PHYSIOLOGICAL PECULIARITIES OF THERMOREGULATION IN BATS

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Thermoregulation in bats has certain important peculiarities which separate these interesting animals from other mammals. The body temperature of bats, excepting in periods of activity, approaches the temperature of the medium, therefore some investigators referred to them as poikilothermic organisms [17, 11 and others]. However, as shown for the first time by A. D. Slonim [5], rather intensive chemical thermoregulation is noted in bats for a definite temperature range during the wakeful period. This was recently confirmed by Hanus [9]. The phenomenon of "warming" after winter hibernation or the daily diurnal "torpor" serve as important evidence of the existence of a physiological regulation of thermoproduction in bats. In this, the animal's body temperature is raised rapidly, having apparently no precedents. According to the data of Eisentraut [7], this rate attains 1.6° after one minute. A. D. Slonim was successful in showing that under the animals' daily living conditions the "warming" has a complex reflex nature and is under control of the central nervous system. The present work is devoted to a study of the physiological mechanism of this interesting phenomenon.

We investigated the electrical activity of the skeletal muscles of bats at complete rest. In homoiothermic animals and humans the defined level of bioelectrical activity of "quiescent" muscles is called thermoregulation tone. A reinforcement or relaxation of the thermoregulation tone coincides with corresponding changes in the level of thermoproduction and plays, evidently, a significant role in chemical thermoregualtion [3, 6, 8 and others].

EXPERIMENTAL METHODS

No special device was needed in order to provoke the phenomenon of "warming" in bats. The removal itself of the animals from their individual cages, where they were in a state of winter hibernation, and the act of fastening them immediately initiated this reaction.

In the laboratory the bats were maintained at 5-10°. The experiments were conducted at room temperatures of 13-18°.

The animals were fastened to wooden plates by strips of sticking-plaster. Thin steel electrodes are placed into the most powerful pectoral muscles (space between electrodes 4-6 mm). The biocurrents were recorded on a recording oscillograph MPO-2 with an amplifier. In a series of experiments electrocardiograms were also registered on the oscillograph. For measuring body temperature a special thin thermistor, which served as the arm of the Wheatstone Bridge, was inserted into the animals' rectum. On the diagonal the bridge contained a specially calibrated, highly sensitive microampere recorder. Such an apparatus enabled us to measure, and at the same time record, the body temepratureon an oscillogram.

A total of 12 animals yielded 21 experiments. All animals (9 long-eared and 3 night bats) were captured in caves in the neighborhood of Leningrad, where they were in a state of hibernation, during February-March, 1960. The weight of the bats was 4-6 g.

RESULTS

In the sum of experiments conducted we found that the "warming" reaction in bats depends upon the general state of the animals and the preceding conditions of confinement. Animals delivered to the laboratory on the first or second day were distinguished by an extremely intensive "warming" reaction. Their body temperature rose rapidly, equalling, on the average, 0.7 to 1.5° after one minute, increasing after 10-20 minutes from 8-15 to 29-32°. At the start of the experiment the body temperature of the animals always exceeded by several degrees the temperature of the surrounding medium in which they were maintained prior to the experiment. This can be explained by the fact that the fastening of the bats, appearing to be the basic stimulus, provoked the "warming", lasting for 3-4 minutes, during which the initial increase in thermoproduction originated. The intensive "warming" reaction is always accompanied by extremely high electrical activity of the muscles (Fig. 1).

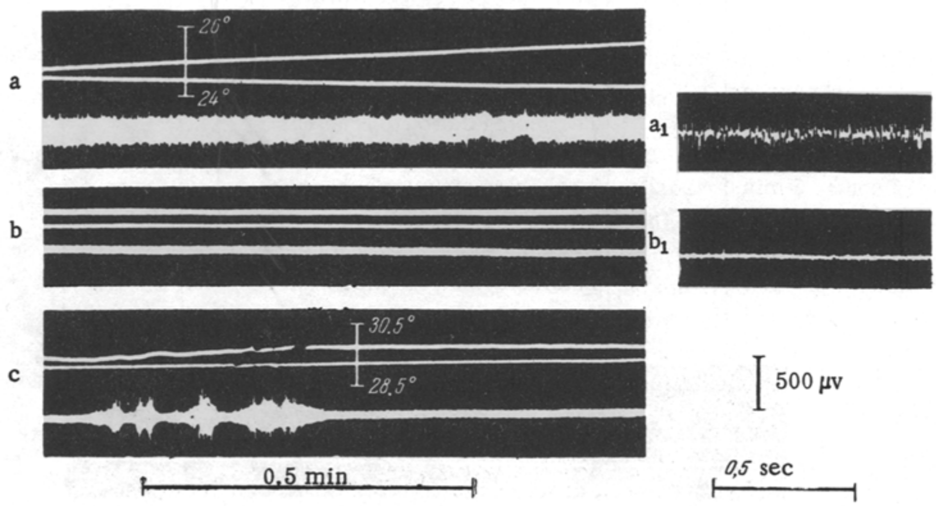

Fig. 1. Changes in the thermoregulation tone and body temperature in bats during intensive "warming". Room temperature 18°. a) Nine minutes from the beginning of "warming": high thermoregulation tone corresponds to a rapid rise in body temperature; the significance of the curves (top to bottom): temperature, line with horizontal mark, electrical activity of the muscle (read from left to right); a_1) Nine minutes from the beginning of "warming"; thermoregulation tone at the high speed of the (ribbon-recording) mechanism; b) Seventeen minutes from the beginning of "warming": thermoregulation tone is absent, the temperature is maintained at the attained level (30.2°); the significance of the curves is the same; b_1) Seventeen minutes form the beginning of "warming"; thermoregulation tone at the high speed of the (ribbon-recording) mechanism; c) Twenty-six minutes from the beginning of "warming": the influence of muscle movement on the body temperature in the absence of thermoregulation tone; significance of the curves is the same.

This electrical activity with a frequency of 150-300 cps and an intensity of separate peaks to 200-400 μv was not related to any kind of muscular contraction. This kind of electromyogram, which retained a uniform character throughout all experiments, speaks for itself, while in voluntary muscle contractions short flashes of potential of higher voltage are superimposed on this background. Typical cooling trembling also appears in the form of periodically ensuing flashes of amplified electrical activity on a background of more or less pronounced thermoregulation tone, which was shown by us earlier [3].

Thus, the constant electrical activity of the muscles in bats at complete rest has a character of thermoregulation tone with relatively high voltage potentials. The cause of this phenomenon may lie in the high frequency asynchronous fibrillization of separate muscle fibers, which does not cause appreciable muscle contraction, but is accompanied by significant increases in metabolism. According to the data of Eisentraut [7], the oxygen consumption in bats during the period of "warming" can increase in comparison to the state of "torpor" by a hundredfold. A greater frequency of heart beat and breathing movements correspond to this. In our experiments heart beat in

Record of Experiment No. 18, March 19, 1960. Temperature at which the Animals Were Maintained Prior to the Experiment Was 10°. The Temperature in the Experimental Room Was 18° The Weight of the Animals Was 4.5 g.

Time	Body temperature	(I) Thermoregulation tone	Frequency of heart beat per minute	Frequency of breathing per min
11 hours 45 min	16.1°	High thermoregulation tone	–	–
11 hours 51 min	19.4°	High thermoregulation tone	–	above 300
11 hours 53 min	22.0°	High thermoregulation tone	–	–
11 hours 57 min	31.7°	Marked relaxation	840	–
11 hours 59 min	32.7°	Thermoregulation tone absent. Strong motor anxiety	–	–
12 hours 02 min	31.8°	Thermoregulation tone absent	–	–
12 hours 04 min	30.3°	Thermoregulation tone absent	600	–
12 hours 10 min	27.5°	Thermoregulation tone absent	–	–
12 hours 13 min	26.5°	Thermoregulation tone absent	–	above 300
12 hours 15 min	26.2°	Weak thermoregulation tone	–	–
12 hours 17 min	25.8°	Weak thermoregulation tone	–	–
12 hours 19 min	25.7°	Weak thermoregulation tone	600	–
12 hours 30 min	25.0°	Thermoregulation tone absent	–	–

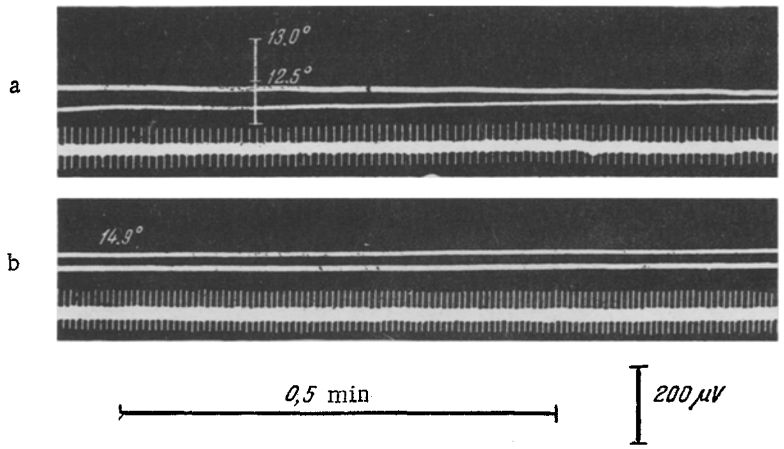

Fig. 2. Body temperature of bats at the absence of thermoregulation tone. Room temperature 16°. a) Five minutes after fastening: thermoregulation tone is absent; b) Thirty minutes after fastening: thermoregulation tone absent (electrocardiogram is seen); body temperature closely corresponds to the outside temperature (read from right to left; in the rest the significance of the curves is the same as on Fig. 1).

bats at "warming" increased their frequency to 500-800 per minute, and breathing movements to 250-300 per minute.

Thermoregulation tone reaches its maximum almost at the very beginning of the observed "warming" process and continues until that time when the rectal temperature is 29-32°. At this moment the thermoregulation tone very rapidly, as though suddenly, disappears. Simultaneously with this the body temperature stops rising. For some time it stays at the attained level,and then begins to decrease. A strong motor anxiety, usually ensuing in the animals at that moment, prevents their rapid cooling (see Fig. 1); however during the fastening of the animals the corresponding effect is shown, apparently, to be insufficient, and the body temperature of the bats continues to drop slowly. These correlations, which were observed in 10 experiments on 10 animals, are illustrated in Fig. 1,and for a record of one of these experiments see the table.

If we attempt to provoke the "warming" reaction in those same animals a second time 1-2 days after the first experiment, we get another picture. At the repetition of "warming" the thermoregulation tone is shown to be very low, not uniform and practically completely absent. Correspondingly, the animal's body temperature rises very slowly, exceeding in the final analysis the temperature of the medium by a total of several degrees. At the complete absence of thermoregulation tone the body temperature can remain at almost the level of the outside temperature (Fig. 2). We also observed a similar pattern in two bats delivered to the laboratory after repeated "warming" phenomena during transportation. At the absence of thermoregulation tone there was a considerably lower frequency of heart beats (150-330 per minute) and breathing movements (20-6) per minute).

Inasmuch as a rapid "warming" in animals always is combined with intensive thermoregulation tone of the muscles, and the absence of this reaction or its very slow course coincides with the absence or extreme relaxation of the corresponding electrical phenomena, it seems possible to us to consider themoregulation tone as one of the most important physiological mechanism of increasing thermoproduction in the organism during the period of "warming" in bats. The considerable intensiveness of thermoregulation tone at this moment is related, evidently, to a high level of metabolism. The turning off of thermoregulation tone after the attainment of a body temperature of 29-32° can be explained by the fact that at this temperature the bats are able to fly (which we observed in our experiments) and, consequently, to maintain their body temperature by active muscular contractions.

Thus, to a definite period of vital activity of animals corresponds, one can assume, a definite mechanism of thermoregulation. The "warming" reaction itself is accompanied by a considerable expenditure of energy reserves. It is possible that the absence of thermoregulation tone at a repeated attempt to arouse the "warming" reaction is explained by the fact that the corresponding reserves were, to a considerable extent, exhausted.

It is well known that a reduction in blood sugars leads to a disturbance in the thermoproduction processes and the disappearance of muscular shivering [2]. As was shown earlier by N. A. Arkhangel'skaya and others [1], in bats the "warming" phenomenon correlates with the blood sugar content. In contrast to laboratory conditions, in nature bats begin to fly immediately after "warming" and make up for their loss of energy by feeding (catching insects). The latter has important significance, since bats are relatively small animals and for the maintenance of homiothermism they require very intensive feedings. It is well known, for example, that in homiothermic animals 3-4 g in weight (some birds, rodents) the quantity of food consumed in one day approximately equals their body weight [10]. Therefore homoiothermism in bats is most pronounced only in flight when the animals are feeding. The motionless state, even forced, as we observed, ultimately leads to a gradual cooling of their bodies. This, however, is not a sign of poikilothermism but rather a characteristic of small homoiothermic animals, since an analagous pattern is observed, for example, in small species of humming birds and some other birds (literature cited by N. I. Kalabukhov [4] and Eisentraut [8]). "Warming" in this sense plays quite a special role, enabling the animal to transform from a state of "torpor" to active work in the shortest possible time.

In conclusion we express our deep gratitude to P. P. Strelkov for assistance in the fulfillment of the present work.

SUMMARY

In bats, intensive "warming" of the body after hibernation is associated with a high electric activity of the skeletal muscles during complete rest of the animal (thermoregulation tone). It is concluded that the "thermoregulation tone" is an important source of sharply increased thermoproduction during this period.

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