calf presence. The above-mentioned distribution of released milk between calf and machine or increased volume of residual milk can probably be ascribed to voluntary keeping the milk for the needs of the calf [18]. However, voluntariness is a very wide explanation. Further investigations will be necessary to know whether peripheral or central mechanisms are involved.

The reduced oxytocin release during milking in the presence of the calf seems to be actively regulated. It can be pointed out from the oxytocin data that the amount of milk in the udder could be an important factor in oxytocin release during machine milking in the calf presence but not during suckling. We have found significantly lower oxytocin levels during milking cows under conditions of relatively empty udder due to suckling. But the oxytocin release was not negatively influenced during suckling if the udder was relatively empty due to previous milking. We suggest that the lower oxytocin release during milking in the presence of calves is caused by psychological disturbance on a central level although mechanisms in the udder cannot be excluded.

In post-partum and early lactation periods, oxytocin secretion in response to suckling was more pronounced in primiparous than in multiparous cows. Oxytocin releases within the central nervous system (CNS), is an important factor to stimulate maternal behaviour in sheep and to decrease the response to stress in rats [19]. Primiparous dams showed a higher incidence of abnormal maternal behaviour after calving than multiparous cows [20]. Thus in primiparouscows higher activity of oxy-tocinneurones possibly causes simultaneously an elevated release of oxytocin within the CNS and to the peripheral circulation and could be important to establish maternal behaviour. Oxytocin and milk removal are also required for post-partum alveolar proliferation and mammary gland function of mice, which could also be important to establish the lactation for primiparous cows.

Hand and Machine Milking: Hand milking induced a more pronounced release of oxytocin than did machine milking [21]. Mechanical stimulation with the milking machine is usually adequate, but machine milking can lead to a lower oxytocin response than manual stimulation indicating the importance of hand preparation of the udder for fast and complete milking. In any case, under ordinary conditions, mechanical stimulation is sufficient to induce normal oxytocin release and milk ejection [14].

The induction of stress or adrenaline administration results in the inhibition of milk ejection. On the other hand, adrenaline is not released in response to milking [22]. Adrenocorticotropin hormone (ACTH), stimulatecortisol release and suppresses milk secretion. However, machine and hand milking or suckling stimulate the release of cortisol [22].

The increase of cortisol during milking was not likely induced by ACTH because there were no changes in ACTH concentrations. Even naloxone, an opioid antagonist, further increased cortisol levels in response to milking but had no effect on ACTH. The increase cortisol during milking under normal conditions seems to be regulated by other mechanisms than stress. It seems that the hypo-thalamus-pituitary-adrenal axis is not activated in response to machine milking. Although the control of the adrenal glucocorticoid secretion has generally been supposed to exclusively depend on the release of ACTH [23]. Under certain conditions the plasma glucocorticoid concentrations were found to be inappropriate to the existing ACTH status. There is evidence that the autonomic nervous system can influence adrenocortical steroidogenesis by splanchnic sympathetic nerve activation. Splanchnic nerve stimulation increases the blood flow through the adrenal gland, which might lead to an increase in steroidogenesis by increasing the rate at which ACTH is delivered to the gland, even though the concentration in the plasma does not change. Machine milkingincreased the heart rate in dairy cows [24].

Though the importance of increased levels of cortisol in response to milking is not clear there is some evidence about the relationship between cortisol and the function of the mammary gland in literature. Glucocorticoids play an important role in the formation and maintenance of mammary tight junctions in vitro in mouse. Tight junctions may be involved in the mammary gland secretion and regulation of milk yield in dairy cows. As recently shown, cortisol seems to be important in the reduction of mammary epithelial cell tight junction leakiness in the udder of dairy cows. But, this effect seems to be effective only under normal conditions because under social isolation the tight junction permeability was negatively influenced and even to a larger extent in cows with higher release of cortisol [25].

Disturbance of Milk Ejection: In dairy cows,problems in the milk ejectionwas referred, to braking the secretion of oxytocin from the posterior pituitary (Central inhibition), or disruption of action of oxytocin (Peripheral inhibition) in the milk glands. In the presence of α-adrenergic receptorantagonists and oxytocin receptor blocking agent, caused peripheral inhibition of milk ejection [26]. In this case, the amount of oxytocin is normal, but its effect on myoepithelial cells has been disabled and missing their contractions and the milk cannot squeeze out alveoli in the drains. Central inhibition of milk ejection is caused by release of oxytocin from the pituitary gland and occasionally occurs in cattle production as a result of various stressors, in which decreased levels of oxytocin and increased levels of β-endorphin, cortisol, ACTH and catecholamines in blood plasma.

Post-partum Period: In primiparousthe immediate inhibition of milk ejection after parturition or delayed several days after parturition caused by a failure of oxytocin release. The delayed release of oxytocin in response to first milking after parturition was also observed in primiparous ewes [27]. Mechanisms responsible for the inhibition of milk ejection in primiparous cows immediately after parturition probably arise from the unknown mechanical stimulus of hand and ma-chine for animals that needs to be conditioned. In pregnant heifers the first hand contact with the udder evoked only a small increase in oxytocin release over the basal level compared with older ones, probably as a result of novel experience [28]. The adaptation to milking (Hand, machine) is typical of dairy but not of primitive cows.

The failure of oxytocin release during milking in the early post-partum period cannot be ascribed to the non-functional neuroendocrine arc. Normal release of oxytocin was observed in response to suckling in primiparous cows with inhibited oxytocin release during milking in the post-partum period. However, the functionality of the neuroendocrine arc of milk ejection is not probably always essential for oxytocin re-lease in response to suckling [28].

Calf Removal: Post-partum calf removal before milking did not influence oxytocin release, milk ejection and milk yield despite the high behavioral activity of cows until the start of milking (Calling, vocalization, looking for). From the stress point of view post-partum calf separation did not influence blood cortisol levels [29]. However, if the calf is separated later, there is a negative effect on milk yield. A stronger negative effect of calf separation on the oxytocin release in early lactation could be due to the higher milk demands of older calves, i.e. also higher intensity of suckling and lower amount of milk stored in the udder [30]. Even total lack of oxytocin secretion during milking occurred in some cows.

Suckling: Removal of her own calf and suckling by an alien her calf caused a failure of oxytocin release. Also suckling by the own calf on day 2 after calving stimulated oxytocin release in 100% of beef cows but suckling by alien calves stimulated oxytocin release in 36.4% of the cows only.

Inhibited release of oxytocin during suckling was observed in the first suckling of dairy cows after several weeks of machine milking [30]. The failure of oxytocin release was observed less frequently in cows with previous suckling experience than cows without such experience in which also the endogenous opioid β -endorphin increased. We have recently shown that under the inhibited oxytocin release during extraordinary suckling the signal reaches the brain because of prolactin and cortisol increased. However, the regulation of reduced oxytocin release in response to the first suckling is not clear yet [30].

Relocation: The inhibition of milk ejection as a consequence of inhibited oxytocin secretion could be related to milking after changing the milking surroundings under experimental and practical conditions [31]. Also relocation even to familiar surroundings reduces the secretion of oxytocin and milk yield. The relocation results in the release of endogenous opioid β -endorphin [31].

The sensitivity to emotional stress induced by relocation could also be influenced in thepresence calf. Suckling of primiparous cows in new surroundings (Parlour) caused a reduction in oxytocin release, but the amount of oxytocin increment was still sufficient to activate the milk ejection reflex. When primiparous cows were first milked in the parlour, oxytocin release was more reduced and in some animals the total inhibition of oxytocin release and milk ejection was observed as compared with suckling in the same place. Suckling has probably a stronger stimulus to release oxytocin under stress conditions than machine milking [32].

Possible Mechanisms: Inhibition of milk ejection can be induced at a central (Brain) or peripheral (Mammary gland) level, but only central inhibition of oxytocin release was observed in dairy practice [33].

Central Inhibition: There are several neural systems in the brain inhibiting the release of oxytocin or activity of oxytocin neurones inparaventricular nuclei (PVN) and supraoptic nuclei (SON) [10]. The main attention to understand the possible mechanisms involved in the central inhibition of the release of oxytocin is paid to the importance of endogenous opioid system – EOP [34]. The opioid system may have a physiological role in controlling oxytocin release at three levels from the neuronal terminals in the neurohypophysis, supraoptic and paraventricular cells in the hypothalamus and inputs to oxytocin neurones [35]. The presence of opioid receptors and opioids in the bovine hypothalamus and neurohypophysissupports the assumption that endogenous opioids could influence oxytocin secretion during milking in dairy cows as it was observed in rats [36].

The release of oxytocin can be affected by the noradrenergic and dopamine systems. The main attention is paid to the noradrenergic cells (A2 cell group) of the nucleus tractussolitarii in medullary structures and to the dopaminergic cells of the posterior and per ventricular hypothalamus acting directly at the hypothalamus [10]. Oxytocin release may be influenced at the level of neurosecretory terminals by noradrenaline containing fibers of the sympathetic nervous system controlling the neurohypophysial blood flow [37].

Opioid Control: The central inhibition of milk ejection means a reduction of oxytocin release in response to stimuli but the mechanisms responsible for this inhibition are not clearly understood in dairy cows During emotional stress evoked by social isolation oxytocin release and milk ejection were suppressed while β–endorphin were increasingβ -Endorphin together with ACTH are parts of the precursor proopiomelanocortin.Both hormones are possibly released concomitantly during stress [37]**.**

The question why naloxone could not overcome the central inhibition of oxytocin release during milking under stress conditions or during suckling by alien calf or during milking of primiparous dairy cows with inhibited milk ejection early post-partum have not resolved yet. Not even naloxone could influence oxytocin release in response to normal milking or during parturition in cows. Possible explanation is that naloxone could not reach the oxytocin neurones (Blood-brain barrier) or naloxone is not able to block EOP receptors in cows [38].

When morphine was injected together with naloxone, naloxone surmounted the inhibitory effect of morphine and even poteentiated the release of oxytocin in response to machine milking [39]. Naloxone in combination with morphine can reverse its inhibitory effect on oxytocin release in potentiated manner in the rat as well naloxone, administered even alone, stimulated and potentiated the release of oxytocin in response to machine milking.

Thus the endogenous opioid system seems to exert an inhibitory effect on oxytocin release during machine milking in dairy cows under normal conditions. Also naloxone is able to reach the brain areas important in the regulation of oxytocin activity. Naloxone is also able to increase the volume of morphine distribution in the brain and thus through changed morphine kinetics induce the inhibition of morphine action in addition to the competitive antagonism at opiate receptors in rats [39].

Further studies are needed to specify the mechanisms responsible for the central inhibition of oxytocin release during machine milking under stress conditions. There are some interesting relationships between released β -en-dorphin and cortisol in different situations. For example, emotional stress induced the release of β -endorphin but not cortisol in sheep but physical stress stimulated cortisol β -Endorphin and motor activity, not cortisol, seem to be indicators of the negative emotional state [40]. Also during transport naloxone was able to potentiate the re-lease of cortisol but not during social isolation in dairy cows. Different effects of various stressors on milk release were confirmed in rats [39]. Reduced milk ejection during stress was not a directconsequence of increased corticosterone. The increased levels of β -endorphin with si-multaneous normal cortisol levels suggest another source of β -endorphin, which could be more effective in oxytocin inhibition, is to be involved. During emotional stress β -endorphin did not probably derive from the anterior lobe but it came from the intermediate lobe, where β -endorphin would not be co-secreted with ACTH [40].

Thus increased β -endorphin in the intermediate pituitary can reach the terminals of axons of oxytocin neuronsin neurohypophysis by local diffusion and influence the oxytocin release. Based on the anatomical localization of immunoreactive oxytocin and β -endorphin in the bovine pituitary, it was concluded that the distribution of oxytocin neurosecretory terminals was denser in that part of the lobus nervous bordering the pars intermediate where β -endorphin staining was confined than in the centre of the lobe. Possibly β -endorphin secreted by the intermediate lobe reflects the amount of β -endorphin released within the brain to act as a neurotransmitter [40].

Noradrenergic Control: Noradrenalin derived from the A2 cells has predominantly excitatory effects on oxytocin neurons [10]. The excitatory effect is mediated via α 1-adrenergic receptors in PVN and SON. The activation of β -adrenergic receptors has inhibitory effects on oxytocin release in rats. β -adrenergic receptors are activated by adrenaline released from the adrenal medulla. It was also documented that the hypophysial portal epinephrine plasma concentration is highly on adrenal source However, machine milking did not induce the release of adrenaline [22]. Intravenous administration of adrenaline reduced the release of oxytocin during milking, which was not confirmed in other works where even the stimulatory effects of catecholamine and oxytocin release were found [22]. One could expect that catecholamines are involved in the central inhibition of oxytocin release under stress conditions. But in dairy cows, the administration of propranolol (β -adrenergic antagonist) was not able to abolish or influence the central inhibition of oxytocin release during milking in unfamiliar surroundings. But more work is needed to specify the effect of exogenous and endogenous catecholamines on milk ejection and milk removal in dairy cows.

CONCLUSION AND RECOMMENDATION

From the milk secreted in the udder only a small amount representing cisternal milk is available for mechanical removal. Thus the alveolar milk ejection induced by the release of oxytocin in response to machine milking and during the entire milking procedure is an essential factor for fast and complete milk removal in dairy cows. The milk removal can be disturbed at central or peripheral levels under different conditions. The central disturbance represents a failure of ejection or insufficient ejection of the alveolar milk into the cistern due to inhibited oxytocin release from pituitary into the blood circulation. If sufficient oxytocin release cannot induce the transfer of milk from alveoli to cistern, peripheral mechanisms are involved. Incomplete milking represents an economic loss and milk remaining in the mammary gland is a propitious medium for microorganisms, potentially causing increased incidence of mastitis. Optimal conditions in practical dairy farming should be respected and the biological requirements of dairy cows should be followed to maintain high production in combination with animal's good health. In conclusion, during machine milking, the physiological requirements of the cows need to be considered with minimizing stressors

Therefore, based on the above conclusion the following recommendation were forwarded:

- Milking should be a pleasant experience for the cow in order to maintain Ejection of milk
- Establishment of regular milking routine to be promoted to induce milk ejection
- A potent stimulus for milk let down is presentation of calf to its mother, so calf Should be near his/her mother during milking
- Udder stimulation is should be maintained to prevent disturbed milk ejection.

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