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Animal Physiological and Behavioural Thermoregulatory Mechanisms: A Review

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Abstract

Thermoregulation refers to the ability of organisms to keep their internal temperature at a given range despite the changing environmental temperatures. It's vital in homeostasis, physiological functions, reproductive success and survival of various animal species. This review paper explores the different physiological and behavioural thermoregulatory mechanisms in animals and their role in homeostasis, reproduction and survival of the animals. Animals are categorized into endotherms and ectotherms basing on the thermoregulatory behaviours that they employ to maintain their body temperature. Thermoregulation is strongly related to energy balance in animals and therefore less energy is used when the ambient temperature is similar to the thermal neutral zone of the animal. In incidences of thermal changes i.e. increased or decreased ambient temperatures, physiological mechanisms like shivering, evaporative cooling are employed to gain and lose heat respectively which increases energy expenditure. Endotherms (mammals & birds) also employ sophiscated behavioural mechanisms like communal huddling, nesting to minimize heat loss and wallowing/panting to facilitate evaporative cooling while ectotherms(reptiles & insects) bask under the sun to gain heat and seek shades to avoid thermal extremes. Behavioural mechanisms lower the animal activity thus reducing metabolic energy costs incurred in cold exposure and also hyperthermia associated with dehydration can be reduced during hot days. Behavioural mechanisms also avoid hypothermia as heat exchange is enhanced among the animals that commune together. Thermoregulation in animals is crucial as it influences various physiological, reproductive functions in the body and therefore understanding the behavioural and physiological thermoregulatory mechanisms provides insights into animals' survival rates and performance in various environments.

Keywords: Behavioural; Physiological; Hyperthermia; Hypothermia; Homeostasis

Introduction

Thermoregulation is a physiological and behavioural process allowing organisms to adjust their body temperature in response to changing environmental conditions, optimizing cellular and molecular functions [1]. It plays a major role in organism homeostasis, involving central, endocrine and metabolic functions [2]. Animal species have developed various ways to maintain an internal temperature to enable efficient functioning of cells and organs, despite a changing external environment condition [3]. These mechanisms include morphological, physiological, and behavioural changes that allow them to confront variable conditions to regulate their physiological capacities [4,5]. Additionally, adaptation plays a major role in temperature maintenance for example the long, highly-vascularized ears of Oryctolagus cuniculus aid in dissipating heat, the development of thermogenesis from brown adipose tissue (BAT) in placental (eutherian) mammals, the reduced thickness of subcutaneous fat in ruminants from arid regions [1].

Endotherms mainly mammals have two broad types of thermoregulating mechanisms: physiological (or reflex) and behavioural. Physiological mechanisms consist of involuntary effectors that produce mostly automatic responses that generate or dissipate heat upon the activation of thermoreceptors and relay of impulses to the brain [1]. Behavioural mechanisms on the other hand depends on voluntary action when the thermal stimuli are detected by thermoreceptors and it's learned over time. Endothermic homeothermy demands high energy levels thus requiring evolution to develop species that minimize energetic costs in resource-limited environments. In order to cope with energy constraints, some mammals and birds exhibit temporal reductions in metabolic rate and body temperature, allowing them to conserve energy during challenging conditions [6]. Some species have specialized thermoregulating organs, like the rat's tail, that dissipate heat quickly due to its large surface area and dense vascularization [7-9]. Conserving a relatively constant core body temperature (37°C) in most mammalian species is essential in maintaining body system functionality and the sensitive chemical and physical processes involved [1]. High temperatures above 45°C cause hyperthermia a condition characterised by fatal brain injuries, while those below 27–29°C cause hypothermia which decreases respiratory rate and causes even death [10,11]. This review, therefore, focuses on the main physiological and behavioural mechanisms of thermoregulation in mammals, their relation to homeostasis and the adverse effects of extreme thermal changes information that can be used in related disciplines and areas of opportunity

Role of the Skin in Thermoregulation

The skin initiates protective measures in response to changes in temperature, solar radiation, and humidity, and its adaptations have led to the development of mechanisms that help to deal with alterations (Daniel Mota-Rojas). Mechanisms like preventing water loss and extracellular liquid through the tallow secreted by sebaceous glands when the temperature is high [12]. Thermal changes are detected by the cutaneous thermoreceptors including transient receptor potential (TRP ion channels) that transduce local temperature into neural signals that are transferred to hypothalamic and brainstem centres that coordinate autonomic and behavioural responses [13]. Mammals have been reported to have 11 TRP channels that are thermosensitive [14,15]. During high temperature, the sensory skin neurones are activated by TRP 1and 2 stimulation while the neurones are activated by TRP 8 stimulation under low temperatures below 27°C [1,13]. The TRP 1 in birds, reptiles, amphibians and insects have been reported to exhibit more sensitivity to high temperatures as compared to the TRP 1 in mammals [16].

Physiological Thermoregulatory Mechanisms

Physiological mechanisms consist of involuntary effectors that produce mostly automatic responses upon the activation of thermoreceptors in the skin and internal organs and the arrival of information to the hypothalamus, relayed through the spinal cord and midbrain. The transferred information is subsequently used to control thermo-effector organs, like brown adipose tissue and muscle, which play a role in thermogenesis. Physiological thermoregulation is mainly observed in homeotherms, and includes shivering thermogenesis in skeletal muscles, non-shivering thermogenesis in brown adipose tissue, and vasodilation/vasoconstriction [13].

Vasolidilation

During heat stress, thermoreceptors are activated to trigger processes such as vasodilation and sweating, leading to a decrease in body temperature. Vasodilation occurs through inhibition of the vasoconstrictor component of the Sympathetic nervous system (SNS) and, the activation of the vasodilator component of the SNS [17]. Activation of the vasodilator augments blood circulation to the periphery thus dissipating heat and it's induced when the Pre optic area (POA) receives excitation or warming stimuli [1].

Sweating

Sweating or evaporative cooling is another mechanism of dissipating heat in animals. When cutaneous vasodilation is unable to meet the thermal homeostatic requirements set by the POA [17], the SNS stimulates sweating by releasing acetylcholine which binds to muscarinic type3 (M3) receptors expressed in the sweat glands [18]. Other mammals dissipate heat by salivation, spreading saliva over the entire cutaneous surface or fur and panting performed through the respiratory tract [19].

Hibernation

On the other hand, during cold stress animals activate various ways to generate heat. Birds and mammals despite the ability to maintain a high and stable body temperature of around 40°C and 36°C, respectively, may enter hibernation, or any state along the continuum in order to conserve body heat. Hibernation is characterized by seasonal and sometimes extreme reductions in body temperature and metabolic rate. Also, upregulation of a mitochondrial enzyme, pyruvate dehydrogenase kinase 4, which inhibits the oxidation of pyruvate (conversion of pyruvate to acetyl-CoA) after glycolysis.

Vasoconstriction

Cooling of the skin activates the cold thermoreceptors which initiate vasoconstriction [17], which reduces heat transfer to the environment and conserves heat in the centre of the organism's body, effectively increasing insulation by the body's shell [4]. When the Preoptic area (POA) detects decrease in the core body temperature, it activates the sympathetic nervous system that innervates the endothelium of the blood vessels by releasing noradrenaline that elicits vasoconstriction.

BAT Thermogenesis

Brown adipose tissue (BAT) thermogenesis is another essential heat producing mechanism in response to cold activity. The BAT tissue is innervated by the sympathetic nervous system that releases norepinephrine [1], this activates brown fat cells causing their mitochondria to leak protons. The norepinephrine increases the amount and activity of uncoupling protein-1 (UCP1), which allows protons to flow across the mitochondrial membrane and produce heat instead of ATP [8]. The BAT contains β_3 adrenergic receptors that are activated by norepinephrine (NE) and consequently activate UCP1 receptors to produce heat [6,20]. Mammals like mice and rats have large deposits of BAT in the interscapular region, while adult species such as sheep have brown adipocytes combined with white adipose tissue because skeletal tissue has a bigger role for thermoregulation. Smith, et al. [21] also reported more β_3 adrenergic receptors in brahman than angus calves which also shrank after 48hours of exposure to cold temperature (4°C) which indicates that this breed may exhaust their BAT reserves shortly after birth in order to adapt to cold stress. Liu, et al. [22] also reported a reduction in perirenal BAT in newly born goats exposed to low temperatures of 6°C.

Sex hormones play a role in the development of BAT activity in animals with estrogen having a stimulatory effect on the BAT adipocytes and also the hypothalamus which activates the sympathetic nervous system [23-25]. Neonate piglets have small fat deposits (around 15 g Kg^{-1}) available in the abdomen and on the back [26], limiting their capacity to produce heat through food consumption [27]. Studies have also indicated that piglets that lack BAT at birth use the process called "browning of white adipose tissue" (WAT) to perform non-shivering thermogenesis [28].

Shivering

Cold exposure also increases metabolic heat production, mainly through skeletal muscle contractile activity/ shivering. The involuntary repeated rhythmic muscle contractions expend metabolic energy which is liberated as heat [1]. Research indicates that the intensity and extent of shivering vary according to the severity of cold stress with more muscle contraction involved as the shivering intensity increases thus increasing the metabolic rate increases. A study on the responses of cold exposure (4°C) in Tibetan (cold tolerant) and Bama (cold sensitive) pigs indicated a higher transcriptional response in the skeletal muscle of Tibetan pigs upon cold stimulation [29]. Involuntary muscle contractions with a frequency of 10 to 20 seconds in horses mainly increases heat production than other functions [30]. The continuous muscle action during shivering requires energy in terms of glucose and lipids and therefore it becomes a challenge to new born animals that have limited energy resources. Some studies highlight the importance of colostrum or glucose supplementation to face hypothermia in newborns [31,32].

Behavioural Thermoregulatory Mechanisms

Behavioural thermoregulation is a crucial in both homeotherms and ectotherms, though it plays more significant roles in ectotherms because their body temperature depends on the environment temperature and they must seek comfortable temperature zones and changes postures to maintain body temperature. Its mechanisms are classified into those performed to prevent hypothermia and hyperthermia. The later involves strategies that dissipate body heat such as panting, specific postures, cold and shade seeking. Some nocturnal species in arid or semi-arid ecosystems spend their day time in thermal refuge, burrows/ tree holes, decreasing their energy and water expenditure which consistently reduces body temperature by 1 to 2 degrees as exemplified in the ground squirrel [11]. Specific postures like exposition to wind, prone position, posting on rocks exhibited by mammals increase the surface-area ratio or the gradient between the organism and the air to promote the conductive heat exchanges between the warm skin and the air [2]. Movement of the highly vascularized ears of elephants has been observed to enhance heat loss and temperature regulation through improved convection on the ear surface [33,34]. Panting in dogs increases respiratory rhythm frequency dissipating huge amounts of body heat through water loss [35,36].

Behaviours that prevent hypothermia in contrast are based on strategies that conserve body heat for example group huddling, nest housing, certain postures like basking. Pigs, seals, bats, rabbits, rats aggregate in numbers to limit energy dissipation and thus decrease the energetic needs for body heat production. Huddling i n New Zealand and Californian rabbits has been noted to reduce hypothermia at cold temperatures of about 18, 15, and 10°C [37]. Nest housing in birds traps the heat lost by the animal and conserves it within the shelter thus increasing the ambient temperature. Energy intake and locomotive activity can also enhance or decrease heat production in animals. A study conducted to evaluate the behavioural response of Korean native calves and steers under cold exposure indicated an increase in standing time in both groups while the lying time was significantly reduced [38]. Similarly, feedlot steers housed at −40–19°C increased their ruminating (32%) and lying down behaviours by 24% [39]. Increased lying time can considered as a heat retention behaviour similar to huddling in rabbits. Increase in the energy (feed) intake has reported as a strategy of meeting the energy requirements to maintain an adequate core body temperature [40]. In contrast, lying and feeding behaviour were not affected by low temperatures (−10°C) in dairy goats with animals maintained at 10 °C showing similar percentages [41]. Domestic animals use certain behaviours to keep their body temperature stable, and these actions along with their internal body responses help them regulate heat during hypothermia.

Thermoregulation and Homeostasis

Ambient temperature and thermoregulation play a major role in balancing body energy by regulating food intake, heat production and energy expenditure. Ambient temperature and food intake inverse relationship across a wide range of temperatures in multiple animal species. Long term exposure to cold temperatures leads to a rise in food intake but it's insufficient to compensate for the increased metabolic output [42], resulting in a progressive reduction of fat mass. On the other hand, high environmental temperature close to the thermal neutral zone suppress food intake. Brown adipose tissue (BAT) thermogenesis plays a central role in the regulation of both body temperature and energy homeostasis, by converting the stored chemical energy into heat instead of ATP thus reducing the energy levels in the animal's body. It also increases lipolysis, fatty acid oxidation and thus activating thermogenic metabolism in BAT exerts beneficial impacts in obesity, type-2 diabetes, dyslipidaemia and cardiovascular pathologies, improving the glucose and lipid homeostasis [43,44]. Shivering thermogenesis involves rapid skeletal muscle contraction burning large amounts of ATP to increase heat production therefore there's an increase in glucose uptake, glycogen breakdown, and fatty acid oxidation in the body. Temperature alters membrane fluidity and protein folding by denaturing proteins and destabilizing membranes during high temperatures and increasing membrane rigidity during cold temperatures thus impairing ion channel function [45].

Effects of Hypothermia in Farm Animals

Hypothermia is defined as a deliberate (therapeutic) or accidental lowering of core body temperature below 35°C. It's subdivided into three basing on degree of severity: mild hypothermia (37°C to 32°C) during which thermoregulatory responses continue to function normally; moderate hypothermia (32°C to 28°C) with gradual loss of thermoregulatory response, especially that of shivering; and severe hypothermia (<28°C) with full suppression of thermoregulation homeostasis and muscle rigidity [46,47].

Hypothermia causes a reduction in metabolic rate and consequent decrease in produced CO2 which lowers the numbers of breaths per minute as well as tidal volumes. The rate of carbon dioxide removal is also low by the lungs due to bradypnea and inefficient alveolar ventilation, this later leads to respiratory acidosis. In anaesthetized animals, a drop in core temperature has been noted to cause considerable complications owing to the lower basal metabolic rate, which in fact reduces 10% for every 1 ^{0}C of reduced temperature [48]. Hypothermia slows heart rate and respiration by causing arrhythmias including fatal ventricular fibrillation in extreme cases and poor tissue perfusion. A case study where dogs were deliberately cooled to cause hypothermia, half of them developed ventricular fibrillation when their body temperature dropped below 23.5°C and systolic cardiac arrest at final stages [49].

Effects of Hyperthermia

Hyperthermia refers to elevation of body temperature above the normal physiological range due to failed thermoregulation. In mammals its usually above 40 ^{0}C though the threshold varies by species. It's caused by excess environmental heat, toxins or pathological conditions. Feedlot animals are at particularly high risk for heat stress because their confinement limits their ability to pursue shade and other natural cooling behaviours, for example sheep kept under feedlot conditions tend to have a rise in rectal temperature by 0.5-1.5°C. Increased respiratory rate /panting as a means of dissipating heat has been noted to double the usual rate of 60 breaths/minute in cattle. Monogastric animals instinctively decrease their feeding activity in response to high ambient temperatures to minimise additional metabolic heat production [50]. Feed intake reduction creates an energy deficit that limits the availability of essential nutrients required for growth and tissue repair, leading to slower weight gain and reduced overall growth rates [51].

Studies have shown that heat stress decreases daily feed intake by up to 15–20% in poultry which translates into a significant drop in body weight gain and overall growth performance [52]. It also reduces egg production and quality due to low intestinal absorption of calcium and suppression of vitamin D_3 synthesis necessary for egg shell formation [53]. The limited ability of pigs to sweat during heat stress causes suppression of immune function, elevated cortisol, metabolic disturbances, and poor growth. Plasma levels of Non esterified fatty acids (NEFAs) and ketone bodies, such as β-hydroxybutyrate, increase, indicating elevated lipid mobilisation. Heat stress-induced hyperthermia has been reported to cause fatal damage to the brain and other vital organs in cattle and sheep [54]. Hyperthermia impairs immune responses especially in monogastric animals (like pigs and poultry) where chronic heat stress suppresses lymphocyte proliferation, reduces function of natural killer (NK) cells, and disrupts cytokine balance (pro- vs anti-inflammatory) [55-64].

Recommendations

Increasing issues of climate change tend to increase ambient temperatures causing heat stress in animals. This is an increasing threat to animal welfare, production, and health. Recent reviews highlight how both physiological processes and behavioural adaptations like shade-seeking, reduced feed intake act together to regulate body temperature but there is a need for a comprehensive integrative synthesis that spans species, links molecular/cellular mechanisms with whole-animal behaviours, and discusses practical mitigation strategies.

Conclusions

Thermoregulation in animals is crucial as it influences various physiological, reproductive functions in the body and therefore understanding the behavioural and physiological thermoregulatory mechanisms provides insights into animals' survival rates and performance in various environments. Temperature regulation in mammals is organised to respond to various stimuli that can generate thermal changes. The skin is a vital organ in thermoregulation and homeostasis because its one of the first detectors of thermal changes in the body, participating in vasomotor responses permit the dissipation or retention of heat through vasodilatation and vasoconstriction.

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