THE OXYGEN AND CARBON DIOXIDE DISSOCIATION CURVES OF HUMAN BLOOD.*

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For many years studies of the combination and dissociation of oxygen and hemoglobin in blood have been based on the dissociation curve of blood as presented by Barcroft (1). This curve is an S-shaped curve, described by Hill's (2) equation

\[
y = \frac{Kx^n}{1 + x^n}
\]

in which \( y \) is the percentage saturation of blood with oxygen, \( x \) equals the oxygen pressure, and \( K \) and \( n \) are constants. Assuming that molecules of hemoglobin fall into aggregates in the presence of salts, Barcroft has interpreted \( n \) in the formula to mean the number of molecules in each aggregate, and \( K \) is regarded as the equilibrium constant. Owing to the conception that there are varying degrees of molecular aggregation of hemoglobin the value of \( n \) is taken as the average value of the aggregates present, 2.5 being the value best fitting the experimental curves thus far determined. Recent studies indicate that 2.2 is a more exact estimate for \( n \). The variations in the dissociation curves of blood of different individuals is considered to be due to change in the value of \( K \) only.

An attempt to verify Barcroft's curve with analyses of blood done with the Van Slyke apparatus failed to confirm previous work and led to the production of dissociation curves on the blood of two of the authors (A. V. B. and G. S. A.) that are not capable of definition by Hill's equation. The variations found are greater

* This is study No. 37 of a series of studies on the physiology and pathology of blood from the Harvard Medical School and allied Hospitals, a part of the expense of which has been defrayed by the Proctor Fund for the study of chronic disease.
than experimental errors would appear to account for, and aside
from theoretical considerations concerning the relations between
hemoglobin and oxygen, many practical points make it advis-
able to publish oxygen dissociation curves as determined with the
apparatus of Van Slyke. In this country the Barcroft-Haldane
blood gas methods are little used. If the discrepancy of our results
with those of previous workers is a matter concerned with the
type of apparatus used, it seems essential that data obtained with
the Van Slyke apparatus should be referred when desirable to
dissociation curves obtained with this method. The most accu-
rate method at present of obtaining the pressure of oxygen in arte-
rial and venous blood, for example, is based upon the oxyhemo-
globin curve, and the value obtained, as shown by the work here
presented, varies greatly, apparently depending on the blood gas
methods used.

This paper, therefore, presents two well defined oxygen disso-
ciation curves for human blood at a CO₂ tension of 40 mm. of Hg
as determined with the apparatus of Van Slyke. Similar curves
on the blood of one of us (A. V. B.), at the following tensions of CO₂,
3, 20, and 80 mm., are given, and Barcroft’s curve is reproduced
for comparison.

Because of the general interest in the relationship of oxygen and
carbon dioxide in blood, the average CO₂ dissociation curves on
oxygenated and reduced blood of one of us (A. V. B.), as well as
the corresponding true plasma curves, are also given. The com-
plete set of curves for both oxygen and CO₂ for the same human
blood may be of interest to other workers in this field.

Methods.

Oxyhemoglobin Dissociation Curves.

1. A set of tonometers of approximately 250 cc. capacity was
prepared with known gas mixtures, CO₂ about 40 mm. of pressure,
O₂ from 2 to 100 mm.

2. After a rest period of 15 minutes about 25 cc. of blood were
drawn, without stasis, from the arm vein of the subject, run at
once into a tube containing a minimum amount of carbonate-free
potassium oxalate to prevent clotting, and stirred gently with a
glass rod. A sample of 2 cc. was taken at once for the first tonom-
eter; the rest of the blood was put on ice.
3. The tonometer was rotated for 20 minutes in a water bath at 37.5°C. An equilibration experiment was carried out to determine the optimum time required for equilibrium to be reached between the blood and the atmosphere in the tonometer. The time found was from 17 to 20 minutes. After equilibration 1 cc. of blood was removed from the tonometer in an Ostwald pipette, calibrated to deliver between marks, and run directly under water into the Van Slyke pipette, the burette of which was calibrated to read to 0.01 cc. The determination of oxygen in the sample was carried out according to the technique described by Van Slyke and Stadie (3). The oxygen was absorbed by pyrogallol after the CO₂ had been removed with 0.2 N NaOH. Blank determinations were carried out to find how much gas was present in the reagents. The tiny bubble formed could not be estimated exactly but a maximum error of 0.005 cc. would occur if no correction were made for this bubble. The solubility corrections for oxygen were taken from Van Slyke and Stadie's table, calculated from Bohr's solubility coefficient.

4. The partial pressures of oxygen and carbon dioxide in the tonometer were determined in the usual way in the Haldane gas apparatus. The equilibration of the blood in the tonometer was carried out with a small positive pressure. Since some uncertainty has been felt as to the method of calculating partial pressures in the water bath from experimental data at room temperature, it seems advisable to state the formula used in the calculations.

\[
x = p(B - w + pp) \frac{273 + 37.5}{273 + t} \frac{V | 7 - 2 + 1}{V - 2}
\]

- \(x\) = partial pressure of CO₂ or O₂.
- \(p\) = percentage of gas.
- \(B\) = barometric pressure.
- \(w\) = vapor pressure at temperature \(t\).
- \(pp\) = positive pressure measured in burette of Haldane apparatus.
- \(t\) = room temperature.
- \(V\) = volume of tonometer.
- \(7\) = "" gas taken into Haldane apparatus.
- \(2\) = "" blood present in the tonometer.
- \(1\) = "" "" removed for analysis.

This formula is based on Dalton's law; the pressure of water vapor at 37.5° does not enter into the calculation because the system is an heterogeneous equilibrium.
5. The partial pressure of carbon dioxide desired in the tonometer was 40 mm. of Hg. An inspection of our data will show that while most of the equilibrations were carried out at this tension or within 2 or 3 mm. of it, numerous points were done at somewhat wider ranges of CO₂ tension. In order to correct all points to a CO₂ tension of 40 mm. of Hg use was made of a correction curve obtained by application of a new formula derived from Hill’s equation, and a formula published by one of us (G. S. A.) in 1921 (18), \[ \frac{1}{K} = au + b. \]

In the new formula,

\[ x_{40} = x_u \left( \frac{40a + b}{(au - b)n} \right) \]

\( x_{40} \) = tension of oxygen at 40 mm. of CO₂.
\( x_u \) = observed tension at \( u \) mm. of CO₂.
\( a \) and \( b \) = empirical constants.

The equation \[ \frac{1}{K} = au + b \] has been shown by Hill to be inaccurate when a wide range of CO₂ tensions is considered, but as an empirical formula it is accurate over the range we require.

**Carbon Dioxide Dissociation Curves.**

For the determination of carbon dioxide in whole blood and plasma the technique used was that described by Austin and his associates (4) with certain minor modifications. Simple gas burettes were used for approximate estimation of the tensions of oxygen and carbon dioxide required in each tonometer and the exact tensions were determined by means of the Haldane apparatus after the blood was removed from the tonometer. The analyses for carbon dioxide were made with the constant volume apparatus of Van Slyke, equipped with a side trap in which the blood reagent mixture was trapped during absorption of carbon dioxide by sodium hydroxide. This modification of the original apparatus enabled us to get more accurate readings than appeared possible when it was used without the side trap.
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<th>Saturation with O₂.</th>
<th>O₂ capacity (combined).</th>
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O₂ and CO₂ Dissociation Curves of Blood

**TABLE I—Concluded.**

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*Oxygen Dissociation Curve of Blood at a CO₂ Tension of 40 Mm. of Hg.*

For the sake of brevity attention in these remarks will be confined to the curve of the blood of A. V. B. The variations of the corresponding curve for the blood of G. S. A. may be determined from comparison of the curves. The small differences found between these two curves appear to be beyond the range of error and are doubtless significant. The points as determined on the blood of A. V. B. are given in Table I, and are plotted in Fig. 1. The curve is drawn free-hand through the points as the most
practical method of determining its character. It will be noted that of a total of 66 points, 28 fall above the curve as drawn, 28 fall below, and 10 are on the curve. If the sum of the squares of all the deviations is taken and the mean square deviation determined, it is found that the square root of this value multiplied by 0.673 gives a "probable error" of about 1 per cent. In other words

![Graph](http://www.jbc.org)

**Fig. 1.**

taking the tensions of oxygen as being correct and considering the error involved to lie in the percentage saturation of the blood with oxygen, the mean error of all the determinations on the curve is 1 per cent above or below the curve as drawn for all tensions above 10 mm. Below a tension of 10 mm. of Hg the deviation is considerably less than this.
As contrasted with the curve of Barcroft's blood, the deviation from it of the blood of A. V. B., shown in Fig. 2, expressed in terms of percentage saturation with oxygen at corresponding tensions is as follows:

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<th>Hg, mm</th>
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</table>

The number of points on each curve below a tension of 10 mm. of Hg, the range of deviation of the points from the curves, and the change in form of the new curve as contrasted with the old,
are well shown for the lower range in Fig. 3. The curve and points for Barcroft's blood are taken from a figure published in 1913 (5).

The dissociation curve of the blood of A. V. B. is characterized at low tensions by an S-deflection much less striking than in the case of Barcroft's blood. Attention is also called to the fact that the former curve attains a saturation of 95 per cent at a tension of about 70 mm. of Hg, as against 90 mm. for the latter curve. This difference in the upper reaches of the curves may be of some significance from the point of view of diffusion of oxygen from the lungs to the blood.

The data for the blood of G. S. A. are given in Table II and the curve is shown in Fig. 4.
### O₂ and CO₂ Dissociation Curves of Blood

#### TABLE II.

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**Fig. 4.**
Oxygen Dissociation Curves of Blood at CO₂ Tensions of 3, 20, and 80 Mm. of Hg.

The 3 Mm. Curve.—In the case of this curve the points are few in number but their accuracy is sufficiently great to establish the
curve as drawn free-hand through them. The data comprise Table III.

The 20 Mm. Curve.—Of 21 points determined on this curve 6 fall above the free-hand curve, 9 fall below it, and 6 points are on the curve. The points are listed in Table IV.

<table>
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The 80 Mm. Curve.—Of 30 points on this curve, 10 fall above it, 14 below it, and 6 fall upon it. The data are given in Table V.
No great degree of accuracy is claimed for these three curves owing to the insufficient number of points by which they were determined. In the experimental work more difficulty was experienced in getting consistent results when the tension of CO$_2$ was at 80 mm. of Hg than at the lower tensions. Whether the equilib-

![](image)

Fig. 5.

rium of the system is more unstable at the higher tension of CO$_2$ or not is a matter for future investigation. The curves are shown in Fig. 5, and may be compared with a similar figure in Barcroft’s book.$^1$

$^1$ Barcroft (1), p. 65.
Hill’s Equation Applied to the Oxygen Dissociation Curve of Blood.

When the oxygen dissociation curves of blood are plotted in the usual way, \( y \), the ordinate, being the fraction of \( \text{HbO}_2 \), and \( x \), the abscissa, the tension of oxygen in mm. of Hg, it will be seen that our curves and Barcroft’s are nearly the same in shape and correspond roughly to the curve of Hill’s equation. The fit in

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<td>87.0</td>
<td>67.5</td>
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the former set of curves, however, is not exact, but the method of plotting makes it difficult to discuss the nature of the deviation. This can be brought out by plotting the relations involved in logarithmic form, according to Hill’s theory, as has recently been done by Brown and Hill (6).
O₂ and CO₂ Dissociation Curves of Blood

\[
\begin{align*}
(Hb) \times (O₂)^n \times K &= (HbO₂) \\
(1 - y) \times (x) \times K &= y \\
\log (1 - y) + n \log x + \log K &= \log y \\
n \log x + \log K &= \log y - \log (1 - y)
\end{align*}
\]

Hence if we calculate \(\log \frac{y}{1 - y}\) and \(\log x\) for each point, and plot the new variables with \(\log x\) as abscissa, the result should be a straight line if Hill’s equation describes the new curves. In Table VI we have calculated the logarithmic variables from the values of \(x\) and \(y\) in Table VII. The results are plotted in Figs. 6 and 7. It will be seen that the lines curve upwards. If Hill’s theory applied over the whole range, the lines would be straight. An empirical formula covering the entire range of tensions would have to include one more term.

\[
n \log x + \log K + b (\log x) = \log y - \log (1 - y)
\]
If the physiological range is considered alone, Hill's formula is accurate enough for all practical purposes, provided the values of \( n \) and \( K \) are used which apply to this range. These calculations are tabulated in Table VIII. \( B_3, B_{20}, B_{40}, \) and \( B_{80} \) are from the oxygen dissociation curves of A. V. B., at 3, 20, 40, and 80 mm. of CO\(_2\), and \( A_{40} \), that of G. S. A. at 40 mm. of CO\(_2\). These observations confirm Barcroft's finding that change of CO\(_2\) tension alters \( K \) rather than \( n \), but they show that \( n \) is not constant over the range from full reduction to full oxidation at constant CO\(_2\) tension. The mean values, \( n = 2.33 \), upper range, and \( n = 2.0 \), lower range, have been used in calculating \( K \).

It will be seen that the value of \( n \) for the upper range of the blood of A. V. B., 2.33, agrees with that of Douglas, and the value of \( n \) for the upper range of the blood of G. S. A., 2.55, agrees with that
O$_2$ and CO$_2$ Dissociation Curves of Blood

of Barcroft. For some time we suspected that the curve for the blood of G. S. A. might be wrong as there were fewer points, but further observations forced us to conclude that there is a difference in the form of the two oxygen dissociation curves. There are other published curves which agree with ours in indicating a low value of $n$ at low saturations. For example, in the curve of J. S. Haldane (7), the value of $n$ for the upper range is 2.2 and for the lower range $n = 2.0$.

The deviation of our curves from those described by Hill’s equation is significant. Since the curve described by this equation fitted the experimental points determined by Barcroft, the latter ascribed physical meanings to empirical constants and upon this basis the Barcroft-Hill (1) aggregation theory of hemoglobin was constructed. Our data do not conform to Hill’s equation, but we have no alternative theory to offer as to the mechanism by which the combination of hemoglobin and oxygen in blood is attained.

**Carbon Dioxide Dissociation Curves.**

The form of the carbon dioxide dissociation curves of fully oxygenated and fully reduced whole blood was determined by Christiansen, Douglas, and Haldane (8). These workers suggested that the greater capacity of reduced blood to combine with CO$_2$ might be due to the fact that reduced hemoglobin was less acid than oxyhemoglobin. That this is probably the case has subsequently been shown by Hasselbalch (9), Parsons (10), and L. J.
Henderson (11). The significance of the form of the CO₂ curve has been discussed by many writers and need not be dwelt on here. In the laboratory this curve is commonly used for two purposes. In the first place, the level of the curve at any given tension of carbonic acid shows the amount of base available for the transport of CO₂. That the quantity of this base in a given individual in health is fairly constant over long periods of time was shown by Christiansen, Douglas, and Haldane (8). In the case of the blood of A. V. B. variations from day-to-day of 1 or 2 volumes per cent only of total CO₂ were encountered over a period of several months. There can be no doubt, however, from a study of many curves in the literature of normal individuals that the level of the curve at any tension of CO₂, e.g. 40 mm., may vary from individual to individual, although it has recently been assumed by Dautrebande, Davies, and Meakins (12) that some of these curves are in error because they do not coincide with that of the blood of Haldane.

**Fig. 8.**
372  O₂ and CO₂ Dissociation Curves of Blood

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<th>Date</th>
<th>CO₂</th>
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<th>Total CO₂ of true plasma</th>
<th>O₂ capacity</th>
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In the second place, the curve may be used in determining the amount of additional CO₂ that will be taken up by the same blood when it is reduced as compared with that of the fully oxygenated state. If one disregards the small change in (H⁺), this added amount at any given tension of CO₂ represents the amount of base transferred from combination with hemoglobin to that combined with carbonic acid. The phenomenon takes place partially in the body with every cycle of the blood through the lungs, the mixed venous blood of normal resting individuals being about 25 to 30 per cent reduced. In the case of the blood of A. V. B., the average difference in the amount of CO₂ between the curves

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of blood fully oxygenated and fully reduced at tensions of CO₂ from 40 to 80 mm. of Hg is 6.3 volumes per cent. The data upon which the curves of whole blood shown in Fig. 8 were constructed are given in Table IX. In the laboratory it is difficult to obtain complete reduction of blood in the tonometers under the conditions of the experiment, but in the case of every point determined for reduced blood correction has been made for the amount of oxygen present by reading off the percentage saturation with oxygen on appropriate oxygen dissociation curves at the tension of oxygen found to be present in each tonometer.

**Straight Line Relationship of the CO₂ Curve.**

Attempts have been made by Warburg (13) and Van Slyke, Austin, and Cullen (14) to express the carbon dioxide absorption curve as a straight line when plotted with pH against bicarbonate.
Peters and his associates (15) have shown that this relationship only roughly approximates a straight line over short ranges of pH and that for the usual range covered by the curve the deviation from a straight line at a tension of 40 mm. of Hg is ± 1.26 per cent. After study of a considerable mass of data on the subject, Peters showed that when the curve is plotted as log

\[ \log[\text{H}_2\text{CO}_3] - \log(\text{BHCO}_3) \]

against log (BHCO₃) the result is more nearly a straight line. The matter was tested in the case of the blood of A. V. B, and the results are shown in Figs. 9 and 10. H₂CO₃ was calculated following the data of Van Slyke, Wu, and McLean, (16), and pH with Hasselbalch's formula, using 6.16 for the value of pK₁, this being the apparent value of pK₁ as calculated from data given in the following paper. The log (H₂CO₃) - log (BHCO₃)
relationship is approximately a straight line for fully oxygenated blood and permits, as Peters has pointed out, determination of the entire CO₂ curve by extrapolation if two points have been experimentally determined.

True Plasma Carbon Dioxide Dissociation Curves.

There are very few data in the literature for true plasma curves determined on plasma from fully oxygenated and fully reduced blood. The most complete curves are those of the blood of J. J. given by Joffe and Poulton (17). The present data are published chiefly to supplement those now available. The data are included in Table IX and the curves are plotted in Fig. 8.

At a CO₂ tension of 40 mm. of Hg, the difference in the CO₂ content between oxygenated whole blood and oxygenated true plasma is 9.5 volumes per cent; at 80 mm. it is 11.6 volumes per cent. For the reduced blood and plasma the corresponding figures are 7.8 and 8.9 volumes per cent. The absence of oxygen obviously reduces the amount of CO₂ taken up by reduced true plasma by 1.7 volumes per cent at a tension of 40 mm. of Hg, probably because a somewhat greater proportion of CO₂ is carried in the corpuscles of reduced blood than in those of oxygenated blood. This follows from the more alkaline character of reduced hemoglobin.

It is shown in the following paper that the tension of CO₂ in the arterial blood of A. V. B. is approximately 40 mm. of Hg, that of the mixed venous blood is 47 mm. of Hg, that the saturation with oxygen of the arterial blood is 95.5 per cent, and that of the mixed venous blood is about 65 per cent. The average oxygen capacity is 20 volumes per cent and the corpuscle volume is 40 per cent. If, for the sake of simplicity, the curve for fully
oxygenated blood is taken to represent the arterial blood, and allowance is made for the reduction of the mixed venous blood, it is possible to read from the curves of Fig. 8 the amount of CO₂ contained in the arterial and mixed venous blood and the amount of CO₂ in the true plasma separated from the blood at the above tensions. The amount of CO₂ taken up in a respiratory cycle by both corpuscles and plasma can then be calculated. The figures are given in Table X. As shown also in the following paper it thus appears that the transport of CO₂ during a respiratory cycle is accomplished by both corpuscles and plasma in the ratio of approximately 40 to 60 per cent.

SUMMARY.

1. The oxygen dissociation curves determined at a CO₂ tension of 40 mm. of Hg for the blood of two normal subjects are given. Similar curves at CO₂ tensions of 3, 20 and 80 mm. of Hg for the blood of one of the subjects are also presented.

2. It is shown that these oxygen dissociation curves do not conform to Hill's formula.

3. Carbon dioxide dissociation curves on fully reduced and fully oxygenated blood as well as the corresponding true plasma curves are given.

4. Both corpuscles and plasma transport carbon dioxide; the former carrying 40 per cent of the total and the latter, 60 per cent.

BIBLIOGRAPHY.

8. Christiansen, J., Douglas, C. G., and Haldane, J. S., J. Physiol., 1914, xlviii, 244.
O₂ and CO₂ Dissociation Curves of Blood

THE OXYGEN AND CARBON DIOXIDE DISSOCIATION CURVES OF HUMAN BLOOD
A. V. Bock, H. Field, Jr. and G. S. Adair


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