probably the same when he discovered that fatigued frog's muscle swells up when placed in water, to a much greater extent than resting muscle. He observed also that sufficient exposure to an atmosphere of oxygen restores to the muscle in a marked degree the osmotic character of resting muscle. It might, therefore, have been supposed that a vigorous circulation of blood through the muscle would have prevented the swelling which we have observed. The fact, however, appears to be that muscle is capable of out-running its oxygen supply with great ease, and this is probably especially true of frog's muscle, in which the opportunities afforded for the acquisition of oxygen are much smaller than in the case of mammalian muscle.

In comparing our result with that of Fletcher, it must be borne in mind that his phenomenon was probably a purely osmotic one; ours may involve, or may not, also some change in the permeability of the vessel walls.

The Effect of the Depth of Pulmonary Ventilation on the Oxygen in the Venous Blood of Man.

By J. F. Twort and Leonard Hill, F.R.S.

(From the Physiological Laboratory, London Hospital Medical College, and Research Fund.)

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We have sought to gain evidence as to whether the arterial blood is saturated with oxygen during its passage through the lungs when the breathing is shallow and the subject lying at rest. Incidentally we have made some observations on:—(1) The effect of work. (2) The local application of heat or cold on the gases in the venous blood.

As means have not been devised for obtaining safely samples of normal arterial blood from man, we have been obliged to content ourselves with samples of venous blood collected from the veins of the arm.

The samples have been collected for us with strict aseptic precautions by Dr. James McIntosh, and in some cases by Dr. Paul Fildes. Their daily practice in collecting blood samples from patients has made our colleagues skilful in the technique of this small operation. We owe them our best thanks for their help.

Neither ligature nor compression was applied to the arm. The needle of the syringe was passed straight into the vein; the arm of the subject rested upon the couch and remained covered with the sleeve until the moment of

collection; 0·1 c.c. of 1-per-cent. sodium citrate solution having been placed in the syringe to prevent clotting, the blood was drawn up exactly to the 1 c.c. mark. The analyses were made by means of the small Barcroft apparatus—the oxygen being displaced by ferricyanide.

The subject rested for some minutes on the couch, and at the time of collection of the blood breathed through a meter so that ventilation of the lungs was recorded. A mouthpiece was employed fitted with wide tubes and mica inlet and outlet valves. The nose was closed with a clip. One sample was collected while the subject breathed quietly, and another from the same, or the other arm, while he breathed forcibly. In the experiments in which oxygen was breathed the subject inhaled from a large bag filled with oxygen and exhaled through the meter.

Double samples taken as controls under the same conditions gave us results which agreed within fairly close limits. For example:—

11·4 per cent., right arm; 12·0 per cent., left arm.

Table I.—Cubic Centimetres of Oxygen per 100 c.c. of Blood.

Subject.	Resting.				Working.	
	Breathing air quietly.	Breathing oxygen quietly.	Breathing air forcibly.	Breathing oxygen forcibly.	Breathing air quietly.	Breathing oxygen quietly.
1	12·9	8·6	—	—	5·5	6·3
2	5·9	9·5	—	—	—	3·2
3	7·6	9·7	—	—	6·8	9·2
4	12·7	13·8	—	—	7·0	6·8
5	2·6	5·0	—	—	2·8	4·7
6	14·0	14·6	—	—	8·2	7·3
7	10·4	8·5	—	—	3·3	1·5
8	8·8	—	—	—	6·5	—
9	11·4	—	—	—	—	—
	12·0	—	—	—	—	—
10	4·5	11·1	—	—	—	—
11	6·3	—	13·0	—	—	—
12	7·4	—	14·6	—	—	—
13	7·5	—	14·6	—	—	—
14	—	13·7	—	14·6	—	—
15	—	13·2	—	13·8	—	—
16	—	12·4	—	12·2	—	—
17	—	8·3	—	9·2	—	—
18	8·3	7·9	—	—	—	—
19	—	15·7	11·6	—	—	—
20	—	16·9	15·2	—	—	—
21	13·4	15·6	—	—	—	—
22	9·1	13·4	—	—	—	—
23	4·6	7·0	—	—	—	—
24	14·1	15·4	—	—	—	—
25	16·0	17·9	—	—	—	—
26	8·6	9·4	—	—	—	—
27	10·8	12·5	—	—	—	—

Considering the slight physiological differences which may arise, *e.g.*, from posture, exposure to cold during the collection of samples, etc., we cannot expect to get closer results. To carry out work the subject grasped a spring ergograph and squeezed it 20 times a minute; the sample was collected immediately at the end of two minutes period of work.

The average of 22 analyses taken when resting and breathing air quietly is 9·5 per cent., breathing oxygen quietly 11·8 per cent.

The average of analyses when working and breathing air quietly is 5·7 per cent., while that when working and breathing oxygen quietly is 5·6 per cent. The corresponding resting analyses in the same subjects gave 9·4 per cent. when breathing air quietly, 10·0 per cent. when breathing oxygen quietly.

Table II.—Effect of Warming One Arm.

Subject.	Arm not warmed.	Arm warmed with bath.	Remarks.
	per cent.	per cent.	
1	9·4	14·8	Air quietly breathed.
2	4·3	11·7	" "
3	10·0	11·6	" "
4	10·3	12·2	Oxygen quietly breathed.
5	12·6	14·2	Air forcibly breathed.
6	15·2	16·4	Oxygen breathed quietly.

The average of the six experiments is 10·3 per cent. for the unwarmed and 13·5 per cent. for the warmed arm.

Table III.—Effect of Forcibly Breathing Air or Oxygen.

Subject.	Forcibly breathing air.	Forcibly breathing oxygen.
	per cent.	per cent.
1	14·2	14·8
2	11·3	11·8
3	13·5	13·1
4	12·9	12·4
5	9·2	9·8
6	17·1	16·8
7	14·1	14·1
8	14·2	16·0
9	11·6	—
10	15·2	—
11	13·0	—
12	14·6	—
13	14·6	—

The average of 13 analyses of samples taken when forcibly breathing air is 13·5 per cent., and of eight breathing oxygen forcibly 13·6 per cent.

To sum up, then, the average results of the analyses are:—

No. of analyses.	Cubic Centimetres Oxygen.
22	9·5 resting, breathing air quietly.
22	11·8 resting, breathing oxygen quietly.
7	5·7 working, breathing air quietly.
7	5·6 working, breathing oxygen quietly.
3	7·9 resting, breathing air quietly, arm not warmed.
3	12·7 resting, breathing air quietly, arm warmed (to produce vaso-dilatation).
3	12·7 resting, breathing oxygen quietly (2), air forcibly (1); arm not warmed.
3	14·2 resting, breathing oxygen quietly (2), air forcibly (1); arm warmed.
13	13·5 resting, breathing air forcibly.
8	13·6 resting, breathing oxygen forcibly.

Our subjects were medical students and laboratory servants. Some of them, when lying on the couch and breathing quietly, gave us low, and some high readings. The difference is an individual one, and cannot be ascribed to errors in technique, for he who gives a low reading when resting gives a low reading when working. Moreover the deep breathing readings are uniformly high. Some of our subjects were emotionally affected by the operative procedure and breathed about 10 litres a minute, while others breathed only 5–6 litres, while resting on the couch. We cannot, however, ascribe the higher reading in all cases to the ampler breathing. All we can affirm is that quiet breathing gives us a certain proportion of low readings in the given number of subjects, while deep breathing gives us uniformly high readings.

Looking at the difference between the average figures for resting and breathing air quietly and breathing oxygen quietly it might be assumed that this was due to the oxygen simply dissolved in the blood according to the law of partial pressures. If pure oxygen were breathed we might expect a little over 2 per cent. O_2 to be simply dissolved, and the tissues, using this oxygen first, would dissociate the hæmoglobin less by the same amount.

The subjects were breathing not 100 per cent. but about 80 per cent. of oxygen, so the amount simply dissolved would not be quite as much as 2 per cent. When, however, we compare the figures obtained during forcible breathing of air or oxygen, we see no evidence of any excess of oxygen due to simple solution under the increased partial pressure of this gas.

Similarly in a very careful series of analyses of cat's blood recorded by Buckmaster and Gardner and obtained by means of the Töpler pump we see no evidence of any increase in oxygen of the arterial blood due to the breathing of oxygen in place of air. The average of 13 analyses, the cats breathing air, was 14·2 per cent., breathing oxygen 14·9 per cent.

The theoretical oxygen capacity determined from the hæmoglobin value was about 17 per cent. These authors say:—

"From the experiments it is a fair conclusion that during its passage through the pulmonary capillaries the blood is rarely fully saturated with oxygen even when oxygen is inhaled. For an explanation, it is probable that parts of the lung, for example the apices, are imperfectly ventilated, and also, since the circulation time in the lung is only about five or six seconds, that complete equilibrium is not attained between the blood and alveolar air."*

We know that anything over 75 per cent. of an atmosphere of oxygen when continuously breathed produces pneumonia, and that exposure to two or three atmospheres of oxygen causes convulsions. A high partial pressure and concentration of oxygen on the blood acts as a poison. It may be that there is at work some mechanism which prevents, within certain limits of oxygen partial pressure, the over-concentration of free oxygen in the blood, and therefore we find no more oxygen in the venous blood on forcibly breathing air than on forcibly breathing oxygen.

Our figures show that forcible breathing of air, or oxygen, equally and notably increases the oxygen in the venous blood above the average result obtained when breathing air quietly. We cannot ascribe this result to vaso-dilatation and accelerated flow through the arm produced by the forced breathing, for G. N. Stewart has shown that forcible breathing diminishes the velocity of flow in the hand by about 40 per cent.† Forcible breathing mechanically interferes with the circulation and the hand tends to become pale and cold when such is continued.

We conclude that the arterial blood is not always saturated with oxygen during the passage through the lungs when the breathing is quiet. Some parts of the lung may remain unexpanded, and the blood passing through these parts is not oxygenated. Forcible breathing ensures the expansion of all parts and the better saturation of the arterial blood. In one case Caske and Barcroft‡ obtained a sample of arterial blood and found it 94 per cent. saturated with oxygen. The sample was obtained from a young woman acting as donor in a direct transfusion of blood. Her artery was opened under local anæsthesia. The emotional conditions probably ensured in her a good pulmonary ventilation.

If it be true that the person engaged in sedentary occupation does not expand the lungs sufficiently to arterialise the blood in all their parts, this

* 'Roy. Soc. Proc.,' B, vol. 85, p. 56 (1912).

† 'Amer. Journ. Physiol.,' vol. 28, p. 190 (1911).

‡ 'Proc. Physiol. Soc.,' 'Journ. Physiol.,' vol. 47, p. xxxv (1914).

may be a contributory cause of a lessened immunity to the organism of disease such as phthisis.

Our results too confirm the need for caisson workers not to rest during decompression but to take exercise and to breathe deeply so as to secure the escape of nitrogen, which has been dissolved in their body fluid during their work in compressed air.

On the Occurrence of an Intracranial Ganglion upon the Oculomotor Nerve in Scyllium canicula, *with a Suggestion as to its Bearing upon the Question of the Segmental Value of Certain of the Cranial Nerves.*

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(Communicated by Prof. A. Dendy, F.R.S. Received January 21,—Revised March 1, 1915.)

During the study of a number of elasmobranch brains made in connection with my work on Reissner's fibre, I noticed, in a specimen of *Scyllium canicula,* a collection of ganglion cells upon a length of nerve lying freely beneath the mid-brain. This particular brain had been sectioned in the longitudinal vertical plane and the ganglionic mass occurred at a place which corresponded with the level of the third cranial nerve. Further examination showed that these cells were undoubtedly related to the oculomotor nerve. They are situated upon it in a scattered group which, beginning at a point about 1·4 mm. from the superficial origin of the nerve, stretches to its severed end (roughly 1·6 mm. from its origin). The cells, though only about 15 in number, are moderately large (averaging $20\mu \times 18\mu$) and are apparently unipolar or bipolar. Their distribution suggested that other cells of the group must have existed distally to the point of severance of the nerve.

Upon the opposite side of the brain the corresponding nerve had been cut away quite close to its superficial origin, when the brain was removed from the cranium.

A second specimen of *S. canicula* in which some 2 mm. of the third nerve had been left attached to the brain, on either side, showed the ganglion well on both nerves.