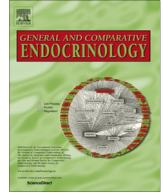




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Differential responses of the somatotropic and thyroid axes to environmental temperature changes in the green iguana



José Ávila-Mendoza^a, Martha Carranza^a, Patricia Villalobos^b, Aurora Olvera^b, Aurea Orozco^b, Maricela Luna^a, Carlos Arámburo^{a,*}

^aLaboratorio de Bioquímica de Hormonas, Departamento de Neurobiología Celular y Molecular, Instituto de Neurobiología, Universidad Nacional Autónoma de México, Campus Juriquilla, Querétaro, Qro. 76230, Mexico

^bLaboratorio de Fisiología Evolutiva, Departamento de Neurobiología Celular y Molecular, Instituto de Neurobiología, Universidad Nacional Autónoma de México, Campus Juriquilla, Querétaro, Qro. 76230, Mexico

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ABSTRACT

Growth hormone (GH), together with thyroid hormones (TH), regulates growth and development, and has critical effects on vertebrate metabolism. In ectotherms, these physiological processes are strongly influenced by environmental temperature. In reptiles, however, little is known about the direct influences of this factor on the somatotropic and thyroid axes. Therefore, the aim of this study was to describe the effects of both acute (48 h) and chronic (2 weeks) exposure to sub-optimal temperatures (25 and 18 °C) upon somatotropic and thyroid axis function of the green iguana, in comparison to the control temperature (30–35 °C). We found a significant increase in GH release (2.0-fold at 25 °C and 1.9-fold at 18 °C) and GH mRNA expression (up to 3.7-fold), mainly under chronic exposure conditions. The serum concentration of insulin-like growth factor-I (IGF-I) was significantly greater after chronic exposure (18.5 ± 2.3 at 25 °C; 15.92 ± 3.4 at 18 °C; vs. 9.3 ± 1.21 ng/ml at 35 °C), while hepatic IGF-I mRNA expression increased up to 6.8-fold. Somatotropic axis may be regulated, under acute conditions, by thyrotropin-releasing hormone (TRH) that significantly increased its hypothalamic concentration (1.45 times) and mRNA expression (0.9-fold above control), respectively; and somatostatin (mRNA expression increased 1.0–1.2 times above control); and under chronic treatment, by pituitary adenylate cyclase-activating peptide (PACAP mRNA expression was increased from 0.4 to 0.6 times). Also, it was shown that, under control conditions, injection of TRH stimulated a significant increase in circulating GH. On the other hand, while there was a significant rise in the hypothalamic content of TRH and its mRNA expression, this hormone did not appear to influence the thyroid axis activity, which showed a severe diminution in all conditions of cold exposure, as indicated by the decreases in thyrotropin (TSH) mRNA expression (up to one-eighth of the control), serum T4 (from 11.6 ± 1.09 to 5.3 ± 0.58 ng/ml, after 2 weeks at 18 °C) and T3 (from 0.87 ± 0.09 to 0.05 ± 0.01 ng/ml, under chronic conditions at 25 °C), and Type-2 deiodinase (D2) activity (from 992.5 ± 224 to 213.6 ± 26.4 fmol I¹²⁵T4/mg h). The reduction in thyroid activity correlates with the down-regulation of metabolism as suggested by the decrease in the serum glucose and free fatty acid levels. These changes apparently were independent of a possible stress response, at least under acute exposure to both temperatures and in chronic treatment to 25 °C, since serum corticosterone had no significant changes in these conditions, while at chronic 18 °C exposure, a slight increase (0.38 times above control) was found. Thus, these data suggest that the reptilian somatotropic and thyroid axes have differential responses to cold exposure, and that GH and TRH may play important roles associated to adaptation mechanisms that support temperature acclimation in the green iguana.

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1. Introduction

It is well known that temperature is a critical environmental factor directly affecting molecular, biochemical and physiological processes, particularly in ectothermic vertebrates (Angilletta et al., 2002; Angilletta, 2009). In reptiles, this factor has a strong

* Corresponding author.

E-mail address: aramburo@unam.mx (C. Arámburo).

influence upon activity levels, metabolism and reproduction rate (Blouin-Demers et al., 2000; Deeming, 2004; Radder and Shine, 2006). Besides, the optimal body temperature in these organisms promote essential functions such as digestion, embryonic development, sex differentiation and somatic growth (Flatt et al., 2001; Ladyman et al., 2003; Zani, 2008). Some of these functions are regulated by complex hormonal systems such as the somatotrophic axis (SA), which is the primary endocrine regulator of growth in all vertebrates, affecting also the metabolism and regulation of cell proliferation and cell differentiation (Rousseau and Dufour, 2007). The main interacting components involved in the SA are several hypothalamic neuropeptides, such as: growth hormone releasing hormone (GHRH), pituitary adenylate cyclase activating polypeptide (PACAP), and somatostatin; the pituitary growth hormone (GH); and insulin-like growth factor I (IGF-I) which is synthesized and secreted primarily by the liver, but also from other peripheral tissues; as well as their respective receptors (Canosa et al., 2007).

In mammals, GHRH and somatostatin play a delicate equilibrium upon GH synthesis and secretion regulation, one being stimulatory and the other inhibitory, respectively (Lamberts, 1988; Ling et al., 1984). However, this hypothalamic regulation appears to be more complex and heterogeneous in non-mammalian vertebrates (Rousseau and Dufour, 2007), since other factors, in addition to GHRH and PACAP, positively regulate GH synthesis and secretion. It is known that thyrotropin-releasing hormone (TRH) not only stimulates thyroid-stimulating hormone (TSH) release from the pituitary thyrotropes, but also GH secretion by somatotropes of fish (Trudeau et al., 1992), amphibians (Gracia-Navarro et al., 1991), reptiles (Hall and Chadwick, 1984) and birds (Ahene et al., 1991; Harvey, 1990). In reptiles PACAP can also stimulate both actions with equal potency as GHRH (Gahete et al., 2009), and it has been described that in some fish GnRH is a potent GH-releasing factor (Li et al., 2002). In contrast, the main inhibitor of pituitary GH release is somatostatin, and this role is phylogenetically conserved (Rousseau et al., 1998). Another mechanism that is evolutionarily conserved is the GH-regulated secretion of IGF-I by hepatocytes (although it is also expressed in several tissues in response to GH and other factors); IGF-I, in turn, is involved in the negative feedback regulation of GH secretion (Rousseau and Dufour, 2007).

On the other hand, TRH and TSH belong to a system that regulates the activity of the thyroid hormones (TH): tetraiodothyronine (T4) and triiodothyronine (T3). TH are produced in the thyroid gland primarily as T4, which can then be metabolized to T3 and 3,5-diiodothyronine (T2) by three types of deiodinase enzymes (D1, D2 and D3) in peripheral tissues (Köhrle, 2000).

Environmental temperature is an abiotic factor that can influence the function of both hormonal systems, somatotrophic and thyroid axes, in ectothermic organisms. With respect to the GH axis, in fish it has been described that its response to environmental temperature changes depends on the species, developmental stage (Li et al., 2007), nutritional status (Gabillard, 2003a), ecological niche (Vargas-Chacoff et al., 2009) and reproductive stage (David and Degani, 2011; Levy et al., 2011) and, in general, the GH-IGF-I axis diminishes its activity at temperatures below the optimum for each species. On the other hand, the thyroid axis is a thermosensitive system that regulates the endocrine thermogenic response of endotherms and its activity increases during cold exposure (Silva, 2001) whereas, in ectotherms, thyroid activity is modified with variations in environmental temperature, increasing during exposure to warmer conditions and decreasing at lower temperatures (Buffenstein and Louw, 1982; Walker, 1973). However, the response of both axes to environmental temperature variations has not been studied in terrestrial ectotherms such as reptiles, species with a strong influence of this factor over its growth (Li et al., 2011).

Therefore, the aim of this study was to evaluate the response of the green iguana's somatotrophic and thyroid axes when exposed to sub-optimal environmental temperatures. Our main results showed that, under these conditions, activity of the green iguana somatotrophic axis increased while that of the thyroid axis decreased, which implies a differential function under these conditions. In addition, results of the present study suggest that TRH could play a role as a crosstalk-mediator between the two axes.

2. Material and methods

2.1. Animals

Eight-month-old green iguana (*Iguana iguana*) juveniles were kindly donated by the Environmental Management Unit (EMU) at Cementos Holcim-Aspasco (Guerrero, México), and by the Conservation Breeding Center of iguanas at Universidad del Mar (Oaxaca, México). Animals were maintained initially in cages at 30–35 °C, with 60–70% relative humidity and a controlled 12-h dark/12-h light photoperiod, and then subjected to 35–38 °C and 25–28 °C in the light and dark period, respectively, mimicking natural conditions. They were fed daily with a vegetable and fruit diet including carrot, pumpkin, apple, and water *ad libitum*. The animals were sacrificed by decapitation following a protocol approved by the Institute's Bioethics Committee (Instituto de Neurobiología, UNAM). Immediately after decapitation, the trunk blood was collected in glass tubes (in less than 2 min), where clot formation was allowed for 20 min at room temperature. Serum was separated by centrifugation at 5000 rpm for 15 min. Simultaneously, the hypothalamus, pituitary, and liver were rapidly dissected from decapitated iguanas. Both the serum and the tissues collected were frozen immediately at –80 °C until used.

2.2. Experimental design

To evaluate the changes of the somatotrophic axis components in response to variations in environmental temperatures, 2 experimental groups composed of 12 iguanas each and one control group with 6 iguanas were formed. The control group was maintained under the conditions described above. The two experimental groups were maintained at a constant environmental temperature, one at 25 °C and the other at 18 °C. After 48 h of exposure to the corresponding conditions, 6 iguanas were sacrificed from each experimental group (acute treatment) as was described above; the remaining 6 were sacrificed after two weeks (chronic treatment). The time of animal sacrifice was always similar in all cases (around 14:00 h), in order to discard variations in the hormone concentrations (including corticosterone) due to circadian rhythm effects.

2.3. Quantification of serum hormones

2.3.1. Growth hormone

Serum GH was measured by a heterologous indirect enzyme-linked immunosorbent assay for chicken GH (ELISA, Martínez-Coria et al., 2002) which has significant cross-reactivity with iguana GH (Ávila-Mendoza et al., 2014). Briefly, 96-well microtiter plates (Immulon 2HB, Chantilly, VA) were coated overnight at 4 °C with 12 ng of recombinant chicken GH (rcGH, American Cyanamid, Princeton, N.J., USA, lot 100) in 100 µl of 0.1 M sodium carbonate buffer (pH 10.3). The plates were washed five times with TPBS (0.01 M sodium phosphate, 0.15 mM NaCl, 0.05% (w/v) Tween-20, pH 7.0) using an automatic microplate washer (Bio-Rad Immunowash, Mod. 1250, Hercules, CA). This wash procedure was repeated after each incubation step. Pituitary extracts (1.75–114 µg of

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