REGULATION OF BLOOD PRESSURE IN SNAKES.

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INTRODUCTION

One can daily observe that the blood pressure regulation system in the arteries is rapidly influenced by gravitational forces. Getting up quickly induces fainting for a few seconds. The pressure in the head after getting up is subtracted by a column of fluid of a height roughly the distance between eyes and heart, and that is just enough to induce fainting. Fortunately a relatively fast regulation system, called baroreceptor reflex, detects this pressure drop in the brain and corrects this with neuronal and cardiac action. Then the mean pressure in the great arteries is about 100 mm Hg (in one heart cycle from 120 to 80 mm Hg) and heart rate is about 80 beats per minute.
So far this example applies to mammals. What occurs in an animal with larger expansions when it gets op, for instance a python of about 6 meters long, with his heart at about 1 m from the head?. What pressure can be recorded when this snake is 'standing up'. Experiments were performed with snakes from aquatic, terrestrial and arboreal habitats. The animals were stretched out and tilted from the horizontal to the vertical position (and positions in between). So when the pyhton is put right up, its heart has to pump blood at least to 1 m to compensate for this fluid column. This means compensation of at least a pressure of 77 mm Hg, and when his mean blood pressure in

horizontal position is about 75 mm Hg, the blood pressure in the brain is not far from zero for a while. So a big problem exists for a simple heart, such as a reptile heart. So a big problem exists for a simple heart, such as a reptile heart.

Before discussing experiments and results, some figures about 'normal' blood pressure in snakes in horizontal position are given in table 1. The experimental results are from papers of Lillywhite (1978, 1983, 1985) and Seymour (1976, 1981).

Habitat	Mean blood pressure	Head-Heart dist. frct. total length
Aquatic	25	1/3
Terrestrial	55	1/6
Arboreal	75	1/6

HYPOTHESIS

The division made in the introduction showed three groups, based on the possibility of getting involved with gravitational influences. The arboreal species will regularly experience these forces and therefore will have a regulation system that enables them to keep pressure in the head adequately. The terrestrial species have restricted possibilities in changing their horizontal position and therefore need a regulation system but less developed than in the arboreal types. The most simple ones in regulation are the aquatics. When they are put right up in the water no difference in hydrostatic pressure between head and heart develops as in air occurs, because outside the animal the water column of exactly the same height helps the heart to overcome the head-heart distance. But when they are outside the water they would be in trouble. Summarizing: increasing possibility to overcome the gravitational force by regulating possibilities in heart and circulation from aquatic to arboreal.

EXPERIMENTS

The protocol of the experiments is as follows. Put a snake in a well fitting tube, not too narrow and not too wide. This tube can rotate in a vertical plane. The rotational axis is located at the place where the heart is supposed to be. The snake is equipped with a pressure transducer that records the pressure in the dorsal aorta at the level of the heart.
For aquatic snakes the tube is put in a watertank so that the animal is completely under water when he is tilted up right. For comparative purposes with the land snakes this aquatic snake is also subjected to the same tilting protocol on land.

RESULTS

In seasnakes, submerged in water, no change in blood pressure in the head can be measured when tilted from horizontal to vertical (head-in-right-up) position. But if this experiment is repeated outside the water a clear decrease in pressure in the centre (heart) can be measured, due to pooling of the blood in the lower part of the snake. The pressure in the head is calculated from the pressure at heart level by subtracting the vertical fluid column between head and heart at one particular angle. In figure 1 the pressure in the heart and head is drawn in case of tilting under water (full) and in air (dashed).
So the aquatic snakes have no (or poorly developed) quickly reacting blood pressure regulation system. They do not need such a system in the

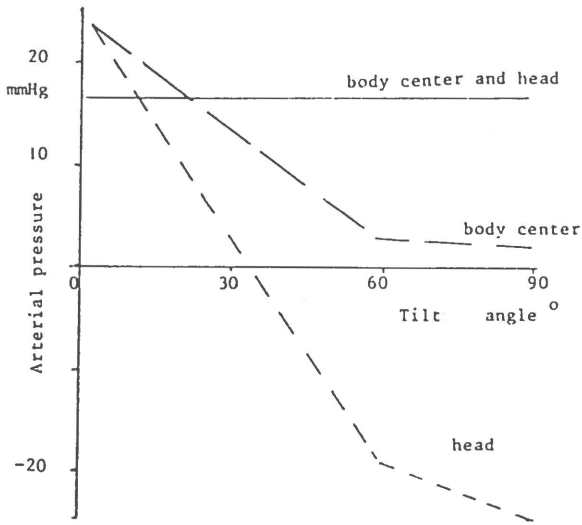

Figure 1: Relation between arterial pressure and tilt angle in a sea snake. The dashed lines show the pressure after tilting in air. The fill line gives the result after tilting under water.

water as the full line shows. But it also makes one aware that arboreal snakes can not live without such a system.
In terrestrial and arboreal snakes the same experiments are carried out. Figure 2 summarizes the data from the three groups (aquatic, terrestrial and arboreal) when they are put in their specific habitat (under water, above water) and tilted from head-down to head-up position. These curves show the calculated pressure in the brain, based on the pressure measurements at body centre level directly after tilting. If pressure has to be constant at brain level the regulation system has to be correct for at least to the horizontal position at the zero angle level.
Because of the elastic nature of vessels, amounts of blood are shifted from the upper part to the

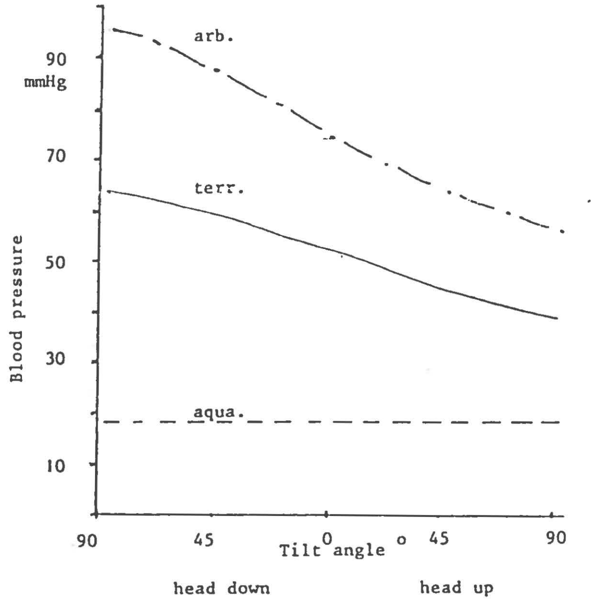

Figure 2: Blood pressure versus tilt angle. For three different habitats the pressure directly after tilting measured in the brain is shown

lower part and effect the pressure regulation system. In case of the arboreal snake, a 125 cm long *Boiga dendrophila*, the pressure in his head is about 60 mm Hg.

REGULATION

The heart acts as a pulsatile pump. This means that only in restricted periods is blood ejected into the arterial system. In the same tissues, especially in the brain, a non pulsatile, constant pressure level is required to maintain exchange of nutrients for proper functioning. This constant level is kept up by means of the elastic behaviour of the arterial wall, consisting of muscle tissue surrounding the arterial cavity. The way it works is comparable with the old 'windkessel' model of the fire engine. Figure 3 shows the schematical setup. The air in the air chamber is compressed during the ejection stroke of the pump, storing energy by increasing air pressure. This energy is released to the circulation when the pump is filling from the reservoir (venous system) and therefore disconnected from the arteries (valve closed). To gain more pressure, there are two possibilities:

1. larger number of ejections in a minute > higher heart rate.

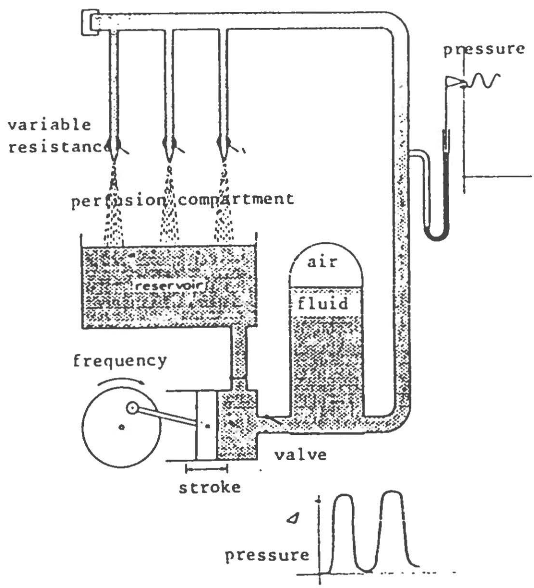

Figure 3: Schematic set up of the circulation. The pump represents the heart, the reservoir represents the venous system, the tubes and air chamber represent the arterial system. The pulsatile pressure in the heart is converted to less variable pressure in the arteries. The cranes will permit perfusion of tissue.

2. better balance between volume and pressure in the air chamber > volume of, and tension in the arterial wall.

The second item needs extra explanation. The tension in the wall of an artery (and a vein) is controlled by the autonomic nervous system. If pressure is too low the nervous system reacts by increasing wall tension so trying to get the volume of the circulatory system down. This increases the pressure in the fluid.

It is this last mechanism that mainly keeps control of the blood pressure in reptiles. An additional effect of this pressure increase is that blood flows faster from the veins to the heart (filling). The heart reacts to this increased filling by ejecting more blood into the aorta. This 'compensation' mechanism is called the Starling mechanism. But it is also responsible for decreased pressure if less blood is flowed to the heart. Heart rate plays a second additional role, because of the temperature dependence of metabolism. This is shown in figure 4. Heart rate increases ten times if temperature increases from 10^0 to 40^0C. In figure 5 it is shown that mean blood pressure only increases twice in the same temperature region. The effect of the so called vasomotor tone on blood pressure is an increase of five times over this temperature range. If pressure drops because of change in position the vasomotor tone restores pressure by decreasing when hanging down or increasing when getting up. Vasomotor tone increase is a process that costs energy. The question arises how effectively the energy supply of the pressure regulation system works at different temperatures. Tilting experiments with *Notechis scutatus* supplied the relation between changing in central blood pressure and angle at different temperatures, shown in figure 6.

From this figure we learn that at lower temperatures central pressure will not increase to compen-

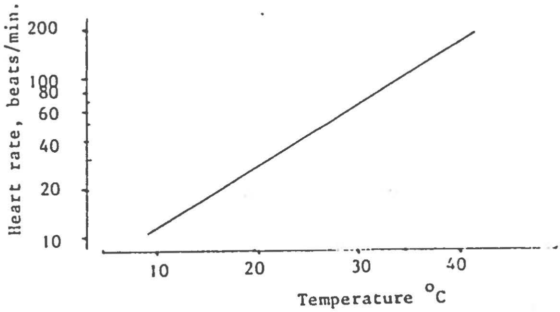

Figure 4: Heart rate as function of temperature. The rate scale is logarithmic.

sate the head heart fluid column. Another finding is that hanging down introduces a decrease in pressure, independent of temperature. This drop is due to dilatation of the blood vessels, which does not cost energy, so is independent of temperature. It prevents the snake from a too high blood pressure in his blood vessels in the brain. This is as important as preventing too low pressures. In case of a too high pressure, fluid in the very small blood vessels (capillaries) will move to the room where the nervous cells are. This fluid extravasation blocks a good exchange of oxygen and carbon dioxide, so forming a strongly dangerous

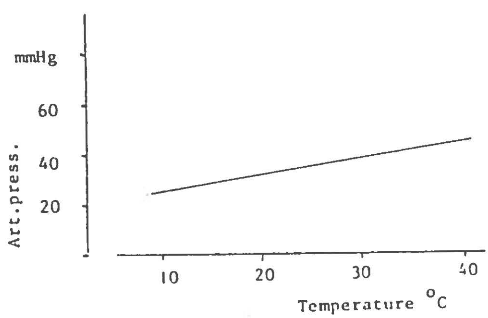

Figure 5: Arterial pressure versus temperature.

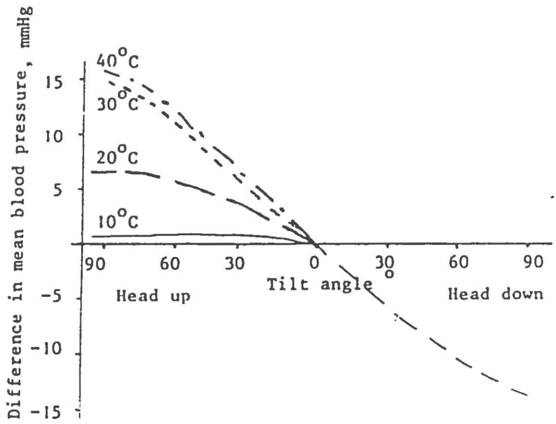

Figure 6: Differences in pressure in the heart after stabilizing from tilting at different temperatures in a terrestrial snake.

situation.
In relation to the importance of minimizing pressure differences in the brain when the snake changes its position it is remarkable that in terrestrial and arboreal snakes the heart is closer to the head than in aquatic ones, to keep the extra energy needed for the heart in getting up within acceptable limits.

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