J. Dairy Sci. 98:1057–1068
http://dx.doi.org/10.3168/jds.2014-8710
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Effect of increasing body condition on key regulators of fat metabolism in subcutaneous adipose tissue depot and circulation of nonlactating dairy cows

L. Locher,*[1,2,3] S. Häussler,†[1,2] L. Laubenthal,† S. P. Singh,†[4] J. Winkler,§ A. Kinoshita,* Á. Kenéz,‡ J. Rehage,* K. Huber,‡ H. Sauerwein,† and S. Dänicke§
*Clinic for Cattle, University of Veterinary Medicine Hannover, Foundation, 30173 Hannover, Germany
†Institute of Animal Science, Physiology & Hygiene Unit, University of Bonn, 53115 Bonn, Germany
‡Department of Physiology, University of Veterinary Medicine Hannover, Foundation, 30173 Hannover, Germany
§Institute of Animal Nutrition, Friedrich-Loeffler Institute (FLI), Federal Research Institute for Animal Health, 38116 Braunschweig, Germany

ABSTRACT

In response to negative energy balance, overconditioned cows mobilize more body fat than thin cows and subsequently are prone to develop metabolic disorders. Changes in adipose tissue (AT) metabolism are barely investigated in overconditioned cows. Therefore, the objective was to investigate the effect of increasing body condition on key regulator proteins of fat metabolism in subcutaneous AT and circulation of dairy cows. Nonlactating, nonpregnant dairy cows (n = 8) investigated in the current study served as a model to elucidate the changes in the course of overcondition independent from physiological changes related to gestation, parturition, and lactation. Cows were fed diets with increasing portions of concentrate during the first 6 wk of the experiment until 60% were reached, which was maintained for 9 wk. Biopsy samples from AT of the subcutaneous tailhead region were collected every 8 wk, whereas blood was sampled monthly. Within the experimental period cows had an average BW gain of 243 ± 33.3 kg. Leptin and insulin concentrations were increased until wk 12. Based on serum concentrations of glucose, insulin, and nonesterified fatty acids, the surrogate indices for insulin sensitivity were calculated. High-concentrate feeding led to decreased quantitative insulin sensitivity check index and homeostasis model assessment due to high insulin and glucose concentrations indicating decreased insulin sensitivity. Adiponectin, an adipokine-promoting insulin sensitivity, decreased in subcutaneous AT, but remained unchanged in the circulation. The high-concentrate diet affected key enzymes reflecting AT metabolism such as AMP-activated protein kinase and hormone-sensitive lipase, both represented as the proportion of the phosphorylated protein to total protein, as well as fatty acid synthase. The extent of phosphorylation of AMP-activated protein kinase and the protein expression of fatty acid synthase were inversely regulated throughout the experimental period, whereas the extent of phosphorylation of hormone-sensitive lipase was consistently decreasing by the high-concentrate diet. Overcondition in nonpregnant, nonlactating dairy cows changed the expression of key regulator proteins of AT metabolism and circulation accompanied by impaired insulin sensitivity, which might increase the risk for metabolic disorders.
Key words: fat metabolism, dairy cow, subcutaneous adipose tissue

INTRODUCTION

Many health disorders in dairy cattle are attributed to the process of uncontrolled lipid mobilization in response to excessive negative energy balance in early lactation (Drackley, 1999; Opsomer et al., 1999; Pravettoni et al., 2004; Roche et al., 2009) and are most likely related to reduced antilipolytic action of insulin (Ji et al., 2012; De Koster and Opsomer, 2013). Overconditioned cows with a BCS > 4.0 (Edmonson et al., 1989) at calving showed higher plasma concentrations of NEFA in early lactation until wk 7 postpartum compared with cows with moderate or low BCS (Pires et al., 2013). Hyperlipidemia in turn caused insulin resistance in dairy cows (Pires et al., 2007), which is in accordance to studies linking high BCS to reduced peripheral insulin sensitivity in the lipomobilization state (Holtenius et al., 2003; Hayirli, 2006; Holtenius and Holtenius, 2007). However, whether changes in

Received August 5, 2014.
Accepted October 24, 2014.
[1]These authors contributed equally.
[2]Corresponding authors: L.locher@med.vetmed.uni-muenchen.de and Susanne.Haeussler@uni-bonn.de
[3]Current address: Center of Veterinary Clinical Medicine, LMU Munich, Sonnenstrasse 16, 85764 Oberschleissheim, Germany.
[4]Current address: Physiology, Reproduction and Shelter Management Division, Central Institute for Research on Goats, Makhdoom, Farah 281 122, Mathura (U.P.), India.

adipose tissue (**AT**) metabolism occur with fattening and possibly account for subsequent insulin resistance in bovine is rarely known.

Beyond the storage and release of metabolites, AT exhibits specific enzymatic patterns. In addition, bioactive molecules, so called adipokines, are secreted from AT. Both specific enzymes and adipokines can affect peripheral organs (Trayhurn et al., 2006). Leptin, an adipokine, regulates energy intake, storage, and expenditure in ruminants (Chilliard et al., 2005). It positively reflects both BCS and nutrient status in cows and heifers (Reist et al., 2003; León et al., 2004) and interacts with insulin depending on the physiological status (Block et al., 2003; Leury et al., 2003). The adipokine adiponectin (**AdipoQ**) improved peripheral insulin sensitivity (Turer and Scherer, 2012), whereas low AdipoQ levels were associated with insulin resistance in humans and rodents (Berg et al., 2002). In dairy cows, reduced plasma AdipoQ concentrations seemed to be an important control variable for the homeorhetic adaptation to early lactation (Giesy et al., 2012; Singh et al., 2014). In addition, plasma AdipoQ was positively correlated with RQUICKI, a surrogate marker for insulin sensitivity, whereas a negative association with BCS in the periparturient period was recently reported by Singh et al. (2014).

The AMP-activated protein kinase (**AMPK**), a target of AdipoQ, controls energy expenditure within the cell by balancing ATP-consuming and ATP-providing pathways (Gauthier et al., 2008; Gaidhu et al., 2009). Both AdipoQ and insulin activated AMPK in isolated 3T3-L1 adipocytes presumably by increasing the AMP/ATP-ratio (Liu et al., 2010). With regard to the whole organism, AMPK activated β-oxidation and reduced glucose and NEFA output into circulation and thus influenced indicators of reduced insulin action in several species (Bijland et al., 2013). In bovine AT, lipolysis during early lactation was associated with an increase in phosphorylation of AMPK and the ratio of pAMPKα1 to AMPKα1 (Locher et al., 2012).

Fatty acid synthase (**FAS**) is one of the key enzymes in de novo synthesis of fatty acids and is positively related to the nutritional status in cattle (Sadri et al., 2011; Khan et al., 2013). Hormone-sensitive lipase (**HSL**) is a key enzyme of adrenergically stimulated lipolysis in adipocytes. This enzyme is activated by protein kinase A (**PKA**) dependent phosphorylation and its activation is controlled by catecholamines and insulin (Holm, 2003; Choi et al., 2010). In dairy cows, an increase in phosphorylation of HSL was associated with the onset of lactation and fat mobilization (Elkins and Spurlock, 2009; Locher et al., 2011). The present study aimed to assess the effect of increasing fat accumulation on key regulator proteins of fat metabolism in subcutaneous AT and circulation of dairy cows. Therefore, we analyzed the enzymes HSL and AMPK with their respective phorphorylated forms, as well as FAS, and AdipoQ in subcutaneous AT on protein level, whereas AdipoQ, leptin, and insulin concentrations were measured in blood. Transcription, translation, and activity of all the aforementioned enzymes and adipokines are largely influenced by pregnancy, parturition, and lactation. Therefore, nonlactating, nonpregnant cows serve as an appropriate model to elucidate the changes of these effectors in the course of overcondition independent from physiological changes related to gestation, parturition, and lactation.

MATERIALS AND METHODS

Animals, Feeding, and Sample Collection

The animal experiment was approved by the Lower Saxony State Office for Consumer Protection and Food Safety, Oldenburg, Germany (File Number 33.9–42502–04–11/0444). The experiment was conducted at the experimental station of the Institute of Animal Nutrition, Friedrich-Loeffler-Institute, Braunschweig, Germany. Nonpregnant, nonlactating, pluriparous German Holstein cows (n = 8) were housed in a free-stall barn with free access to straw and water. The cows were gradually adapted to a high-energy ration (corn-grass-silage with increasing the proportion of corn silage), including a successive increase of the proportion of the concentrate feed (within 6 wk from 0% up to 60% of the DM of the daily ration). The ration composition during conditioning and feeding regimen as well as the analyzed composition of the diet are given in Tables 1 and 2 and have been described in detail elsewhere (Dänicke et al., 2014). Blood samples from a jugular vein were collected monthly. Plasma was analyzed for glucose, NEFA, and BHBA concentrations using an automatic analyzer system (Eurolyser CCA180, Eurolab, Hallein, Austria) and were used for calculation of the surrogate indices for insulin sensitivity stated below. Plasma insulin concentration (determined in EDTA plasma) was measured by RIA (IM3210, Immunotech, Beckman Coulter Inc., Brea, CA). Biopsies from AT were taken before conditioning (wk 0) and at wk 8 and 15 of the trial. Animals were given 4 mL of procaine (Procaine 2%, Selectavet, Weyarn-Holzolling, Germany) as a lumbosacral epidural anesthesia. After preparation of the surgical field, a 5.0-cm skin incision was made in the region of the tailhead and subcutaneous AT from the underlying fat layer was collected. The biopsies from wk 8 and 15 were each made on the contralateral side of the preceding biopsy. To reduce surgically induced blood contamination, the sample was shortly rinsed

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