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Environmental heat stress modulates thyroid status and its response to repeated endotoxin challenge in steers

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ABSTRACT

The objective of this study was to evaluate in cattle, the effects of acute exposure to a heat stress (HS) environment on the status of the pituitary (thyrotropin, TSH)–thyroid (thyroxine, T_4)–peripheral tissue T_4 deiodination (type 1 5'-deiodinase [D1]; triiodothyronine [T_3]; reverse-triiodothyronine [rT_3]) axis, and the further response of this pituitary–thyroid–peripheral tissue axis (PTTA) to perturbation caused by the induction of the proinflammatory innate immune state provoked by the administration of gram-negative bacteria endotoxin (lipopolysaccharide [LPS]). Ten steers (318 ± 49 kg body weight) housed in controlled environment chambers were subjected to either a thermoneutral (TN: constant 19°C) or HS temperature conditions (cyclical daily temperatures: 32.2°C–40.0°C) for a total period of 9 d. To minimize the effects of altered plane of nutrition due to HS, steers in TN were pair-fed to animals in HS conditions. Steers received 2 LPS challenges 3 d apart (LPS1 and LPS2; 0.2 μg/kg body weight, intravenously, *Escherichia coli* 055:B5) with the first challenge administered on day 4 relative to the start of the environmental conditioning. Jugular blood samples were collected at 0, 1, 2, 4, 7, and 24 h relative to the start of each LPS challenge. Plasma TSH, T_4, T_3, and rT_3 were measured by radioimmunoassay. Liver D1 activity was measured in biopsy samples collected before the LPS1 (0 h) and 24 h after LPS2. Before the start of LPS1, HS decreased ($P < 0.01$ vs TN) plasma TSH (40%), T_4 (45.4%), and T_3 (25.9%), but did not affect rT_3 concentrations. In TN steers, the LPS1 challenge decreased ($P < 0.01$ vs 0 h) plasma concentrations of TSH between 1 and 7 h and T_4 and T_3 at 7 and 24 h. In HS steers, plasma TSH concentrations were decreased at 2 h only ($P < 0.05$), whereas plasma T_3 was decreased at 7 and 24 h ($P < 0.01$). Whereas plasma T_4 concentrations were already depressed in HS steers at 0 h, LPS1 did not further affect the levels. Plasma rT_3 concentrations were increased in all steers at 4, 7, and 24 h after LPS1 ($P < 0.01$). The patterns of concentration change of T_4, T_3, and rT_3 during LPS2 mirrored those observed in LPS1; the responses in plasma TSH were of smaller magnitude than those incurred after LPS1. The LPS challenges reduced ($P < 0.01$) hepatic activity of D1 in all animals but no differences were observed between steers subjected to TN or HS environment. The data are consistent with the concept that acute exposure of cattle to a HS environment results in the depression of the pituitary and thyroid components of the PTTA, whereas a normal capacity to generate T_3 from T_4 in the liver is preserved. The data also suggest that LPS challenge further suppresses all components of the PTTA including liver T_3 generation, and these PTTA perturbations are more pronounced in steers that encounter a HS exposure.

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1. Introduction

Thyroid status is an important determinant of metabolic rate [1], and in domesticated farm animals, affects the amount of nutrients partitioned for maintenance, growth [2], and lactation [3]. Thyroid hormones may directly influence metabolic rate of individual organs, the liver in particular, and impart differences in sensitivity of various tissues to other regulatory hormones especially the multifunctional catecholamines [4]. Thyroxine (T_4), the predominant thyroid hormone in the circulation, has no inherent biological activity and is synthesized only in the thyroid gland. The most metabolically active thyroid hormone, triiodothyronine (T_3) is mainly produced in several extrathyroidal tissues by the removal of one iodine from the outer ring of T_4 by type 1 5'-deiodinase (D1) or type 2 5'-deiodinase (D2) [5]. In contrast, biologically inert compound, reverse-triiodothyronine (rT_3) is produced by deiodination of the inner ring of T_4 by 5-deiodinase (D3) [5]. In euthyroid mammals, almost all of the circulating T_3 is generated by 5'-deiodination by D1 expressed predominantly in liver and kidney [6] and because of the central role played by the liver across metabolic responses and adjustments to stresses, the liver is the principle target of interest as a peripheral tissue.

Thyroid hormones are critical for the regulation of thermogenesis [1] and therefore are an important consideration in the adaptation to heat stress (HS) [7]. Thyroid axis status, the integrated functioning and signaling between the hypothalamo–pituitary unit, the thyroid gland, and the peripheral tissues, allow for the adjustment of metabolic rates in favor of decreased energy utilization and heat production during exposure to elevated ambient temperatures (along with humidity) that demand a homeostatic response for normalization of interior body core temperatures [8]. It has been shown in cattle that high environmental temperatures reduced circulating concentrations of T_4 [9] and T_3 [10,11]. In Holstein calves, changes in plasma T_3 concentration during thermoneutral (TN), HS, and postheat compensatory periods were positively correlated with daily weight gains [12]. In addition, the degree of plasma T_3 reduction was related to the ability of different cattle breeds to adapt to thermal stress [13].

Thyroid axis status is also compromised in a variety of acute and chronic infections, inflammatory illnesses, and toxin-mediated disease states [14]. Endotoxin (lipopolysaccharide [LPS]), a major component of the outer membrane of gram-negative bacteria, is a highly potent activator of the innate immune system and constitutes an important marker of pathogen recognition for the host's defenses against gram-negative pathogens [15,16]. After the binding of LPS to cell membrane–associated toll-like receptor 4 proteins, a transient burst of proinflammatory cytokines, especially tumor necrosis factor-α (TNF-α), triggers a cascade outpouring of proinflammatory response mediators including vasoactive and pyrogenic factors such as interleukins (ILs), arachidonic/eicosapentanoic acid compounds, acute phase proteins (APPs), adrenomedullin, and a number of reactive oxygen and nitrogen species [17,18]. In experiments conducted by our laboratory, intravenous injection challenge with *Escherichia coli* LPS at doses between 0.2 and 2.5 μg/kg body weight (BW) have always resulted in a measurable increase in circulating plasma concentrations of TNF-α that peak at approximately 1 to 2 h after challenge, and measurable increases in the APP such as serum amyloid A (SAA) and/or haptoglobin 24 to 48 h after challenge [18]. Parasitic infection or LPS challenge has been shown in cattle to decrease circulating concentrations of T_4 and T_3 and to inhibit hepatic activity of D1 [19,20]. However, no studies to date have taken the approach of defining how HS might impact the intensity and duration of changes in an animal's status of pituitary (thyrotropin [TSH])–thyroid (T_4)–peripheral tissue (liver) T_4 deiodination (T_3, rT_3, D1 activity) axis (PTTA) during response to innate immune challenge.

The purpose of this study was to evaluate in cattle the activity of the PTTA during short-term adaptation to HS and the response of this modified PTTA status to immune challenge induced by repeated LPS administrations. Changes in circulating concentrations of TSH, T_4, T_3, and rT_3, as well as in hepatic activity of D1, were estimated.

2. Materials and methods

2.1. Animals and experimental design

Study protocol and procedures involving animals were approved and conducted in accordance with the University of Arizona Institutional Animal Care and Use Committee and the USDA Beltsville Animal Care and Use Committee. To address the issue in a manner devoid of animal-to-animal variability due to reproductive or lactation status of female cattle [21,22], Holstein steers were used as the test model. Growing Holstein steers ($n = 10$, average BW 318 ± 49 kg, 11–13 mo of age) were paired by weight and divided and assigned in equal numbers to individual tie stalls in 1 of 2 environmental chambers in the University of Arizona's William J. Parker Agriculture Research Complex. Throughout the experiment, steers were fed an 86% concentrate diet primarily composed of steam-flaked corn and alfalfa hay formulated to meet or exceed National Research Council recommendations [23] at 6 AM and 5 PM. Feed intake and water intake were recorded daily. The steers were transferred to their respective environmental chambers for a 9-d period of acclimation under ambient temperature conditions. After adjusting to the environmental chambers, steers were exposed to either a TN environment (constant 19°C, 20% humidity) or HS conditions (cyclical daily temperatures: 32.2°C–40.0°C; 20% humidity) for 9 d. To account for confounding alterations in HS-associated changes in feed intake per se, each TN steer was pair-fed daily to the intake level of its HS weight-paired cohort with the adjustment to feed offered to TN steers made 24 h after the intakes of HS steers were measured. To facilitate the acquisition of blood samples or administer LPS, an indwelling catheter was introduced into the jugular vein on each side of the neck 1 d before the first LPS challenge and maintained for the duration of the trial. Catheters were maintained patent with the instillation of a solution of sterile heparinized (10 U/mL) saline at a volume equivalent to 90% of void volume of catheter to minimize inadvertent heparinization of animals. Solution of LPS was prepared in pyrogen-free saline and,

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