Why is thermoregulation important?

In all living organisms there is a complex series of chemical reactions occurring, the rate of which is dependent of temperature. In order for these chemical reactions to occur and thus sustain life all animals exhibit some way of regulating their body temperature. This process is known as thermoregulation. This regulation is achieved in various ways, either by behavioural or autonomic means. Homeothermic animals take advantage of both behavioural and autonomic means of regulating their body temperature in response to temperature fluctuations. Homeotherms have complex means of maintaining core body temperature within very narrow limits. For example, humans are able to regulate skin blood flow through the vasodilation and vasoconstriction of blood vessels redirecting blood so as to conserve heat in cold conditions or to increase heat loss in the cold. This process is further reviewed later on. Other autonomic processes utilized by homeotherms are shivering and non-shivering thermogenesis. Poikiotherms do not have the means to regulate their body temperature in such a precise way. Their body temperature is more dependent on the environmental temperature and they regulate this primarily by behavioural means. Such animals include bees, fish, amphibians and reptiles. However current knowledge on how this behavioural thermoregulation operates is not very high. Heterotherms exhibit the characteristics of both homeotherms and poikilotherms. One such example are bats which when active utilize autonomic means to maintain their relatively high body temperature. At rest however the metabolic cost of maintaining this body temperature is too high thus they substantially reduce their metabolic rate, at such time they can be described as being poikiothermic. This review will focus in some detail on the various mechanisms by which different animals thermoregulate, some of the benefits and drawbacks associated with thermoregulation and how this complex system has evolved across different groups of animals. I will draw on knowledge from various pieces of literature to give a comprehensive overview of this important life process.

Behavioural and autonomic means of thermoregulation

As discussed earlier homeotherms are utilise autonomic means to regulate their internal body temperature. It has been postulated that there is a hierarchy of structures responsible for maintaining the internal body temperature of these animals. The preoptic area of the hypothalamus plays a key role in autonomic thermoregulatory process. Early thermal studies identified the preoptic area as the centre of the thermoregulatory response. This area is synaptically connected to the lower brain stem and thus enables precise regulation of body temperature. Early research suggested that an increase in temperature in this preoptic region would lead to the excitation of neurons, resulting in the heat loss organs bringing about a reduction in preoptic temperature. In the same way, a reduction in preoptic temperature would excite neurons and lead to the heat production organs bringing about an increase in preoptic temperature. More recent research however has demonstrated that there is a far greater number of warm-sensitive neuron than cold-sensitive. These warm-sensitive neurons, play a much bigger role in the thermoregulatory process. During pre-optic warming these warm sensitive neurons significantly increase their firing rates and because of the synaptic connection with the lower brain stem, effector neurons are able to bring about heat loss responses. The median forebrain bundle is an important pathway that may be utilized here carrying signals to effector areas. In this way autonomic responses such as skin blood flow and shivering are controlled. Figure 1 demonstrates that in addition to bringing about heat loss responses, the increased firing rate of warm sensitive neurons inhibits nearby cold sensitive receptors preventing heat production. During pre-optic cooling the firing rate of warm sensitive neurons decreases thus reducing synaptic inhibition of the cold sensitive neurons. In turn the cold sensitive neurons increase their firing rate and induce heat production responses and heat retention.

The preoptic region is also involved in afferent signals, detecting peripheral temperature changes through receptors in the skin. This information is integrated with central temperature information and the appropriate thermal response is activated.

Most preoptic neurons are actually temperature insensitive, but do serve a purpose in thermoregulation. It has been postulated that they are involved in the comparison of excitatory and inhibitory synaptic inputs from both warm sensitive and temperature insensitive neurons. It is this that forms the basis for set point temperatures, therefore playing a vital role in heat loss, heat retention and heat production responses. Figure 1 demonstrates the activity of a temperature insensitive neuron. If a neuron is inhibited by a warm sensitive neuron and excited by a temperature insensitive neuron it will act as a cold sensitive neuron. Once the preoptic temperature drops below a certain point i. e. the set point, it will increases it firing rate and bring about heat production and heat retention responses.

If thermoregulation does not operate properly it may result in fever. This can be caused by the presence of endogenous substances like pyrogen. Pyrogen affects the activity of the pre-optic thermosensitive neurons. It can inhibit the firing rate of the warm sensitive neurons resulting in heat loss responses not occurring and elevated set point temperature. Also because of the synaptic inhibition between the warm-sensitive and cold-sensitive neurons, this decreased firing rate will result in an increased firing rate in the cold-sensitive neurons and bring about heat production responses further elevating the set point temperature. As a result fever occurs.

Skin blood flow

The preoptic area is able to coordinate correct efferent response in response to various internal and external thermal stimuli. One of these responses is the control of skin blood flow in humans. The vasodilation of blood vessels and the resultant increased blood flow to the skin is vital to heat dissipation during heat exposure. The increased skin blood flow significantly increases convective heat transfer from the body to the periphery. In conjunction with this increased skin blood flow, the evaporation of sweat from the skin results in cooling of blood in the dilated vessels. This process continues until the internal temperature returns to normal, at which point sweating stops and skin blood flow returns to normal. Skin blood flow in humans is controlled by vasoconstrictor and vasodilator nerves. The vasoconstrictor system is continually active, detecting even detecting subtle changes in ambient temperature. Through this activity maintenance of normal body temperature is achieved. Even small changes in skin blood flow can cause relatively large changes in heat dissipation. The vasodilator system on the other hand is only activated when an increase in internal temperature is detected. This may be during exercise or as a result of environmental heat exposure. Humans have many eccrine sweat glands distributed around the body which are responsible for thermal sweating. These sweat glands are innervated by sympathetic nerves which when stimulated results in secretion. The sweating response is only of benefit when it is coupled with evaporative heat loss. It is for this reason that environmental conditions like humidity and wind speed play an important role in this thermoregulatory process. Sweating and vasodilation are functionally linked however changes in one does not necessarily reflect changes in the other. An example of this is during exercise, as the threshold for cutaneous vasodilation is increased bit the threshold for the sweating response is not. During exercise blood cannot be redirected to the skin at the same level as blood flow to the muscle must be maintained. During cold exposure vasoconstriction of blood vessels and the redirection of blood flow to the core is essential for heat retention. When vasoconstriction occurs its results in a decrease in heat dissipation from the skin. Any alteration in this process can have serious implications, impairing the body’s ability to thermoregulate. As temperature decreases further shivering occurs. These muscular contractions help to maintain core body temperature.

Humans are not the only animals to utilize evaporative heat loss process. Despite the fact that most mammals do not have sweat glands many of them are able to use this process in different ways. Birds lack sweat glands and some mammals like cats or dogs only have sweat glands on their feet. In such animals evaporative heat loss occurs by increased air movement over moist mucosal surfaces of the mouth and upper respiratory tract. This is brought about by rapid shallow breathing along with increased salivation. Another way of utilizing this process is seen in rats and kangaroos when they spread saliva on their fur. Tests in rats have shown that warming of the pre optic area of the hypothalamus results in increased saliva secretion. It also resulted in body extension which improves heat loss through the increase in effective body surface area.

Many small mammals and those that hibernate exhibit another process in the thermoregulatory process. This process known as non-shivering thermogenesis occurs in response to the cold and it is regulated by the pre-optic area of the hypothalamus. It is a result of increased metabolic activity in the brown adipose tissue. The brown fat cells there are numerous fat droplets interspersed with many mitochondria. The brown adipose tissue has a rich supply and is also innervated by many sympathetic nerves. In cold conditions this non-shivering thermogenesis is activated by impulses passing down these sympathetic nerves or by the release of noradrenaline from the adrenal medulla. The free fatty acid store are burned up with the help of mitochondria and heat is produced. The rich blood supply to the area ensures blood is transported back to the core thus increasing core temperature. This process is seen in animals that hibernate, evident from the amount of brown fat found in such animals.

Behavioural thermoregulation

As indicated before the preoptic region plays a key role in autonomic thermoregulation, it does not however play such an important role in behavioural thermoregulation. Currently there is a lack of knowledge to indicate exactly which area of the hypothalamus is involved in behavioural thermoregulation. Behavioural responses to changes in environmental temperature occur before the internal body temperature elevates. It is from this that the assumption has been made that receptors in the skin play a key role in behavioural thermoregulation. Research has shown that the neurons responding to thermal stimulation of the skin are located in the spinal cord, with the signals from these reach areas in the cerebral cortex. However these signals, whether detected as hot or cold, cannot be a direct cause of activating the behavioural process. The reasoning behind this is that if a cold stimulus is applied to the skin of a resting animal, they perceive this as unpleasant and move away from it. However during exercise the same cold stimulus applied to the skin may be perceived as pleasant. It is because of this that the behavioural mechanisms of thermoregulation appear to be based around thermal comfort and discomfort. It has been postulated that the parastrial nucleus and the dorsomedial hypothalamic region are involved in eliciting behavioural responses. Further research however needs to be done to confirm this, possibly by examining the effect of lesions of the two areas on behavioural responses. Once the area directly responsible for eliciting behavioural responses further research can then be done into the relationship between behavioural and autonomic responses.

One example of an animal that exhibits mainly behavioural thermoregulation is the lizard. Lizards are ectothermic mainly obtaining heat from external sources. Lizards are able to maintain a relatively high body temperature, unlike most other ectotherms they can do this very precisely. Much research has been carried out into the thermoregulatory process of reptiles. An early concept that was developed was that of the preferred body temperature (PBT), which is related to homeostasis. The idea being that the PBT is the optimum temperature at which the animal’s physiological processes take place. The PBT varies across species and in some lizards the PBT can change along with the seasons. There are a number of different ways in which the lizard obtains heat from the environment. The absorption of solar radiation or the conduction from hot air or surfaces are the main ways in which lizards gain heat. If internal temperature is too high they may reduce this by radiation from the surface, convection or conduction to a cooler surface. Like other animals discussed before lizards are able to utilize evaporative cooling processes. In temperate climates lizards maintain a high PBT and obtain heat through absorption of solar radiation by basking in the sun, these are known as basking heliotherms. Different species of lizard exhibit different behaviour in relation to basking. The Lacerta vivipara emerges and begins to bask at a time when the activity temperature can be reached in the least time. This way they do not unnecessarily make themselves vulnerable to predators. Other lizards may emerge at a constant time independent of temperature. When basking lizards will adopt a specific posture in order to maximise body surface area and thus maximising their heat gain from the surroundings. They do this by sprawling on the ground with outstretched legs. During the day lizards will alternate between periods of activity and periods of basking. When they achieved their activity temperature they will stop basking and may begin actively foraging for food. During this time their internal body temperature is continually dropping and once it reaches a certain point they will have to bask again. This is a continual cycle throughout the day, observed in species known as shuttling heliotherms. Species which obtain most of their heat by conduction from hot rocks are known as thigmotherms, they are only able to in regions with intense solar radiation. Although the information on how lizards monitor their body temperature and how they use this to elicit the appropriate behavioural response is limited, the assumption is made that they must have thermal receptors in the skin. While maintaining a high body temperature the lizard will exhibit a lower metabolic rate than mammals, the reason being that they obtain most of their heat by thermal radiation. However lizards do generate some heat by metabolism but as they do not have fur, feathers or other insulatory means seen in hometherms this heat is lost very quickly. Research has shown that heart rate can effect thermoregulation in these animals. During cooling the animals heart rate decreases thus decreasing blood flow and conserving heat. As seen in other animals, these reptiles exhibit some control over peripheral blood flow through the sympathetic vasoconstriction or vasodilation of blood vessels.

Evolution of homethermy

Endotherms like birds and mammals are different from ectotherms in that they have substantially higher standard metabolic rate. When the ambient temperature is reduced endotherms may raise their metabolic rate to generate heat, as opposed to ectotherms such as the lizard which simply allow their body temperature to drop. The evolution of this process of homeothermy may have occurred in stages with the first being the development of behavioural thermoregulation. As seen in the lizard this can become very precise. Once this level of thermoregulation had been achieved enzymes may have become adapted to function optimally at the PBT. Along with a gradual increase in the importance of metabolic heat and development of fur, feathers and subcutaneous fat to retain the heat homeothermy eventually evolved.

Consequences of homethermy

The evolution of homethermy has many advantages, in that it gives such animals independence from changes in environmental temperature. There are however some downfalls to this process. In order to maintain their high body temperature they must also maintain a high metabolic rate. To do so homeothermic animals must eat a lot more than poikiotherms and they must do so continually. This can be a big problem for small mammals or birds which lose heat fairly quickly. These smaller animals must feed voraciously just to maintain their body temperature.

Adaptions to cold

Many animals have had to adapt to survive in climates where they are exposed to severe cold conditions. There is a number of ways in which they do this, either through migration, adapting itself to tolerate the cold or it can go into hibernation. Some poikiotherms such as faced with extreme cold have demonstrated adaptions to avoid freezing through the secretion of glycerol. Through this they are able to reduce the freezing point of the body fluids. Another adaption to surviving extreme cold conditions is known as supercooling. This phenomenon is the ability to tolerate temperatures lower than the typical freezing point. One experiment demonstrated that fish taken from deep water had a freezing point between -0. 9 and -1. 0 C, yet the temperature of the water from which they were taken was -1. 73C. Thus they are demonstrating supercooling. It is through this process that deep water fish are able to survive such low temperatures. Another adaption to climatic stress is hibernation. During hibernation, body temperature decreases to approximately that of the surrounding environment. Heart rate and metabolic rate also drop to a minimal level. Animals that hibernate are homeothermic during the summer but under the cold conditions of winter they become poikilothermic. During hibernation the animal remains inactive with greatly reduced metabolic requirements. The animal sustains these small requirements through its energy stores. If surrounding conditions get too low the animal's metabolic rate may increase to generate heat.

Some species also exhibit another process in regulating their body temperature. This process is a cycle between phases of intense activity with phases of torpor. This is a daily cycle exhibited in small birds and mammals that have high metabolic rates. An animal that exhibits such behaviour is the insectivorous bat. Their particular aerial habits inhibit them from carrying large energy stores. Studies have shown that torpor is important in energy maintenance during the summer diurnal roosting of the N. geoffroy.

While resting, the energetic cost of maintaining a constant, high (normothermic) body temperature (Tb) in small bats rises steeply when ambient temperature (Ta) decreases below about 30_C (Herreid and Schmidt-Nielsen 1966; Kulzer et al. 1970; Genoud 1993; Geiser and Brigham 2000). Hence, thermoregulation throughout the diurnal rest phase can be energetically expensive, even at relatively high roost Ta.
Furthermore, during cool weather, insect activity and therefore
foraging success and energy intake of insectivorous bats typically
declines dramatically (Paige 1995; Hickey and Fenton 1996). Torpor is likely

an important factor in allowing insectivorous bats to manage their energy expenditure nd survive in temperate climates