THE CARBON DIOXIDE EQUILIBRIUM IN ALVEOLAR AIR
AND ARTERIAL BLOOD.

III. EXERCISING SUBJECTS.*

BY D. B. DILL,† J. S. LAWRENCE,‡ L. M. HURXTHAL,
AND A. V. BOCK.

(From the Medical Laboratories of the Massachusetts General Hospital,
Boston.)

(Received for publication, June 6, 1927.)

It is a familiar thesis that if the diffusing apparatus of the lung
permits 95 per cent saturation of the blood with oxygen, substan-
tial equilibrium between the carbon dioxide pressures on opposite
sides of the alveolar membrane will be attained. The principal
supporting argument is the fact that carbon dioxide diffuses 20 to
30 times as rapidly as oxygen. It is assumed that the transfer
of each gas is a diffusion phenomenon. That such an equilibrium
exists in resting subjects has been demonstrated experimentally
by Bock and Field (1) and Dautrebande (2).

Krogh and Lindhard (3) have studied the changes in alveolar
carbon dioxide pressure in exercise, but, in common with many
others, doubt the accuracy with which such determinations portray
the arterial carbon dioxide pressure. It has been our purpose to
investigate the possibility of collecting, during exercise, alveolar
air which will measure the average carbon dioxide pressure of
arterial blood.

* The expenses of this research were defrayed in part by the Tutorial
Fund of Harvard University.

A preliminary report of this research was presented to the Society for
Clinical Investigation at Atlantic City, May 3, 1926.

† National Research Fellow in Chemistry.
‡ Edward Hickling Bradford Fellow in Medical Research, Harvard
Medical School.

313
EXPERIMENTAL.

In each of these experiments, unless otherwise noted, the subject rode at a constant speed on a stationary bicycle. By suitable adjustment of the brake, any metabolic level up to 10 times the basal rate could be reached. The apparatus was arranged so that the subject inspired outdoor air and expired through a mixing chamber of 7 liters capacity into a calibrated spirometer. Samples of expired air for analysis could be drawn from the mixing chamber as often as desired. The ventilation rate could be determined by reading the spirometer gauge at intervals of 1 minute or longer. At a convenient time, usually after a steady state had been reached, arterial blood was withdrawn under novocaine anesthesia from the radial or the brachial artery. During its withdrawal, samples of alveolar air were taken by the Haldane-Priestley method. In a few experiments, additional alveolar samples were collected automatically, by use of the Müller valve as described by Henderson and Haggard (4).

The pressure of carbon dioxide in arterial blood was determined as previously described (1). The volume and composition of the air expired during a measured period immediately preceding or following the withdrawal of the blood established the metabolic level.

In the early experiments, the Haldane-Priestley samples were collected by giving the instruction "blow" at the end of a normal expiration. Bock and Field (1) had found that for resting subjects samples collected in this manner were in approximate carbon dioxide equilibrium with arterial blood. The results of our early exercise experiments indicated that at high metabolic levels there is a slight piling up of carbon dioxide during the delay incident to this method of sampling, as suggested by Krogh and Lindhard (3). Experiments were then undertaken in which the instruction "blow" came as the subject began his expiration. Such samples were found to have essentially the same carbon dioxide pressure as that of arterial blood. This method was adopted, therefore, for all later experiments.

In the course of this investigation, twenty-two arterial punctures were made. In twenty of these experiments, samples of alveolar air were collected and the equilibration of the blood was carried to a satisfactory conclusion. Accidents prevented the comple-
## TABLE I.
Carbon Dioxide Pressure of Arterial Blood and of Alveolar Air at Various Metabolic Levels.

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Subject</th>
<th>Date</th>
<th>Oxygen used per min.</th>
<th>Arterial blood $pCO_2$ (mm.)</th>
<th>Alveolar air $pCO_2$ (mm.)</th>
<th>Blood-air $pCO_2$ (mm.)</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>A.V.B.</td>
<td>Jan. 13</td>
<td>1450</td>
<td>38.8</td>
<td>38.8</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>“</td>
<td>19</td>
<td>1250</td>
<td>38.0</td>
<td>39.7</td>
<td>-1.7</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>“</td>
<td>26</td>
<td>1600</td>
<td>35.2</td>
<td>39.4</td>
<td>-4.2</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>Feb. 3</td>
<td>1440</td>
<td>38.8</td>
<td>38.5</td>
<td>+0.3</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>“</td>
<td>17</td>
<td>1770</td>
<td>35.4</td>
<td>36.4</td>
<td>-1.0</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>Mar. 26</td>
<td>800</td>
<td>37.0</td>
<td>36.1</td>
<td>+0.9</td>
<td>3rd minute after stopping work.</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>Apr. 6</td>
<td>1230</td>
<td>39.4</td>
<td>38.4</td>
<td>+1.0</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>D.B.D.</td>
<td>Jan. 15</td>
<td>1710</td>
<td>47.6</td>
<td>48.1</td>
<td>-0.5</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>Feb. 11</td>
<td>1730</td>
<td>41.0</td>
<td>40.9</td>
<td>+0.1</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td></td>
<td>“</td>
<td>26</td>
<td>2110</td>
<td>42.7</td>
<td>45.4</td>
<td>-1.8</td>
</tr>
<tr>
<td>11</td>
<td></td>
<td>Mar. 23</td>
<td>2100</td>
<td>43.3</td>
<td>43.9</td>
<td>-0.6</td>
<td>4th minute after work began.</td>
</tr>
<tr>
<td>12</td>
<td></td>
<td>Apr. 14</td>
<td>2200</td>
<td>44.7</td>
<td>44.1</td>
<td>+0.6</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>J.S.L.</td>
<td>Feb. 12</td>
<td>250</td>
<td>42.7</td>
<td>43.1</td>
<td>-0.4</td>
<td>Resting</td>
</tr>
<tr>
<td>14</td>
<td></td>
<td>Apr. 8</td>
<td>800</td>
<td>33.0</td>
<td>32.5</td>
<td>+0.5</td>
<td>3rd and 4th minutes after stopping work.</td>
</tr>
<tr>
<td>15</td>
<td>L.M.H.</td>
<td>Jan. 8</td>
<td>360</td>
<td>40.0</td>
<td>39.0</td>
<td>+1.0</td>
<td>Sitting on bicycle.</td>
</tr>
<tr>
<td>16</td>
<td></td>
<td>“</td>
<td>8</td>
<td>800</td>
<td>43.8</td>
<td>44.9</td>
<td>-1.1</td>
</tr>
<tr>
<td>17</td>
<td></td>
<td>Feb. 9</td>
<td>9</td>
<td>1720</td>
<td>38.1</td>
<td>42.2</td>
<td>-4.1</td>
</tr>
<tr>
<td>18</td>
<td></td>
<td>Mar. 19</td>
<td>1540</td>
<td>42.5</td>
<td>41.9</td>
<td>+0.6</td>
<td>$pCO_2$ by automatic valve, 41.8 mm.</td>
</tr>
<tr>
<td>19</td>
<td>C.P.</td>
<td>25</td>
<td>1500</td>
<td>39.2</td>
<td>43.1</td>
<td>-3.9</td>
<td>Inexperienced subject; $pCO_2$ by automatic valve, 42.3 mm.</td>
</tr>
<tr>
<td>20</td>
<td>F.A.</td>
<td>Apr. 27</td>
<td>1400</td>
<td>43.0</td>
<td>46.4</td>
<td>-3.4</td>
<td>Inexperienced subject.</td>
</tr>
</tbody>
</table>

The results of these twenty experiments are summarized in Table I. Sixteen of these twenty experiments were made on trained sub-

tion of the other two experiments.
jects during exercise. The results of the sixteen experiments are arranged in two series in Table II. In the seven experiments of the first series, the samples of air were collected at the end of expiration. In the other series, they were collected at the beginning of expiration.

In Table III, is found the complete record of a single exercise experiment in which no arterial puncture was made. Alveolar air was collected at the beginning and at the end of expiration as well

**TABLE II.**

Haldane-Priestley Samples of Alveolar Air in Exercise. Comparison of Samples Collected after Expiration with Samples Collected at Beginning of Expiration.

Two series of experiments on four experienced subjects.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Date</th>
<th>Blood-air pCO₂</th>
<th>Subject</th>
<th>Date</th>
<th>Blood-air pCO₂</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>mm.</td>
<td></td>
<td></td>
<td>mm.</td>
</tr>
<tr>
<td>L.M.H.</td>
<td>Jan. 8</td>
<td>-1.1</td>
<td>D.B.D.</td>
<td>Feb. 11</td>
<td>+0.1</td>
</tr>
<tr>
<td>A.V.B.</td>
<td>&quot; 13</td>
<td>0.0</td>
<td>A.V.B.</td>
<td>&quot; 17</td>
<td>-1.0</td>
</tr>
<tr>
<td>D.B.D.</td>
<td>&quot; 15</td>
<td>-0.5</td>
<td>D.B.D.</td>
<td>&quot; 26</td>
<td>-1.8</td>
</tr>
<tr>
<td>A.V.B.</td>
<td>&quot; 19</td>
<td>-1.7</td>
<td>L.M.H.</td>
<td>Mar. 19</td>
<td>+0.6</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 26</td>
<td>-4.2</td>
<td>D.B.D.</td>
<td>&quot; 23</td>
<td>-0.6</td>
</tr>
<tr>
<td>&quot;</td>
<td>Feb. 3</td>
<td>+0.3</td>
<td>A.V.B.</td>
<td>&quot; 26</td>
<td>+0.9</td>
</tr>
<tr>
<td>L.M.H.</td>
<td>&quot; 9</td>
<td>-4.1</td>
<td>J.S.L.</td>
<td>&quot; 8</td>
<td>+1.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>D.B.D.</td>
<td>&quot; 14</td>
<td>+0.5</td>
</tr>
</tbody>
</table>

Average: -1.6 mm. Average: 0.0 mm.

as by the automatic method of Henderson and Haggard (4). A summary of this and thirteen similar experiments appear in Table IV.

**DISCUSSION OF RESULTS.**

In all but four of the experiments in Table I, fair agreement existed between the carbon dioxide pressure of arterial blood and that of alveolar air. The difference in pressure did not exceed 1 mm. in twelve cases.

These experiments covered a metabolic range up to 10 times the
basal rate. Evidently, in exercise of this grade, it is possible to collect samples of alveolar air which have essentially the same carbon dioxide pressure as that of arterial blood. It is interesting to note that in the four experiments in which the automatic method was used, the results checked the HP method.

The changes observed in the alveolar carbon dioxide pressure in exercise are similar to those recorded by other investigators.

### TABLE III.

**Comparison of Carbon Dioxide Pressures of Haldane-Priestley with Henderson-Haggard Alveolar Air Samples in Exercise.**

Summary of fourteen experiments on five normal subjects.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Date</th>
<th>Oxygen used per min.</th>
<th>Respiration per min.</th>
<th>Tidal air.</th>
<th>No. of samples</th>
<th>HP samples at beginning of expiration</th>
<th>HH samples</th>
<th>pCO₂</th>
<th>pCO₂</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Average pCO₂</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mm.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mm.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mm.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A.V.B.</td>
<td>Apr. 6</td>
<td>1200</td>
<td>20</td>
<td>1500</td>
<td>5</td>
<td>37.9</td>
<td>1</td>
<td>39.4</td>
<td>-1.5</td>
</tr>
<tr>
<td>D.B.D.</td>
<td>Mar. 17</td>
<td>1700</td>
<td>20</td>
<td>1600</td>
<td>4</td>
<td>42.3</td>
<td>4</td>
<td>42.5</td>
<td>-0.2</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>1700</td>
<td>20</td>
<td>1600</td>
<td>4</td>
<td>40.1</td>
<td>4</td>
<td>41.5</td>
<td>-1.4</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>1700</td>
<td>20</td>
<td>1600</td>
<td>4</td>
<td>39.8</td>
<td>3</td>
<td>42.2</td>
<td>-2.4</td>
</tr>
<tr>
<td></td>
<td>22</td>
<td>900</td>
<td>15</td>
<td>1300</td>
<td>3</td>
<td>41.4</td>
<td>2</td>
<td>42.0</td>
<td>-0.6</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>2100</td>
<td>23</td>
<td>1900</td>
<td>2</td>
<td>43.9</td>
<td>2</td>
<td>44.3</td>
<td>-0.4</td>
</tr>
<tr>
<td>A.V.B.</td>
<td>Apr. 6</td>
<td>1900</td>
<td>21</td>
<td>1800</td>
<td>4</td>
<td>42.8</td>
<td>4</td>
<td>42.1</td>
<td>+0.7</td>
</tr>
<tr>
<td>L.M.H.</td>
<td>Mar. 17</td>
<td>1700</td>
<td>16</td>
<td>2100</td>
<td>4</td>
<td>42.6</td>
<td>4</td>
<td>39.3</td>
<td>+3.3</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>1700</td>
<td>16</td>
<td>2100</td>
<td>4</td>
<td>40.0</td>
<td>4</td>
<td>39.9</td>
<td>+0.1</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>1500</td>
<td>15</td>
<td>1900</td>
<td>4</td>
<td>41.9</td>
<td>1</td>
<td>41.8</td>
<td>+0.1</td>
</tr>
<tr>
<td>A.V.B.</td>
<td>Apr. 1</td>
<td>2800</td>
<td>23</td>
<td>2600</td>
<td>3</td>
<td>41.6</td>
<td>1</td>
<td>39.7</td>
<td>+1.9</td>
</tr>
<tr>
<td>C.P.</td>
<td>Mar. 25</td>
<td>1500</td>
<td></td>
<td></td>
<td>3</td>
<td>43.1</td>
<td>2</td>
<td>42.3</td>
<td>+0.8</td>
</tr>
<tr>
<td>G.C.C.</td>
<td>31</td>
<td>1800</td>
<td></td>
<td></td>
<td>2</td>
<td>47.0</td>
<td>1</td>
<td>47.3</td>
<td>-0.3</td>
</tr>
</tbody>
</table>

After a steady state is reached, the carbon dioxide pressure is not far from the resting level. There is often an abrupt drop after stopping work. This is illustrated by Experiment 14; both blood and air reached a level of about 32 mm., which was about 6 mm. below the exercise level.

It is curious that the last two experiments in Table I showed

1 HP is used to designate the Haldane-Priestley method; HH, the Henderson-Haggard valve method.
such unsatisfactory results. We are inclined to attribute this to the inexperience of the subjects. Each was somewhat agitated during the withdrawal of the blood. Upon hearing the signal "blow," F. A. increased his speed considerably. However, the fact that the HH and the HP samples of Experiment 19 checked,

**TABLE IV.**
Comparison of Carbon Dioxide Pressures of Haldane-Priestley with Henderson-Haggard Alveolar Air Samples in Exercise.

Representative experiment on D.B.D. while using 1300 cc. of oxygen per minute.

<table>
<thead>
<tr>
<th>Time</th>
<th>HP samples</th>
<th>HII samples</th>
<th>Respirations per min.</th>
<th>Pulse</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>End of expiration</td>
<td>Beginning of expiration</td>
<td>mm.</td>
<td>mm.</td>
</tr>
<tr>
<td>min.</td>
<td></td>
<td></td>
<td>End</td>
<td></td>
</tr>
<tr>
<td>9-11</td>
<td>46.8</td>
<td>42.9</td>
<td>18</td>
<td>112</td>
</tr>
<tr>
<td>16</td>
<td>43.0</td>
<td>44.6</td>
<td>18</td>
<td>112</td>
</tr>
<tr>
<td>21</td>
<td>45.1</td>
<td>44.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>46.5</td>
<td>44.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24-26</td>
<td>42.8</td>
<td>43.7</td>
<td>20</td>
<td>114</td>
</tr>
<tr>
<td>27</td>
<td>44.4</td>
<td>43.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>43.5</td>
<td>42.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>31-33</td>
<td>43.1</td>
<td>43.2</td>
<td></td>
<td>114</td>
</tr>
<tr>
<td>35</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>40-42</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>50</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>52</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>53-55</td>
<td>44.0</td>
<td>43.1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

suggests that here there may have been an error in determining the carbon dioxide pressure of the blood.

When the results on experienced, exercising subjects are classified according to the method of collecting the alveolar samples (Table II), it is seen that the HP samples collected at the beginning of expiration show but one discordant figure. The average carbon
dioxide pressure of the blood in this series is precisely that of the alveolar air. The two most discordant results came in the early group when we were collecting the samples of alveolar air at the end of expiration. We were then less experienced; hence it is not possible to ascribe these irregularities solely to the method of sampling.

The several experiments of Tables III and IV were undertaken in the light of our accumulated experience. They establish the difference between alveolar airs collected by different methods from exercising subjects. The typical experiment of Table III makes it clear that samples collected at the end of expiration have an appreciably greater pressure than samples collected at the beginning of expiration. Those collected at the beginning of expiration check those obtained automatically.

During exercise, then, the automatic device of Henderson and Haggard gives an accurate measure of the carbon dioxide pressure of the arterial blood. Its ability to do so, despite its failure with resting subjects is quite likely due to the fact that the HP samples collected during exercise at the beginning of expiration come from the same phase in the respiratory cycle as the HH automatic samples.

In view of these results it does not appear necessary to utilize the volume of the dead space to obtain the pressure of CO₂ in alveolar air during exercise as suggested by Krogh and Lindhard (3). Owing to the rapidly changing pressure of carbon dioxide in the lungs during exercise, it is in the nature of fortuitous chance that experimental procedures yield as good results as can be obtained with respect to the equilibrium of carbon dioxide in arterial blood and pulmonary air. The data above cover a range of moderate exercise only.

SUMMARY.

It has been shown that Haldane-Priestley samples of alveolar air collected during exercise at the beginning of expiration measure approximately the average carbon dioxide pressure of arterial blood. Samples collected by the Henderson and Haggard automatic method are similar, but Haldane-Priestley samples collected at the end of expiration are more divergent and tend to give higher values.
BIBLIOGRAPHY.
THE CARBON DIOXIDE EQUILIBRIUM
IN ALVEOLAR AIR AND ARTERIAL
BLOOD: III. EXERCISING SUBJECTS
D. B. Dill, J. S. Lawrence, L. M. Hurxthal and
A. V. Bock


Access the most updated version of this article at
http://www.jbc.org/content/74/2/313.citation

Alerts:
• When this article is cited
• When a correction for this article is posted

Click here to choose from all of JBC's e-mail alerts

This article cites 0 references, 0 of which can be accessed free at
http://www.jbc.org/content/74/2/313.citation.full.html#ref-list-1