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ON THE MILK EJECTION MECHANISM IN COWS UPON AN INCREASE IN MILK YIELD PER MILKING

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Abstract

Sympathetic nervous system regulates milk flow through the udder duct system. However, the mechanisms of contraction of the alveoli upon accumulation of different amounts of milk in the udder have not been studied. In the paper, it is found for the first time that the removal of an increased amount of milk is accompanied by a change in the parameters of the udder blood supply caused by an increase in the contractile response of the alveolar complex. Thus, the goal of the paper is to investigate the mechanism of contractile reaction of the alveolar complex and milk removal in cows with an increased milk yield per milking. Nine black-and-white dairy cows of the 2-5th calving were tested, 7 times each, in the first half of lactation (All-Russian Scientific Research Institute of Physiology, Biochemistry and Nutrition of Farm Animals, Kaluga Province). A serial ADU-1 milking machine and a counter sensor (Latvia) were used to record milking parameters. The milk yield per milking ranged from 3.4 to 6.7 kg in the control period and was 24.5 % higher ($p < 0.001$) in the test period. The mammary blood flow (MBF) was assessed by the electromagnetic flowmetry method. A blood flow probe (Nihon Kohden, Japan) was fixed on the external pudendal artery of the udder. The average MBF values were recorded for 3 minutes prior to milking (initial period) and in milking. The points characterizing udder blood supply were marked on the MBF curve, i.e., the beginning of udder irritation, a sharp increase in the blood supply, its maximum and the baseline restoration. The time intervals until a sharp increase in MBF and an increased blood supply period were calculated. The average and maximum MBF values and an increase in mammary blood flow during milking in relation to the initial indicators were determined. The parameters of the udder blood supply were used to assess the contractile response of the alveolar complex. The latent period until milk ejection was determined based on the time from the beginning of udder irritation to a sharp increase in udder blood supply. It was established that the milk yield per milking affects the parameters of milking and the udder blood supply. The increased milk yield per milking led to a shorter period for removal of the first portion of milk ($p < 0.001$), an increase in the average intensity ($p < 0.001$) and maximum intensity ($p < 0.001$) of milk removal as well as an increase in the machine milking period ($p < 0.001$). The increased milk secretion was also accompanied by an increase in the udder blood supply. I.e., the period before the udder blood flow increased sharply shortened ($p < 0.05$), while the average ($p < 0.05$) and maximum ($p < 0.05$) MBF values during milking, as well as period of intensive blood supply to the udder ($p < 0.001$) increased. The increased mammary blood flow during the test period resulted from an increased contractile response of the myoepithelium and alveoli. The intensive contraction of the alveoli, with the increased contraction amplitude and duration, leads to a shorter latent period of milk ejection. The milk ejection and removal are under regulation of the sympathetic nervous system. Probably, the excitation of the udder sympathetic nervous system depends on the amount of accumulated milk. The udder tone during milk ejection determines both the alveoli contraction and the rate of milk movement through the milk ducts and its removal through the nipple. The increased udder tone when low filling with milk resulted in a delayed ejection, delayed of removal first portion of milk, low contractile response of the alveoli, and low milk removal. With an increase in the amount of milk in the udder, its tone decreases, resulting in a shorter latent period of milk ejection and faster removal of the first portion of milk, strengthening the contractile response of the alveoli and increasing the intensity of milk removal. Therefore, the latent period of removal of the first portion of milk can be proposed to characterize the tone of the udder sympathetic nervous system.

Keywords: cows, milk yield per milking, milk removal parameters, udder blood supply, milk ejection, udder sympathetic tone, alveoli, contractile activity

Secretion and motor activity are the udder functions. The sympathetic nervous system directs the functional activity of the udder in cows [1]. The hormones prolactin [2] and serotonin [3] are important to regulate the secretory function. The local mechanism of its regulation becomes apparent during more frequent milking of one of the udder halves during early lactation [4, 5]. Milk production and accumulation in the alveoli occurs continuously. To maintain a high secretory activity of the mammary gland, cows should be milked in a timely manner [6]. In conventional machine milking, milking intervals are relatively constant. The installation of an automatic milking system with more frequent milking leads to changes in the milk composition [7]. There is a positive genetic correlation between the automated milking frequency and milk productivity of dairy cows [8].

The motor function of the udder is realized during milk ejection, providing rapid forcing of alveolar milk into the milk duct system and cisterns under by contracting myoepithelial cells, active milk flow along the duct system and its removal from the udder. To characterize the intensity of milk ejection, intramammary pressure (IMP) [9, 10] and milk removal parameters during conventional milking [11-13] or automated milking [14]. The IMP and milk removal are influenced by the milk yield per milking. The milk yield positively correlates with machine-on time [13] and the milk removal intensity [11, 13]. Milking intensity and duration increase if the milk yield per milking increases [12, 15]. A positive relationship was found between IMP and the milk yield at quarter level [9], and it was also shown that with an increase in the filling of the udder, the maximum IMP value at forcing milk ejection [10].

The mechanisms regulating milk movement along the system of udder ducts are intensively studied. A decrease in the contractile response of the teat sphincter muscles to manual stimulation led the authors to suggested that a change in the tone of the udder sympathetic nervous system plays a role in milk removal [16]. This hypothesis was confirmed experimentally when α- and β-adrenergic receptors were found in the teat [17-20] and in large milk ducts of the cows' udder [19, 20]. The milk removal is regulated by the sympathetic nervous system through the influence on the adrenergic receptors of the smooth muscles of the milk ducts, udder cisterns and teats. Stimulation of α-adrenergic receptors of the udder causes contraction of the teat sphincter [17] and excretory ducts of the udder [21], decreases the milk removal [22] and the peak flow rate during milking [21, 23]. Prazosin blocks the udder α-adrenergic receptors, prevents contraction of the teat sphincter and causes relaxation of the muscles of its sphincter [24]. In response to β-adrenergic agonists, the muscles of the teat sphincter relax [17] and the intensity of milk flow rate during machine milking increases [21, 23]. It is assumed that in the udder, the smooth muscles of the large milk ducts of have a greater effect on the intensity of milk flow rate than the muscles of the teat and its sphincter [21, 23]. The individual ability of cows to milk ejection is determined by the ratio of α- to β-adrenergic receptors in the teat [18]. In the udder parenchyma, the concentrations of adrenoreceptors are low, so the effect of the sympathetic adrenergic system on the alveolar complex may be low [19, 20]. The IMP and milk removal parameters enable early assessment of milk ejection but not the contraction activity of myoepithelium and alveoli.

Earlier, we found a close relationship of the main parameters of milk flow with the udder blood supply before [25] and during machine milking [26]. We assumed [27] that greater blood flow to the udder is due to a higher vascular tone generated by contracting alveoli. The udder blood supply level during milking reflects contractile response of the alveolar epithelial cells.

This paper shows that an enhanced blood supply to the udder due to the contractile activity of alveolar complex provides a higher milk yield.

Our goal was to investigate contractile mechanisms in the alveoli in relation to milk removal when the milk yield per milking increases.

Materials and methods. A crossover trial was performed on nine black-and-white cows (*Bos taurus taurus*) in the first half of the second to fifth lactation (All-Russian Research Institute of Physiology, Biochemistry and Nutrition of Farm Animals, Kaluga Province). Test parameters were measured in each period in a 7-fold repetition. During the control period, the milk yield per milking per cow ranged from 3.4 to 6.7 kg, in the experimental period, the values were 24.5 % ($p < 0.001$) greater due to regulation by between-milking intervals.

Wet hygiene of the teats was carried out for 10 s, then a milking machine ADU-1 (Russia) was attached. The milk removal parameters were calculated based on the records obtained with a bucket meter-sensor (Latvia) [11].

Mammary blood flow (MBF) was estimated by electromagnetic flowmetry. A blood flow probe (Nihon Kohden, Japan) was attached to the external pudendal artery of the udder. The average MBF values were recorded for 3 min before milking (initial period) and during milking. The characteristic points of the MBF curve were i) the beginning of the udder irritation, ii) a sharp increase in the blood flow, iii) its maximum, and iv) the MBF return to the initial level were. The interval until a sharp increase in MBF, the duration of increased blood supply, the average MBF, maximum MBF and its increment during milking compared to the initial level were calculated.

The parameters of the udder blood supply were used to assess the intensity of the contractile response of the alveolar complex. The interval from the beginning of udder irritation to the moment when blood flow sharply increases indicates a latency period of milk ejection [27]. The duration of increased blood supply corresponds to the contractile reaction of the alveoli. The increase in MBF during milking characterizes the amplitude of alveolar compression and expansion.

Statistical processing, correlation and regression analyzes were performed using the Microsoft Excel package. The mean values (*M*) and standard errors of the means (±SEM) were calculated. Statistical significance of the differences was assessed using the Student's *t*-test.

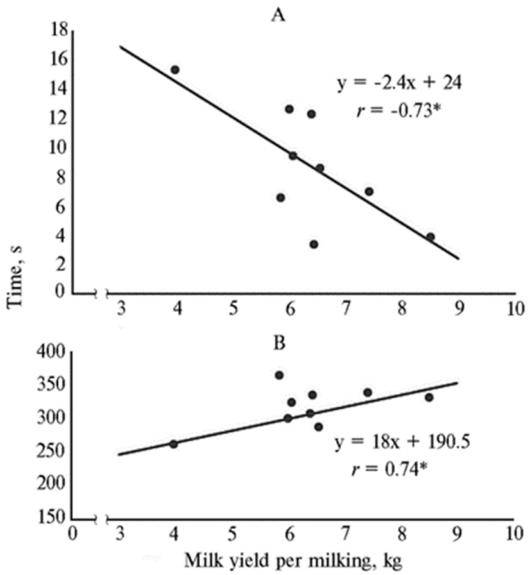
Results. As the milk yield per milking increased, milk removal parameters changed (Table 1), that is, the latency period of milk flow shortened while the average and maximum milk flow rates increased.

1. Milking parameters in black-and-white cows (*Bos taurus taurus*) in the first half of the second to fifth lactation, as influenced by milk yield per milking (n = 9, M±SEM, All-Russian Research Institute of Physiology, Biochemistry and Nutrition of Farm Animals, Kaluga Province)

Parameter	Period	
	control	experimental
Milk yield per milking, kg	5.11±0.12	6.36±0.15*
Total milk yield (machine milking), kg	4.51±0.13	5.77±0.16*
Machine stripping, kg	0.61±0.03	0.58±0.03
Milk flow rate, kg/min:		
average	1.19±0.04	1.38±0.04*
maximum	2.23±0.05	2.52±0.05*
Completeness of milking for the first 2 min, %	65.1±2.5	62.6±2.4
Latency period of milk flow, s	12.3±0.8	7.8±0.7*
Milking time, s:		
entire milking period	265.7±6.4	283.0±6.8
machine milking period	186.3±5.0	207.0±5.6*
machine stripping period	79.4±2.8	76.0±2.9

N o t e. Control and experimental periods are described in the *Materials and methods* section.
* Differences from the control are statistically significant at $p < 0.001$.

A higher milk yield per milking drives an increase in the machine milk yield and machine milking time with a clear tendency to lengthen the entire milking period. We did not find the effect of the milk yield on the machine strip yield, machine stripping time and the completeness of milking for first 2 min. In the experiment period, the milk yield per milking and latency period of milk flow correlate ($r = -0.73$; $p < 0.05$). Figure (A) shows calculated parameters of the linear regression for these two variables.



The relationship of the time period to the first portion of milk (A) **and the duration of increased blood flow to the udder** (B) **with milk yield per milking in black-and-white cows (*Bos taurus taurus*) in the first half of the second to fifth lactation** ($n = 9$, All-Russian Research Institute of Physiology, Biochemistry and Nutrition of Farm Animals, Kaluga Province).
* Statistically significant at $p < 0.05$.

The regression equation indicates that as the milk yield per milking increases, the time interval to removal of the cisternal milk fraction shortened. A shorter time to the first milk portion, an increase in the average and maximum milk flow rates with a greater amount of milk being milked indicated a faster milk flow and a higher milk ejection of a cow.

Our findings are consistent with the report of Bruckmaier et al. [10]. In machine milked cows with high udder filling, they revealed greater milk yield and higher milk flow for a longer time. Stimulation of β-adrenergic receptors in the udder of cows causes an increase in milk yield, the maximum milk flow in machine milking [21], and an increase in milk amount and its removal through the catheter [17]. Stimulation of α-adrenergic receptors in the udder resulted in a decrease in milk yield and maximum milk flow [23]. The blockade of α-adrenergic receptors contributed to the enhanced milk removal [24].

With a decrease in the tone of the sympathetic adrenergic nervous system of the mammary gland, teat relaxation accelerates milk removal [17]. The time until the first portion of milk directly depends on the tone of the teat sphincter. In our experiment, milk increased in yield while ejected for a shorter period ($p < 0.001$). A shorter interval to the cisternal milk ejection during the experimental period indicated a lower tone of the teat sphincters and, therefore, of the udder sympathetic innervation.

Obviously, the sympathetic tone of the mammary gland depends on the amount of milk stored in the udder before milking. At low filling, the sympathetic tone before milking is increased. In such cows, milk movement through the ducts and removal through the teat are low-efficient. Milk accumulation in the capacitive system of the gland helps to reduce its tone and thus accelerates milk removal.

The milking period depends on the parameters of milk removal. In case of no changes in the udder tone and milk flow rate in the experiment period, the milking time would increase by 24.5 %, as would the milk yield per milking. However, due to a decreased udder tone and a higher milk flow rate, the milking

time increased only by 6.5 %. Given the functional relationship, milking time should be considered a function of milk flow rate.

Higher milk yield per milking stimulated the udder blood supply (Table 2). In the experimental period, the MBF sharply increased in a shorter time and did not decrease for or a longer time than in the control. When increased milk yield per milking, the average MBF, maximum c and ΔMBF vs. basal MBF exceeded the control.

In the experimental period, we found close positive correlation ($r = 0.74$; $p < 0.05$) between the milk yield per milking and duration of increased blood flow (see Fig., B). The regression equation sows (see Fig., B) that the duration of higher blood flow to the udder increases as the udder filling increases.

2. Blood supply to the udder of in black-and-white cows (*Bos taurus taurus*) in the first half of the second to fifth lactation as influenced by milk yield per milking ($n = 9$, M±SEM, All-Russian Research Institute of Physiology, Biochemistry and Nutrition of Farm Animals, Kaluga Province)

Показатель	Period	
	control	experimental
MBF basal, l/min	2.97±0.10	3.21±0.11
Increase in MBF:		
time to onset, s	89.7±2.0	82.1±2.2*
duration, s	255.2±6.7	305.5±6.3**
MBF during milking, l/min:		
average	3.95±0.11	4.31±0.12*
maximum	4.88±0.18	5.41±0.14*
MBF increment, l/min:		
average	0.98±0.07	1.22±0.07*
maximum	1.99±0.10	2.31±0.11*

N o t e. MBF — mammary blood flow. Control and experimental periods are described in the *Materials and methods* section.
*, ** Differences from the control are statistically significant at $p < 0.05$ and $p < 0.001$, respectively.

The MBF values before milking and during milking in the control (see Table 2) are consistent with our earlier findings [26, 27]. The trend towards an increase in MBF before milking in the experiment was due to an increase in the milk yield per milking. This conclusion is in line with the relationship between MBF in half of the udder and the milk yield per milking [25].

The alveolar contractile response assessed via blood flow parameters showed that the alveolar complex regulates removal of an increased amount of milk. In the experimental period, the latency period of milk flow was 8.5 % shorter ($p < 0.05$) whilst the contractile reaction of the alveoli was 19.7 % longer ($p < 0.001$). In the control, the average and maximum compression amplitudes of the alveolar complex were 0.98±0.07 and 1.99±0.10 conventional units, respectively. The increase in milk yield per milking in the experiment caused a 24.5 % increase in the average compression amplitude ($p < 0.05$) and a 16.1 % increase the maximum compression amplitude ($p < 0.05$). A reduced latency period of milk ejection, the increased amplitudes and longer contraction of the alveoli in the experiment indicate higher contractile activity of the alveolar complex. An increase in the contractile reaction is a response to a decrease in the tone of sympathetic nervous system of the udder under higher degree of the udder filling.

The delay from the start of milking until commencement of milk ejection, a shorter time for reaching maximum intramammary pressure (MIMP), an increase in MIMP during milking with an increase in milking intervals [10] may indicate an increase in milk ejection. According to the authors, the less the filling of the alveoli with milk, the more time it takes for myoepithelial cells to efficiently movement the alveolar milk through the ducts. It is believed that the

sympathetic nervous system influences milk removal not through regulation of milk ejection , but through stimulation and inhibition of adrenergic receptors in large ducts and cisterns of the mammary gland [20].

Due to small number of adrenergic receptors in the udder parenchyma [19, 20], the sympathetic nervous system cannot directly affect the myoepithelial cells. Their contractile activity is regulated by oxytocin the release of which from the neurohypophysis is also controlled by the sympathetic nervous system. In our experiment, the decrease in the latency period and the increase in the contraction amplitude and duration in the alveoli indicate the possible involvement of oxytocin. The release rate and concentration of oxytocin can regulate the contractile activity of the alveolar complex. The release, delivery and blood concentration of the hormone is likely to increase as the amount of milk in the alveoli increases.

Thus, milk yield per milking in dairy cows affects the parameters of milk removal and blood supply to the udder. A 24.5 % increase in milk yield per milking did not affect completeness of milking for the first 2 min, the machine stripping and machine stripping time, but fastened removal of the first cistern milk fraction, increased the milk flow rate and machine milking time. The changes indicate accelerated and more intensive removal of an increased amount of milk. The blood supply to the udder also increased. Namely, period to sharp growth in blood flow to the udder was shorter, the average and maximum mammary blood flow rates increased during milking, and the increased blood supply to the udder lasted longer. The increased blood supply to the udder was due to higher contractile activity of the myoepithelium and alveoli. The amplitude and duration of alveolar contractions increased which shortens the latency period. The sympathetic nervous system influences milk ejection and removal. We assume that the degree of udder filling influences the tone of the udder sympathetic nervous system. Udder tone during milk ejection and removal determines both the alveolar contractile response and the milk movement through the ducts and teats. The increased tone of the udder with low filling leads to the delay from the start of milking until commencement of milk ejection, low contractile response of the alveolar complex and low milk flow rates. As the amount of milk in the udder increase, the udder tone decreases providing a reduction in the latency period and an increase in the contractile reaction and milk flow rate. The latency period necessary for cisternal milk removal can characterize the functional state of the teat sphincter and the tone of the udder sympathetic nervous system.

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