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# Normal and disturbed milk ejection in dairy cows

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**Abstract**

More than 80% of the milk stored in the udder, i.e. the alveolar fraction, only available after milk ejection is induced by the release of oxytocin and myoepithelial contraction. Milk ejection is induced by tactile teat stimulation, either manually or by the milking machine. The time from the start of a tactile stimulation until the occurrence of milk ejection spans from 40 s up to more than 2 min and increases with decreasing degree of udder filling. Therefore, cows need a longer pre-stimulation in late stages of lactation or if the milking is performed shortly after the previous milking whereas in full udders, pre-stimulation is less important. Milk ejection can be disturbed under several conditions, for example, during milking in unfamiliar surroundings or for several weeks after parturition in many primiparous cows. We found that a disturbed milk ejection is due to a reduced release or complete absence of oxytocin from the pituitary. During milkings with disturbed milk ejection in unfamiliar surroundings, the concentrations of cortisol and beta-endorphin were elevated. While exogenous glucocorticoids could not induce the disturbance, morphine caused inhibition of oxytocin release during milking. However, spontaneously occurring disturbance of milk ejection could not be abolished by the opioid-antagonist naloxone. On the other hand, severity of disturbed milk ejection and coping capacity towards novel milking environment was inversely related to the cortisol release in response to ACTH, i.e. adrenal cortex activity. Therefore, the susceptibility of individual cows to the inhibition of oxytocin release and milk ejection could be predicted by an ACTH challenge test.


*Keywords:* Milk ejection; Inhibition; Dairy cows

## 1. Introduction

In the dairy cow, most of the milk, i.e. 80–100%, is stored in the alveolar compartment of the udder. Therefore, the occurrence of milk ejection is crucial during calf suckling and

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machine milking to allow the removal of alveolar milk. Concomitantly, complete removal of the alveolar milk at each suckling or milking is a prerequisite to maintain milk synthesis and secretion on a high level throughout an ongoing lactation. Alveolar milk ejection is induced by the neuropeptide oxytocin which is released from the posterior pituitary in response to tactile teat stimulation by the calf, hand or milking machine. In cases where release of oxytocin is impaired, milk ejection is inhibited, thus causing production loss and increased risk for mammary infection.

## 2. Distribution and availability of milk fractions before milking

Between milkings, the milk secreted by the epithelial cells accumulates in alveolar and cisternal spaces, while the milk in large mammary ducts and cisternal cavities (cisternal fraction) is immediately available for milking. Milk stored in alveolar spaces and lumena of small mammary ducts (alveolar fraction) is fixed by capillary forces and requires an active expulsion into the cistern. This is called milk ejection or milk let down. The cisternal fraction usually amounts to less than 20% of the stored milk after an interval of 12 h from previous milking [1]. Shortly after milking, there is almost no cisternal milk present [2–4]. Thereafter, the rate of milk transferred into the cisternal compartment is increasing with time from previous milking [2]. Cisternal milk yield and fraction are highest at peak lactation and decrease towards the end of lactation [1,3]. Thus, lowest amounts of milk available for milk removal before milk ejection are present after short intervals from previous milking and in late lactational stages. A close positive correlation between cisternal size and lactation number was shown ($r = 0.90$) and the largest cisternal fractions were measured in the oldest cows [5].

The alveolar fraction is, due to almost missing cisternal milk, largest at short intervals from previous milking and in late lactation [3], i.e. in all situations of low udder filling. To have this fraction available for milk removal, milk ejection is essential.

## 3. Oxytocin release and milk ejection

Milk ejection is the active transport of alveolar milk into the cisternal compartment. It consists of: (1) contraction of the myoepithelial cells that surround the alveoli like a basket and (2) transfer of the milk through the milk duct system. Milk ejection is an innate reflex that occurs in response to tactile stimulation of the mammary gland through a neuroendocrine reflex arc [6].

In response to elevated oxytocin blood concentrations, binding to the oxytocin receptors of the myoepithelial cells causes alveolar contraction [7]. As a consequence, alveolar milk is forcefully shifted into the cisternal space.

Alveolar milk ejection causes a rapid increase of pressure within the cistern [8] and an enlargement of the cisternal cavity size [9]. However, due to the limited cisternal space, not all alveolar milk can be ejected if milk is not simultaneously removed from the udder. Further milk is ejected during the course of suckling or milking [10,11].

## 4. Induction of milk ejection before and during milk removal

The lag time from start of tactile teat stimulation until onset of milk ejection normally ranges from 40 s to more than 2 min and depends on the degree of udder filling [3,10]. The degree of udder filling is low at late stages of lactation and/or at short intervals from previous milk removal. At extremely low udder filling, milk ejection may occur as late as 3 min after the start of tactile teat stimulation. In an experiment, mean lag time from start of stimulation until milk ejection commenced was 50 s in early lactation after 12 h and 90 s in late lactation after 4 h from previous milking [3]. The variable occurrence of milk ejection is not due to a variation of oxytocin release. During the course of lactation, the release of oxytocin at the start of milking is not reduced or delayed [12]. The delayed milk ejection at low degrees of udder filling is obviously due to a delayed response to the oxytocin at the level of the mammary gland. Much more myoepithelial contraction is needed to expel milk from an incompletely filled alveolus than from a completely filled one. More contraction of myoepithelial cells needs more time and the period until alveolar milk occurs in the cistern is delayed. A long lag time until the onset of milk ejection corresponds with very low amounts of cisternal milk at low degrees of udder filling [3]. Interestingly, the lag time from the start of teat stimulation until milk ejection occurs is independent of the intensity of the stimulus. At a minimum stimulation, like keeping a teat cup liner attached to the teat without pulsation, sufficient oxytocin is released to induce immediate milk ejection [8,13]. In particular at low udder filling, an adequate pre-stimulation, i.e. a stimulation of the teats to induce milk ejection without simultaneously removing milk at the full vacuum level, helps to avoid negative effects of milking on empty teats at the start of milking on the further course of milk removal [14]. Because milk ejection is a continuous process throughout suckling or milking [10,11], an emotionally stress-free environment for the cow is crucial to achieve continuous oxytocin release throughout milk removal and, hence, complete udder emptying.

## 5. Disturbance of milk ejection

Under various conditions, the milk ejection may be disturbed in dairy cows either at the site of oxytocin release from the posterior pituitary (central inhibition) or at the site of oxytocin action in the mammary gland (peripheral inhibition). Peripheral inhibition of milk ejection in cows can be experimentally induced by administration of $\alpha$-adrenergic receptor agonists or an oxytocin receptor blocking agent. However, peripheral inhibition of milk ejection is limited to experimental approaches and occurs in the presence of normal oxytocin release but inappropriate contraction of the smooth muscles in the milk duct system [11,15]. Central inhibition of milk ejection, i.e. inhibition of oxytocin release from the pituitary gland, occurs frequently in dairy practice during various types of emotional stress. Thus, milking in unfamiliar surroundings has been demonstrated to result in an inhibition of milk ejection which could nevertheless be abolished by small dosages of exogenous oxytocin [16]. The same effect occurs in primiparous cows milked for the very first time [17] as well as for cows being switched from suckling to machine milking [18]. When cows are repeatedly transferred to initially unfamiliar surroundings,

oxytocin release reaches its normal level when the animals get gradually used to the procedure [19].

To overcome central inhibition of milk ejection, it is necessary to elevate oxytocin blood concentrations either by exogenous oxytocin or by applying nervous stimuli such as vaginal stimulation which are strong enough to induce endogenous oxytocin release [17]. In contrast to tactile stimulation of the teat, which fails to induce oxytocin secretion in certain stress situations, vaginal stimulation might be able to trigger oxytocin release in many cases. Examples for this are anecdotally known from milking cows at primitive rural settings.

The missing oxytocin release in unfamiliar surroundings is accompanied by increased plasma levels of β-endorphin and cortisol [11,16]. When the cows get used to the new surroundings, the concentrations of these hormones decrease while oxytocin release is gradually normalized [19]. These observations led to the concept that endogenous opioid peptides play a role within the mechanisms causing the central inhibition of milk ejection. This hypothesis is supported by experiments in which oxytocin release and milk ejection could be experimentally inhibited by the exogenous opioid morphine [20]. This effect could be abolished by administration of naloxone, an opioid antagonist. However, naloxone application could not abolish the lack of oxytocin release in cows milked in unfamiliar surroundings [21,22] or in primiparous cows shortly after parturition [23]. The role of endogenous opioids in the regulation of milk ejection and mechanism of inhibition of oxytocin release in cows remains unclear.

Cortisol does not seem to have an influence on central inhibition of milk ejection since intravenous administration of cortisol has no effects on milk ejection in cows [24]. During routine milking, plasma cortisol concentrations increase physiologically in cows [16]. Also catecholamines do obviously not cause central inhibition of milk ejection in cows [21,25]. However, there are relationships between the adrenal cortex sensitivity and its release of cortisol in response to adrenal cortex activity (ACTH) and heart rate on one hand and the disturbance of milk ejection on the other hand, although this relationship might not necessarily be a causal one. The cortisol release in response to ACTH challenge could be related to the severity of inhibition of milk ejection in unfamiliar surroundings. The adrenal response to ACTH challenge tended to be higher in cows with more alveolar milk ejected during the first milking in an unfamiliar surroundings [22]. Furthermore, the increase of cortisol levels during the first milking in unfamiliar surroundings as compared with control milkings tended to be lower in cows with total inhibition of milk ejection during all relocations compared with cows that showed similar positive reaction in oxytocin release in response to milking or after vaginal stimulation. Thus, animals with a higher adrenal sensitivity to ACTH or to stress had less pronounced inhibition of milk ejection as a consequence of more oxytocin released [22].

To examine the relationship between the adrenal cortex sensitivity and the coping process during the changeover from conventional milking to an automatic milking system, an ACTH challenge experiment was performed independent of milking [26]. Cows which released more cortisol in response to ACTH injection had a less enhanced heart rate and a less disturbed milk ejection during the first milking in the new environment. In conclusion, the degree of central inhibition of milk ejection, i.e. the coping capacity towards new milking environment, varies widely between cows. The course of adaptation to the novel milking environment can be predicted by testing the adrenal cortex sensitivity to ACTH. There is,

however, no proof of a causal relationship between adrenal cortex sensitivity and disturbance of milk ejection.

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