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Endogenous and dietary lipids influencing feed intake and energy metabolism of periparturient dairy cows

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ABSTRACT

The high metabolic priority of the mammary gland for milk production, accompanied by limited feed intake around parturition results in a high propensity to mobilize body fat reserves. Under these conditions, fuel selection of many peripheral organs is switched, for example, from carbohydrate to fat utilization to spare glucose for milk production and to ensure partitioning of tissue- and dietary-derived nutrients toward the mammary gland. For example, muscle tissue uses nonesterified fatty acids (NEFA) but releases lactate and amino acids in a coordinated order, thereby providing precursors for milk synthesis or hepatic gluconeogenesis. Tissue metabolism and in concert, nutrient partitioning are controlled by the endocrine system involving a reduction in insulin secretion and systemic insulin sensitivity and orchestrated changes in plasma hormones such as insulin, adiponectin, insulin growth factor-I, growth hormone, glucagon, leptin, glucocorticoids, and catecholamines. However, the endocrine system is highly sensitive and responsive to an overload of fatty acids no matter if excessive NEFA supply originates from exogenous or endogenous sources. Feeding a diet containing rumen-protected fat from late lactation to calving and beyond exerts similar negative effects on energy intake, glucose and insulin concentrations as does a high extent of body fat mobilization around parturition in regard to the risk for ketosis and fatty liver development. High plasma NEFA concentrations are thought not to act directly at the brain level, but they increase the energy charge of the liver which is, signaled to the brain to diminish feed intake. Cows differing in fat mobilization during the transition phase differ in their hepatic energy charge, whole body fat oxidation, glucose metabolism, plasma ghrelin, and leptin concentrations and in feed intake several week before parturition. Hence, a high lipid load, no matter if stored, mobilized or fed, affects the endocrine system, metabolism, and feed intake, and increases the risk for metabolic disorders. Future research should focus on a timely parallel increase in feed intake and milk yield during early lactation to reduce the impact of body fat on feed intake, metabolic health, and negative energy balance.

1. Introduction

Mammals developed different lactation strategies to meet their specific substrate and energy demands for milk production. When looking at 2 extremes, some mammals such as bears, seals, and baleen whales rely entirely on the utilization of stored energy depots for milk synthesis while fasting, whereas smaller mammals such as shrews, mice, and rats may rapidly increase their food intake up to 3-fold during early lactation [1]. However, these 2 opposing strategies are not exclusively reflected by the different metabolic rate or the body mass of large vs small animals. Among larger animals, rhinoceroses and horses cope with the increased nutrient requirements for milk synthesis by increasing feed intake and only marginally by mobilization

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of body fat [1,2]. When normalized to lactation intensity, peak energy output, and lactation length, milk composition differs between animals according to their feeding and mobilization strategies, with low-fat high-carbohydrate in rhinoceroses and horses and high-fat low-carbohydrate in some seals [1]. Thus, the amount of particular substrates required by the mammary gland, depends largely on the amount and composition of milk produced and hence on the amount of body reserves, the ability to increase feed intake, and the composition of feed ingested. If the mother is unable to meet the demands of the mammary gland by dietary intake, she reduces milk output, mobilizes precursors from endogenous tissues or employs some combination thereof. Thus, milk composition reflects also the evolutionary habituation of the mare during nesting.

Modern dairy cows provide the precursors for milk production during early lactation from 2 sources, from the increase in feed intake and the mobilization of body reserves. Within the process of selecting dairy cows for high milk yield in early lactation, body weight and stature as a prerequisite to store body reserves has increased as well [3]. On the other hand, the capacity for feed intake has not increased in parallel with the increase in milk yield. The correlated response in feed intake from selection on milk yield alone can cover only 40% to 48% of the extra requirements for the increased yield [4]. Part of this gap is encountered by improved feed conversion efficiency but a significant portion of the deficit is just because of a greater mobilization of body reserves resulting in a negative energy balance (NEBAL) during early lactation [5]. Body reserves mobilized during early lactation are glycogen and protein stored in liver and muscle tissue but mainly triglycerides deposited in adipose tissue. Thus, selecting cows for high milk yield in early lactation also led to the unintentional selection of cows with a high capacity to accumulate and mobilize body fat reserves throughout the lactation cycle. More specifically, larger and fatter cows with an intrinsically high potential to mobilize their body fat reserves in early lactation transfer more mobilized nonesterified fatty acids (NEFAs) to the mammary gland as compared with smaller and thinner cows [6]. Consequently, larger and fatter cows with a high loss of body condition score (BCS) produce more milk fat or fat-corrected milk yield (FCM) but also confine their increase in feed intake, thereby entering into a stronger NEBAL [7,8].

The extent of body fat mobilization in early lactation is determined by the degree of body fat accretion occurring in the preceding late lactation and dry-off period. Energetic oversupply during the prepartum period and the accompanied overconditioning before calving influences BCS loss, feed intake, milk fat content, fat-corrected milk yield, and energy balance after calving [9,10]. However, the overconditioning effect could not be achieved by supplementing the diet with rumen-active fat prepartum because it immediately reduced feed intake when compared with cows fed the nonsupplemented diet [11]. Yet, feeding a ration enriched with rumen-protected fat prepartum as compared with an isoenergetic and isonitrogenous starch-based diet prepartum increased fat content in milk, exacerbated NEBAL, and reduced feed intake of cows fed the same ration in early lactation [12]. Conversely, the reduction of the prepartal dietary energy supply as compared with ad libitum feeding confines body fat accumulation and consequently body fat mobilization in early lactation, resulting in a reduction in milk fat yield [13], whereas increasing the level of feed intake in early lactation [10,14].

The mechanism balancing the utilization of nutrients from dietary and endogenous sources and the mechanisms partitioning dietary and endogenous metabolites toward the mammary gland are under homeostatic and homeorhetic control. The endocrine system, involving a reduction in insulin secretion and systemic insulin sensitivity and orchestrated changes in plasma insulin, insulin growth factor-I, growth hormone (GH), glucagon, leptin, glucocorticoids, catecholamines and so forth controls the metabolism in specific tissues. For example, concerted endocrine changes in the transition period prioritize nutrient partitioning toward the mammary gland by reducing the metabolic load in less-priority organs such as in muscle and by increasing the synthesis capacity of high-priority organs such as the liver. However, the endocrine control system is highly sensitive and responsive to an overload of fatty acids. Conclusively, the amount of lipids no matter whether ingested with the diet, stored in adipose and muscle tissue or mobilized and released into circulation plays a pivotal role in the control of feed intake, energy balance, and partitioning nutrients toward the mammary gland. The objective of the present article is to review the current knowledge about endocrine and molecular mechanisms underlying the effect of dietary and endogenous lipids on energy metabolism and feed intake of periparturient dairy cows.

2. Signals controlling feed intake and energy balance

The capacity for dry matter intake (DMI) of dairy cows is the most critical factor determining the amount of energy and nutrients available for milk production. Besides the animal's genetic background, the amount of feed ingested by a cow depends on environmental (extrinsic) and animal-related (intrinsic) factors. Among extrinsic factors, feed quality, management, and climatic conditions are most critical for the level of feed intake [15,16]. At given husbandry and management conditions, cows reduce their feed intake at temperature-humidity-indices exceeding the thermal comfort zone to prevent excessive endogenous heat production and to maintain constant body temperature. Neurons located in the hypothalamus sense the blood temperature which is compared against the hypothalamic set point. Thus, oscillations of the tympanic temperature (which is close to the temperature at the hypothalamus) are highly associated with the dynamics of feed intake of cattle [17].

Among feed-related factors such as taste and smell, dietary fiber, protein and fat contents are known to influence feed intake of ruminants [18]. Preabsorptive, endogenous signals participating in the regulation of feed intake originate in the wall of the rumen, the abomasum, and the intestine, for example, when feed is detected by mechano- and chemosensors or when specific nutrients in the lumen of the digestive tract are sensed by enterocytes producing