CXLVII. THE AEROBIC AND ANAEROBIC METABOLISM OF THE COMMON COCKROACH (*PERIPLANETA ORIENTALIS*). PART I.

By JOHN GILBERT DAVIS
AND WILLIAM KERSHAW SLATER (*Beit Memorial Research Fellow*).

*From the Department of Physiology and Biochemistry,
University College, London.*

(Received November 1st, 1926.)

INTRODUCTION.

WHEN the common cockroach (*Periplaneta orientalis*) is deprived of oxygen, it enters into a state closely resembling anaesthesia. This condition can be produced by replacing the air by nitrogen or any inert gas, by immersing the cockroach in boiled water, or even by evacuating the vessel in which it is contained.

If the deprivation has not been continued for too long a time, the re-admission of air quickly revives the cockroach, and after a time depending upon the duration of the anaerobiosis it becomes to all appearances normal. These observations have been made by at least two workers in the past, but there appears to be no published account in scientific literature.

The anaerobic existence of the cockroach provides a suitable set of conditions for the study of the energy-producing reactions which replace the oxidation process during oxygen lack.

In the present work an attempt has been made to measure the oxygen used by the cockroach under normal circumstances, and after a period of oxygen lack. In particular it was desired to show whether the cockroach incurs an oxygen debt as the result of anaerobiosis, similar to that produced by violent exercise in man.

METHOD.

Measurements of three types are required for the solution of the problems under consideration.

(1) It is necessary to know the oxygen intake of the cockroach under normal conditions and after anaerobiosis. This measurement must be made in air, the carbon dioxide being absorbed during the experiment.

(2) In order to obtain an approximate value for the respiratory quotient the difference between the volume of oxygen used and the carbon dioxide evolved must be known. This necessitates the measurement, in air, of the total change in the volume of the gases in which the cockroach is living.

(3) The measurement of the increase in volume of the gas in which the cockroach is living, due to the evolution of carbon dioxide during anaerobiosis.

The apparatus used resembled that designed for blood-gas analysis by Haldane [1920]. This gives readings of volume changes at constant pressure, and by the use of a compensating bulb avoids correction for small changes in temperature and pressure during the experiment.

The bulbs used to contain the cockroaches are shown in Figs. 1 and 2. The smaller type of bulb with only one chamber was used when the carbon dioxide was to be absorbed continuously throughout the experiment. It had the advantage that the air in the gas space could be rapidly replaced by nitrogen or *vice versa*. The larger type of bulb was used where the carbon dioxide was only absorbed during a portion of the experiment, the second bulb containing

Fig. 1.

Fig. 2.

the potash being connected to the respiration bulb by means of a wide bore tap. In this apparatus a longer time had to be allowed for the nitrogen to replace completely the air in both chambers.

Except where it is otherwise stated all the experiments were carried out at 25°, the respiration bulb and its control being immersed in a thermostat which maintained that temperature within 0.05°.

In order to represent the results as uniformly as possible, they are calculated in mm.³ per g. weight of cockroach, per hour.

Variations in the insects used.

The insects used were *Periplaneta orientalis*, which can be caught at all seasons of the year in warm places such as a boiler house. The insects were stored in open beakers in a cupboard which was kept at 20°.

In the experiments described below a variety of specimens was used, particularly in the preliminary experiments designed to determine the normal metabolic rate. Body-weight and activity influenced the metabolic rate, and the diet the respiratory quotient.

Influence of body-weight on the metabolic rate.

A series of experiments was carried out on cockroaches, which were as nearly as possible uniform in all other respects save that of body-weight. The results are shown on the accompanying graph (Fig. 3) in which the weight in each individual experiment is plotted against the oxygen intake per g. per hour, measured in mm^3 . It will be seen that the results lie upon a rough curve, showing a rapid fall in metabolic rate as the body-weight increases from 0.08 up to 0.2 g. From this point onwards increase in body-weight does not materially affect the oxygen uptake. It is necessary to mention at this point that the weight of a cockroach is very small, a specimen measuring about an inch in length rarely weighs more than 0.3 g.

Fig. 3.

It will be noticed that as the weight increases the metabolic rate becomes more uniform; thus the percentage mean deviation for fifteen experiments with insects between 0.15 and 0.4 g. was 10.5, whilst that for nine insects between 0.4 and 1.0 g. was only 6.6. These deviations are, however, too great to assume a mean value for the anaerobic experiments, so that in each experiment of this type the normal oxygen uptake was determined for the individual cockroach used.

Influence of activity on metabolic rate.

Changes in activity during an experiment produced very anomalous results. It was found that if the movement was restricted to the antennae and the mandibles, no great change in the oxygen uptake took place, but if the cockroach moved about the vessel the uptake increased rapidly. Fortunately, only in rare cases did the insects show movement of this kind after they had once become settled in the bulb. Where marked movement was observed during the readings the experiment was abandoned.

Influence of diet on the respiratory quotient.

In order to determine the respiratory quotient the normal oxygen uptake was first measured. The tap connecting the respiration chamber with the potash bulb was then closed and the total change in volume measured. If it be assumed that this total change of volume is the sum of the volume changes of the oxygen and the carbon dioxide, it is possible, by subtracting the normal value for oxygen intake, to obtain a value for the carbon dioxide output, and hence for the respiratory quotient.

The investigations which have been made on these lines have not proved very satisfactory, owing to the difficulty which is experienced in ascertaining when the cockroaches have eaten. The mere presence of available foodstuff in the beakers with the insects cannot be taken as evidence. In some cases the cockroach was seen to begin to eat at once, whilst in others a cockroach which has been starving for over a week would not take any food at all. As a result of this, five determinations of the respiratory quotient of animals kept with food varied between 0.72 and 1.0. It is of interest, however, that five similar determinations on starving cockroaches all lie between 0.75 and 0.85, suggesting that the quotient is depressed by starvation in the same way that it is in the higher animals.

Metabolism in nitrogen.

For each experiment a cockroach was selected, which was as nearly normal as possible. It was placed in a bulb with air, potash being present to absorb the carbon dioxide, and the normal metabolic rate was determined. The air was then swept out by nitrogen as quickly as possible, and the cockroach kept under anaerobic conditions for a definite time, usually from half to one hour. At the end of this period the nitrogen was replaced by air, and the oxygen uptake following the anaerobiosis measured, until a normal oxygen uptake was again registered.

In the majority of the experiments the carbon dioxide was absorbed continuously throughout the experiment; under these conditions the gas volume during the anaerobic phase was constant within the limits of normal experimental fluctuations. If, however, the carbon dioxide is not absorbed whilst the nitrogen is present, an increase in volume is noted. This confirms the observations of Spallanzani [Foster, 1924] on snails, where carbon dioxide is evolved during oxygen lack. This carbon dioxide is probably due to the action of the lactic acid formed on the bicarbonates of the tissues.

The accompanying curves (Fig. 4) represent the oxygen uptake during two typical experiments. The continuous line gives the actual oxygen absorbed. The lower portion *AB* shows the normal uptake of the cockroach at the beginning of the experiment. At the point *B* nitrogen is introduced, and the uptake ceases until the point *C* is reached, when air is readmitted. The dotted line *BB'* shows the oxygen which it may be assumed would have been used if there had

been a continuous supply, whilst CC' indicates the oxygen which the cockroach would require, if it commenced to respire at the normal rate when the nitrogen was removed. It will be seen from the curves that when air is re-admitted the cockroach takes up more oxygen than it normally requires, until an excess has been retained, which is equal to the volume the cockroach would have used during the time it was deprived of oxygen. The following examples illustrate this more definitely.

Fig. 4.

Experiment No. 44. Animal No. 19. Weight 0.31 g. Time of anaerobic existence = $\frac{1}{2}$ hour. Time of recovery = $2\frac{1}{2}$ hours (?). Temperature 25°.

Experiment No. 56. Animal No. 45. Weight 0.29 g. Time of anaerobic existence = $1\frac{1}{2}$ hours. Time of recovery = $3\frac{1}{2}$ hours. Temperature 25°.

Exp.	Duration of anaerobiosis (hours)	Calculated oxygen debt (mm. reading)	Excess oxygen in					
			$\frac{1}{2}$ hr.	1 hr.	$1\frac{1}{2}$ hrs.	2 hrs.	3 hrs.	4 hrs.
			(mm. reading)					
1	0.5	15	7	11	14	16	16	—
2	0.5	14	5	9	14	18	—	—
3	0.5	29	16	21	27	27	—	—
4	1	43	—	14	—	33	43	45
5	1	35	—	20	—	26	35	—
6	1.25	67	—	17	—	40	64	72

It is concluded from these results, that when the cockroach exists anaerobically it goes into debt for oxygen, in a manner similar to that which has been shown in man performing heavy physical work.

DISCUSSION OF THE RESULTS.

The earlier experiments dealing with the relation between body-weight and metabolic rate, and between period of starvation and the respiratory quotient, are of interest primarily as controls, but they further serve to indicate the

general similarity between the metabolism of the cockroach and the higher animals. It is interesting to find in a cold-blooded animal like the cockroach the relation between body-weight and metabolic rate, but this may be accounted for by the fact that the majority of the smaller animals were very young, and that the phenomenon here observed is intrinsically one of age and not of body-weight. Some support is lent to this view by the fact that there is little variation in the metabolic rate after a definite weight (*i.e.* age) has been attained.

The power to go into debt for oxygen is of interest, and particularly, the close agreement between the volume of the debt and the volume of oxygen which would have been used during a time equal to the period of anaerobiosis. These observations suggest that the reaction producing energy under anaerobic conditions consists of the breakdown of one compound to another, which, though it has a lower energy content, requires an equal quantity of oxygen for its complete combustion. Such a reaction is the glycolytic formation of lactic acid, which supplies the energy in the anaerobic phase of muscular contraction. That a similar process, and not some entirely strange reaction, supplies the energy in the anaerobic existence of the cockroach is suggested as a working hypothesis.

This hypothesis is further supported by the similarity of the curves given above to those obtained by A. V. Hill and his co-workers on man. The only way in which these curves differ is in the time of recovery, which for the cockroach is much longer than for man.

The research is now being continued by an attempt to estimate the glycogen and lactic acid present in cockroaches before and after anaerobiosis, and by a further study of the respiratory quotients under these conditions. It is hoped by these means to establish definitely that in the case of the cockroach anaerobiosis is maintained by the same mechanism as that which supplies the energy for the anaerobic phase in the contraction of mammalian muscle.

SUMMARY.

(1) The relation between body-weight and oxygen usage in the cockroach (*Periplaneta orientalis*) has been investigated: also the relation between starvation and the respiratory quotient.

(2) It has been shown that the cockroach whilst living in nitrogen goes into debt for oxygen, and that when the cockroach is returned to air an excess of oxygen over the normal uptake is consumed until the debt has been discharged.

The expenses of this research have been largely defrayed by a grant from the Royal Society.

REFERENCES.

- Foster (1924). Lectures on the History of Physiology, p. 251.
Haldane (1920). *J. Path. Bact.* 23, 443.