THE RELATION BETWEEN FOVEAL VISUAL ACUITY AND ILLUMINATION UNDER REDUCED OXYGEN TENSION

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INTRODUCTION

Numerous studies have demonstrated that a diminished partial pressure of oxygen in the inspired air produces marked alterations in the functioning of the central nervous system (McFarland, 1932). All the tissues of the body, and particularly the nervous tissue, are extremely sensitive to anoxia and to variations in the concentration of carbon dioxide. Certain functions that involve the retina, morphologically a part of the brain and metabolically resembling it (Weinstein, 1932), also manifest extensive changes upon exposure to low oxygen tensions. It has not been possible, however, to determine to what extent the effects of anoxia on vision are due to alterations in the central nervous system, or in the sense organ itself.

Studies of dark adaptation have shown that alterations in light sensitivity offer an unusually delicate test of the initial effects of anoxia at partial pressures of oxygen where other sensory tests have failed to show reliable changes (McFarland and Evans, 1939). The dark adaptation curves (threshold against time) were progressively elevated on the log I axis with increasing oxygen deprivation, the magnitude of these changes being 0.10 of a log unit at 15.8 per cent O$_2$ (7,400 ft.), 0.22 at 13.7 per cent O$_2$ (11,000 ft.), and 0.40 at 11.7 per cent O$_2$ (15,000 ft.). Subjectively, there appears to be a general darkening of the visual field during anoxia. Subsequent exposure to oxygen results in a marked increase in the brightness of lights (Goldmann and Schubert, 1933). These changes are probably not concerned with the photochemical processes in the retina, but with the neural elements of both the retina and the central nervous system (Bunge, 1936–37; McFarland and Evans, 1939). In careful experiments on one subject, McDonald and Adler (1939) have recently reported that anoxia causes an equal elevation of rod and cone thresholds, whereas vitamin A deficiency produces a greater change in the rod threshold.
Changes in certain other visual processes have been observed under conditions of acute oxygen deprivation. Schubert (1932-33) and Gellhorn (1936) have observed a considerable decrease in visual intensity discrimination while inhaling 8 to 10 per cent oxygen. They used Masson discs, which provide a rather crude measure of this function. A decrease in critical fusion frequency for flickering light was reported at 10.6 per cent O$_2$ by Seitz (1940). Gellhorn and Spiesman (1935) noted a lengthening of the latent period of the negative after-images or even a complete absence of any after-images. Alterations in negative after-images were also observed by McFarland (1937) in subjects acclimatized to 17,500 ft. and 20,000 ft. in the Chilean Andes. The effects of anoxia on the central visual field have been studied by Evans and McFarland (1938). In experiments in a low oxygen chamber, they found that with progressive oxygen deprivation, beginning at a concentration corresponding to an altitude of 13,000 ft., there was a progressive widening of the angioscotoma (Evans, 1938) (projected defect related to the retinal perivascular spaces). The visual field was obliterated except for an area 8 to 10° about the macula. The measurements were made on a stereocampimeter with test objects of about 0.5 mm. diameter, at 190 mm. from the eye.

The effects of anoxia on peripheral visual fields have been studied by several investigators with somewhat contradictory results. Wilmer and Berens (1918) reported a narrowing of the fields for form and color, in all quadrants, at altitudes of 15,000 ft. and above, simulated in a low pressure chamber. Goldmann and Schubert (1933) found decrements in only the nasal and superior fields. Upon repetition of their experiments, however, Kyrieleis, Kyrieleis, and Siegert (1935) observed no changes in the fields beyond the limits of error. It is possible that these discrepancies were due to differences in experimental conditions and technique. Significant changes in color vision due to oxygen deprivation have been described by Vishnevskiy and Tsyrlin (1935), Velhagen (1936), and Schmidt (1937-38).

Previous investigations of visual acuity under low oxygen tensions have not been very conclusive. In none of them has the role of illumination been taken into consideration. Wilmer and Berens (1918), using a rebreather and a low pressure chamber, reported experiments on twenty-five normal males with the Ives visual acuity test object. They found no change in 60 per cent of their subjects, improvement in 12 per cent, and a decrease of an unstated amount in 28 per cent, from which they concluded that anoxia causes a decrease in visual acuity. On the other hand, Bagby (1921) also using a Henderson rebreather and the Ives test object, found
no significant change in visual acuity until just previous to collapse, when there was a marked deterioration not only of the sensory function but also of attention and ability to cooperate. More recently Berger and Bøje (1937) made a study of the ability of two emmetropic subjects to resolve two squares while breathing air containing 8.7 per cent oxygen. Two methods were used: luminous squares on a dark field, and black squares on a white field. In spite of marked oxygen lack, they reported that the resolving power was unchanged or only slightly decreased while using the luminous squares, whereas with black squares on a white field a considerable decrease was found. The thresholds rose 30 per cent in one subject and 100 per cent in the other. The brightness of the background corresponded to a log $I$ in photons of 2.875. They attributed the changes in this case largely to an alteration in the intensity discrimination threshold (cf. Gellhorn, 1936).

Visual acuity is dependent, among other things, upon the intensity of illumination. Uhtoff (1886, 1890) made the first thorough investigation of this problem over a great range of illumination using white and colored lights. A few years later Koenig (1897) made such comprehensive observations that his data have become classic. The most adequate and precise measurements of this relationship were described recently by Shlaer (1937–38). His apparatus was constructed so as to avoid certain variables which were uncontrolled in previous investigations, namely size of the pupil, distance of the test object, and an extensive surrounding field equal in brightness to that of the test field. The latter is necessary in all measurements involving a stationary state of adaptation of the eye.

The data of Shlaer, as also those of Koenig, when plotted as the logarithm of visual acuity (ordinate) against the logarithm of the intensity of retinal illumination (abscissa) (Hecht, 1937), are consistent with the theory that the retina is a double sense organ. Using white light, a discontinuity appears in the curve at a visual acuity = 0.16. All values below this are mediated by the rods, and those above by the cones. The two portions of the curve were shown by Shlaer to fit a theoretical equation derived by Hecht (1934) upon the simplest assumptions concerning a photoreceptor.
FOVEAL VISUAL ACUITY AND LOW OXYGEN TENSION

system. If red light, to which the rods are believed to be relatively insensitive, is used instead, the rod portion is deleted and the data fall upon a continuous curve which represents a function of the cones alone, and also corresponds to Hecht's equation (Shlaer, Smith, and Chase). This is also apparent in Koenig's data when plotted as a double-logarithmic function (Hecht, 1937). Under most situations, the visual acuity mediated by the cones is probably of greater importance than that which involves the rods. For this reason, and also in order to simplify the treatment of our data, the experiments to be described were made with the use of red light rather than white.

Apparatus and Procedure

Visual Acuity Apparatus.—The apparatus we employed for the measurement of visual acuity at various intensities of illumination was that described by Shlaer (1937-38). The illumination was varied discontinuously in steps of approximately 0.3 of a log unit by means of neutral Wratten filters placed just within a 2 mm. artificial pupil. A No. 70 Wratten (red) filter was also placed at this point. The size of the test object could be varied continuously over a range of about 1:100, at a fixed distance of 1 meter from the eye. It was located in the center of a uniformly illuminated field 30° in extent. In our study it appeared as a black figure against a red background. The test object used was a Landolt broken circle, or C, in which the width of the line and the gap is \( \frac{1}{2} \) the total outside diameter of the letter. It could be rotated about its optic axis so as to be presented in eight different meridians, 45° apart. The apparatus was placed in a room with black walls and ceiling, and the subject was shielded from extraneous light.

The test object was set by the experimenter so as to be too small for the subject to resolve it. The latter turned a knob, which caused the size of the object to increase, in steps of about 0.010-0.020 of a log unit of visual acuity. The subject paused between adjustments to observe the object, until he was able to report the meridian in which the opening of the C was located. If he was correct, the scale reading of the visual acuity was taken, and the test object was reset below the threshold for another determination. If the response was incorrect the meridian was changed and the subject allowed to proceed. The order in which the meridian settings were made was according to a predetermined pattern. Readings on the visual acuity scale were made to 0.001-0.002 of a log unit, depending on the part of the scale employed. With trained subjects successive determinations usually agreed within 0.030 of a log unit or better.

Low Oxygen Apparatus.—The various mixtures of oxygen and nitrogen were inhaled by the subjects from a rubber mask which covered the mouth and nose and fitted tightly against the face. Cylinders of these gas mixtures were prepared and their composition verified by analysis of samples in duplicate on the Haldane apparatus. The gases

\[ 2 \text{ More precisely, as pointed out by Hecht (1937): "It is not that the rods do not function in red light; it is that in red light the cones have about the same intensity thresholds as the rods; but since the cones are closer together in the fovea than are the rods in the periphery, they can resolve smaller distances and therefore dominate the measurements by recording the correspondingly higher visual acuities."} \]
entered a 50 liter Douglas bag from which they passed during inspiration through a one-way mercury valve to the mask. Upon expiration this valve closed and the expired gases passed through a flutter valve on the mask into the room. Changes from one gas mixture to another could be made by the experimenter without the subject being aware of it.

Subjects.—The subjects were eleven males, of sedentary occupation, all but two of whom were medical students. Their age range was 20–25 years with the exception of one (F. B.) who was 43. All were emmetropic and free of organic diseases. They were, on the average, in fair physical condition, the test having been made during the latter part of their summer vacation.

EXPERIMENTAL PROCEDURE

Two series of experiments were performed as follows:

Series 1 consisted in measurements of visual acuity over practically the entire range of illuminations mediated by the cones, while the subjects breathed normal air and while they breathed an oxygen mixture containing 10.34 per cent O₂. The partial pressure of oxygen in such a mixture corresponds to that at an elevation of 18,000 feet, according to Bureau of Standards data for constant temperature of 15°C. (cf. McFarland, 1938).

The two subjects whose data we present were first given an extensive amount of practice. They made observations at each of the light intensities used in the experiment over a period of several days, so that they exhibited no further learning and their measurements were quite consistent.

The actual experiment required about 4 hours. The subject was first dark-adapted for about 10 minutes, and measurements were begun at the lowest intensities. The subject kept his eye as close to the artificial pupil as possible. Before making observations at any given intensity he fixated the center of the illuminated field for 3 minutes so as to reach a stationary state of adaptation at this intensity. Four observations were made at each intensity, each usually requiring 1 to 3 minutes. If any one of these varied from the others by more than 0.030 of a log unit, it was rejected and another taken in its place; this step was rarely necessary. After 5 minutes of observation, the subject was allowed to rest for 1–2 minutes with his eyes closed. Such rest periods were followed by a 3 minute period of adaptation to the illuminated field before observations were resumed.

Having completed the observations with normal air at all the light intensities employed, the subject was allowed to rest for 20 minutes. Then administration of the low oxygen mixture was begun and the entire procedure described in the preceding paragraph was repeated in a similar manner.

Upon completion of the measurements under these conditions, 100 per
cent oxygen from a cylinder was delivered to the mask and the subject was
again allowed to dark adapt for 10 minutes. This change in composition
of the inspired gases was made without the subject's being aware of it.
Visual acuity determinations were then made at the lowest light intensity
which had been used during the tests with the low oxygen mixture.

Series 2.—Nine subjects were tested at two intensities of illumination.
One was near the low end of the range for cone vision (log \( I \) in photons =
1.159) and the other, nearly 10,000 times as bright (log \( I \) = 3.120) or great
enough to elicit nearly maximal visual acuity. Two low oxygen mixtures
as described below, were employed.

The practice period of about 2 hours was first given in which the subjects
were trained to make observations at these intensities. Practice was also
given at an intensity about 0.4 of a log unit lower. (See below.)

The duration of each experiment was about 2½ hours. The same general
procedure was observed as in series 1. After the measurements in normal
air had been completed at the two illuminations, determinations were made
under the following conditions and in the following sequence:

(a) 14.31 per cent oxygen, equivalent to 10,000 feet.
(b) 10.34 per cent oxygen, equivalent to 18,000 feet.
(c) 100 per cent oxygen, as a control.

Each gas mixture was breathed for 15 minutes before the measurements
were begun. Since, as will be seen later, only slight changes occurred at
the high illumination, this was employed only at 10.34 per cent oxygen.
At least six readings were made at each point, depending on the rapidity
with which they could be made, and on their consistency with each other.

RESULTS

Series 1.—The data\(^3\) of two subjects are presented in Table I, and are
plotted in Figs. 1–3. Each datum of log visual acuity represents an aver-
age of four measurements. In Figs. 1 and 2, where the description is by the
photochemical stationary state equation (Hecht, 1934), with visual acuity
taken as proportional to \( x^2 \), the theoretical curve has been superimposed
on the normal air data, and then translated horizontally to the right along

\(^3\) Definitions of units employed:

Visual acuity is expressed as the reciprocal of the angle, in minutes, subtended by the
finest detail distinguishable, which here corresponds to the gap in the C used as the test
object.

Retinal brightness is given in photons (Troland, 1916) and is expressed as external
brightness in millilamberts times 10/\( \pi \) times pupil area in square millimeters (photons =
millilamberts \( \times 10/\pi \times \) pupil area in square millimeters).
Fig. 1. The data for subject F. B. (Table I) showing the relation between log visual acuity and log retinal illumination with normal air and with 10.34 per cent oxygen. The curve corresponding to Hecht's stationary state equation (1) (see Discussion) has been superimposed on the normal air data; it has then been translated horizontally to the right to obtain a fit for the low oxygen data. The + represents a final control with 100 per cent oxygen, after completion of the measurements with 10.34 per cent oxygen.

Fig. 2. The data for subject M. O. (Table I). See legend for Fig. 1.
the log $I$ axis until a fit for the low oxygen data was obtained. For subject F. B., this shift amounted to 0.38 of a log unit, and for M. O. it was 0.66 of a log unit. In Fig. 3, the same data for subjects M. O. and F. B. have been fitted by the probability integral (cf. Crozier, 1937, 1939). Administration of oxygen to each subject at the end of the experiment resulted in complete recovery of visual acuity at an illumination at which it had been most severely affected.

**TABLE I**

Visual Acuity in Relation to Illumination; Normal Air and 10.34 per cent $O_2$
(Series I). (Cf. Figs. 1–3)

<table>
<thead>
<tr>
<th>Log $I$ in photons (photons)</th>
<th>Subject F. B.</th>
<th>Subject M. O.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Normal air</td>
<td>10.34 per cent oxygen</td>
</tr>
<tr>
<td>2.757</td>
<td>1.049</td>
<td>Not measurable</td>
</tr>
<tr>
<td>1.159</td>
<td>1.394</td>
<td>1.046</td>
</tr>
<tr>
<td>1.478</td>
<td>1.584</td>
<td>1.355</td>
</tr>
<tr>
<td>1.781</td>
<td>1.885</td>
<td>1.726</td>
</tr>
<tr>
<td>0.166</td>
<td>Equivalent</td>
<td>0.38</td>
</tr>
<tr>
<td>0.815</td>
<td>0.245</td>
<td>0.152</td>
</tr>
<tr>
<td>1.147</td>
<td>0.396</td>
<td>0.375</td>
</tr>
</tbody>
</table>

**Series 2.**—Table II contains the data for nine subjects breathing normal air, 14.31 per cent oxygen, 10.34 per cent oxygen, and 100 per cent oxygen in that sequence. Each datum of visual acuity represents an average of six to ten measurements. The average values are plotted in Fig. 4. Two points, accurately determined, are sufficient to locate the theoretical curve; this was drawn through the normal air data. It was then translated horizontally to the right so as to coincide with the point representing the measurements at the low intensity, at each of the conditions of decreased oxygen tension. The curve thus drawn through the lower point at 10.34 per cent $O_2$ coincides with the upper point as well. This is confirmed by the fact that the maximum log visual acuity, as calculated from the means of the data in Table II according to Hecht's stationary state equation (cf. Discussion) is 0.330 in normal air, and 0.314 in 10.34 per cent oxygen. The standard deviations of the means of log visual acuity upon which the
computations are based (cf. Table II) are as high as 0.155, with corresponding standard errors up to 0.052. Consequently the difference of 0.016 between log maximum visual acuity in normal air compared with 10.34 per cent oxygen is negligible, and leads to the conclusion that the translation

**TABLE II**

*Visual Acuity Data for Nine Subjects (Series 2). (Cf. Fig. 4)*

<table>
<thead>
<tr>
<th>Subject No.</th>
<th>Logarithm of visual acuity</th>
<th>Dim Illumination, log ( I = 1.159 ) in photons</th>
<th>Bright Illumination, log ( I = 3.130 )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Initial control, Normal air</td>
<td>14.31 per cent O(_2)</td>
</tr>
<tr>
<td>1</td>
<td>1.386</td>
<td>1.305</td>
<td>1.132</td>
</tr>
<tr>
<td>2</td>
<td>1.412</td>
<td>1.069</td>
<td>2.823</td>
</tr>
<tr>
<td>3</td>
<td>1.396</td>
<td>1.033</td>
<td>2.950</td>
</tr>
<tr>
<td>4</td>
<td>1.086</td>
<td>1.005</td>
<td>2.899</td>
</tr>
<tr>
<td>5</td>
<td>1.221</td>
<td>1.053</td>
<td>2.917</td>
</tr>
<tr>
<td>6</td>
<td>1.314</td>
<td>1.192</td>
<td>2.928</td>
</tr>
<tr>
<td>7</td>
<td>1.336</td>
<td>1.201</td>
<td>1.094</td>
</tr>
<tr>
<td>8</td>
<td>1.408</td>
<td>1.308</td>
<td>1.224</td>
</tr>
<tr>
<td>9</td>
<td>1.349</td>
<td>1.101</td>
<td>2.747</td>
</tr>
</tbody>
</table>

Mean .................... 1.312                     1.141                                       2.968                                       1.353                                       0.309                                       0.283 |
Standard deviation of mean. 0.104                     0.116                                       0.155                                       0.118                                       0.097                                       0.098 |
Corresponding visual acuity, per cent of normal .... 100                     68                                           45                                           110                                           100                                           94 |
Difference from normal .... -0.171                     -0.344                                       +0.041                                       -0.026 |
Standard deviation of difference. -0.093                     0.158                                       0.046                                       -0.034 |
Standard error of difference. -0.031                     0.053                                       0.015                                       -0.011 |
Critical ratio. -5.52                     6.54                                           2.73                                           2.40                                           |
\*P .................... Less than 0.01                     Less than 0.01                     0.03                                           -0.026 |

\*\( P \) is equivalent to the probability that the observed difference is due to chance. Statistically significant differences are represented by values of \( P \) which are 0.05 or less (Fisher, 1932).

of the curve has no appreciable vertical component, under the conditions of our experiments. The maximum visual acuity is not affected by anoxia, although a higher illumination may be required to elicit it.

This consideration justifies our having translated the curves in Figs. 1 and 2 horizontally, although in the case of subject M. O. (Fig. 2) the visual acuity at the highest illumination in anoxia suggests a comparatively slight vertical translation as well. The low value for this one point was probably
Fig. 3. The data of Table I plotted on a probability integral grid (see Discussion). Visual acuity, as per cent of the estimated maximum, is plotted against the logarithm of retinal illumination in photons. The open circles represent the data in normal air, and the solid circles, those at 10.34 per cent oxygen. The estimated maxima of log visual acuity which were used as parameters are as follows:

<table>
<thead>
<tr>
<th>Subject</th>
<th>Normal Air</th>
<th>10.34 per cent O₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. O.</td>
<td>0.461</td>
<td>0.410</td>
</tr>
<tr>
<td>F. B.</td>
<td>0.413</td>
<td>0.383</td>
</tr>
</tbody>
</table>

Fig. 4. Mean data for nine subjects, Table II. The curve derived from the stationary state equation (1) has been superimposed on the two points in normal air. It was then shifted horizontally until it coincided with the one point at log I = 1.159 for each of the other conditions.

The fact that the curve superimposed in this manner on this point in 10.34 per cent oxygen runs precisely through the point at log I = 3.120 as well, leads to the conclusion that there is no appreciable vertical component to the translation which is produced by oxygen deprivation. (See Results, Series 2.)
due to the fact that by the time these measurements were made, the subject was suffering from marked effects of anoxemia, such as headache and vertigo, and it was difficult to obtain his full cooperation. The data for series 2 is more reliable since more determinations at each point were made, and the results for nine subjects are averaged.

The amount of translation of the curve corresponding to the mean values of Table II and estimated from Fig. 4 was 0.24 of a log unit at 14.31 per cent O₂, and 0.47 of a log unit at 10.34 per cent O₂. In Table III are presented the corresponding values for each subject, estimated graphically in a similar manner from the data in Table II. The individual differences of the effects due to anoxia were quite large. Their means correspond to the figures estimated from Fig. 3. The amount of translation of each curve on the log I axis is denoted by Δ log I. The antilog of each Δ log I, therefore, represents the factor by which the illumination corresponding to a given level of visual acuity, in normal air, must be multiplied to obtain an equal acuity during oxygen deprivation.

The standard deviations are computed from the formula $\sigma = \sqrt{\frac{\sum d^2}{n - 1}}$ where $d$ is the deviation of each datum from the mean, and $n$ represents the number of data. The reliability of the differences in Table II was computed by Fisher's (1932) method for unique samples, and is denoted by $P$ which

<table>
<thead>
<tr>
<th>Subject No.</th>
<th>14.31 per cent O₂</th>
<th>10.34 per cent O₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.11</td>
<td>0.33</td>
</tr>
<tr>
<td>2</td>
<td>0.45</td>
<td>0.75</td>
</tr>
<tr>
<td>3</td>
<td>0.37</td>
<td>0.48</td>
</tr>
<tr>
<td>4</td>
<td>0.11</td>
<td>0.24</td>
</tr>
<tr>
<td>5</td>
<td>0.23</td>
<td>0.40</td>
</tr>
<tr>
<td>6</td>
<td>0.17</td>
<td>0.54</td>
</tr>
<tr>
<td>7</td>
<td>0.20</td>
<td>0.33</td>
</tr>
<tr>
<td>8</td>
<td>0.15</td>
<td>0.27</td>
</tr>
<tr>
<td>9</td>
<td>0.36</td>
<td>0.82</td>
</tr>
</tbody>
</table>

Mean ................................ | 0.24             | 0.46             |
Antilog of mean ................... | 1.74             | 2.88             |
Standard deviation of mean ...... | 0.13             | 0.21             |
represents the probability that the observed difference is due to chance. Values of $P$ of 0.05 or less indicate statistically significant differences.

**DISCUSSION**

These data may be fitted by a variety of more or less empirical curves. The stationary state equation, for example, has been shown by Shlaer (1937-38) to fit the data of visual acuity, and it is interesting to compare the data obtained in this experiment with the expectation based on the theory of photoreception (Hecht, 1934). Assuming a photosensitive material $S$ which is changed by light to photoproducts $P$, $A$, $B$ ... and which is reformed again by a thermal reaction of some of these products, the equation was derived as

$$Kx = \frac{x^n}{(a - x)^m}$$

where $I$ is the light intensity, $(a - x)$ and $x$ are the concentration of sensitive material and photoproducts respectively, $m$ and $n$ are constants giving the orders of the photochemical and thermal reactions, and $K$ is a constant. Shlaer found that in the case of visual acuity mediated by cones, $m = n = 2$, with visual acuity taken as proportional to $x^2$ and illumination proportional to $KI$. When these are plotted in the forms of their logarithms, the shape of the curve is independent of the values of $K$ and $a$ which may be assumed, and of the units employed. The value of $K$ merely determines the position of the curve along the intensity axis, while $a$ determines the asymptotic value; the maximum visual acuity corresponds to $a^2$. The equation may also be written as:

$$KI = \frac{V.A.}{(V.A._{max} - V.A.)^3}$$

These experiments suggest that under reduced oxygen tension the same relationship holds between visual acuity and illumination as under normal oxygen tension, the only change being a shift of the curve to the right along the intensity axis which is equivalent to a decrease in the value of $K$ in the above equation. This means that for any given visual acuity the illumination must be greater at a reduced partial pressure of oxygen than with normal air. One might thus consider the effect of anoxia as being equivalent to placing before the eye of the subject a filter, of a density corresponding to the amount the curve shifts. Subjectively most of the observers reported that the appearance of the field at $\log I = 1.159$ while they breathed 10.34 per cent oxygen resembled that at an illumination 0.4
of a log unit lower during the normal air tests. (This was the reason for giving the subjects of series 2 practice periods at the latter intensity.)

As a consequence of the nature of the relationship between visual acuity and illumination as expressed by the curve in logarithmic coordinates, a shift to the right results in a relatively great decrease in visual acuity at low illuminations. It must be remembered that on a logarithmic scale, equal distances between points represent equal proportional differences. The vertical distance between the curves, which represents the change in logarithm of visual acuity, becomes smaller with increasing illumination and becomes negligible at very high illumination. (This fact explains the inconclusiveness of the previously reported experiments on this problem, since they were performed at a level of illumination at which the changes in visual acuity with anoxia are relatively slight.) The average data of series 2 in our experiments show that at an illumination of 0.144 photons the size of the smallest resolvable detail increased at 14.31 per cent O₂ to 1.48 times that with normal air, and at 10.34 per cent O₂ to 2.21 times normal. At an illumination of 1,320 photons, on the other hand, it increased to only 1.06 times normal, even at 10.34 per cent O₂. It is interesting to note that the behavior of these differences is strikingly uniform for each observer; specifically, the logarithm of the ratio of visual acuity in normal air compared to visual acuity under conditions of reduced oxygen is an inverse function of log I, which approaches zero as I is increased indefinitely.

The figures representing the amount of shift of the curve on the intensity axis are of the same order of magnitude as the shift of the dark adaptation curves upward on the log I axis in anoxia, as reported by McFarland and Evans (1939). The data of the two experiments, however, are not strictly comparable. Several conditions were different in the earlier report. White light was used, yielding data which represent largely the behavior of the rods; no artificial pupil was used; and the observations were binocular.

The results of these experiments and their relation to the data of dark adaptation might be interpreted in accordance with Hecht's (1928) explanation of visual acuity and illumination. Visual acuity depends upon the resolving power of the retina which is composed of discrete rods and cones. Its resolving power is therefore dependent upon the number of functional elements in a unit area. The thresholds of these elements are distributed in a statistical manner similar to that of other populations. As the intensity is increased the total number of elements whose threshold is exceeded also increases, and with it the visual acuity, which is thus determined by the integral form of this distribution curve. At the highest illumination all the cones are functional and no further increase in visual acuity is possible.
The elevation of light threshold during dark adaptation in low oxygen may be considered as indicative of a shift of the distribution curve of the thresholds of the visual elements to the right, toward increasing intensity. This would result in a similar shift of its integral curve—which corresponds to the visual acuity curve—along the intensity axis. That the latter does actually occur is shown by the present experiments. Further, the fact that the maximal visual acuity during anoxia, as computed from (2), is the same as that in normal air would follow from the consideration that under both conditions the maximal visual acuity is determined by the total number of cones per unit area, at least in the emmetropic eye.

The studies of Crozier (1937, 1939, 1940) have demonstrated that various visual data can be fitted at least as well by the probability integral of Gauss as by the stationary state equation. In the case of flicker, when $m = n$ and critical fusion frequency ($F$) is proportional to the first power of $x$ in equation (1), this equation is mathematically identical with the Verhulst logistic,

$$x = \frac{a}{1 + e^{-p \log KI}}, \quad \text{or} \quad F = \frac{F_{\text{max}}}{1 + e^{-p \log KI}}$$

in which $p = 1/n$. The shape of this function differs only slightly from the probability integral. In order to determine which fits a set of data more accurately, a large range of very precise data must be available.

In the case of cone visual acuity, which is proportional to the second power of $x$ in equation (1), the goodness of fit of the stationary state equation (1) cannot be tested by plotting the data as per cent of $V.A_{\text{max}}$ on a logistic grid; the relationship is not linear. However, by slightly decreasing the value of the parameter $V.A_{\text{max}}$ and plotting the data as per cent of estimated maximum visual acuity on a probability integral grid, a rectilinear relationship can be obtained. In Fig. 3 we present the data for subjects M. O. and F. B. treated in this manner. It is to be noted that the fit is certainly as good as with the photochemical (stationary state) equation. The slopes (i.e., $1/\sigma_{\text{log} I}$) are equal for M. O., although for F. B. a very slight and probably not significant increase of slope in anoxia was noted. In order to obtain a good linear fit for the low oxygen data of both subjects, a lower estimated maximum visual acuity had to be used as parameter than for the normal air data. The evaluation of this parameter in these data is influenced chiefly by the value of one point, that at the highest illumination. As we have already described (cf. Results), the mean data of nine subjects (in series 2), which were obtained under conditions which permitted more measurements at each intensity and are consequently more
reliable, contradict such a decrease in maximum visual acuity in low oxygen, although this may be obscured by the averaging process.

The fact that our data can be well fitted by the probability integral is consistent with Crozier's (1940) conception of the determination of visual functions by processes in the central nervous system. Indeed, experiments on the effects of anoxia on the light sense (dark adaptation) suggest that the photochemical system is not affected by anoxia (McFarland and Evans, 1939). Some process further back in the visual mechanism, probably involving the nervous mechanisms of the brain and retina, seems to be altered. However, our data are certainly not inconsistent with Hecht's description of the relationship between visual acuity and illumination under constant conditions by means of the photochemical hypothesis.

The changes in visual acuity which were observed in this experiment may be attributed directly to the effects of anoxia for the following reasons. When 100 per cent oxygen was inhaled from a cylinder, through the same breathing equipment but unknown to the subject, normal visual acuity was restored immediately. This occurred at an illumination where the acuity had been severely affected and to a degree which was even somewhat above the acuity while breathing normal air at the beginning of the experiment. Thus, fatigue, the wearing of the mask, and other such factors can be excluded as possible causes of the changes, which were progressive with progressive decrease in oxygen tension. Moreover, although it is well known that anoxia causes psychic disturbances, the changes observed in these experiments are not attributable to a decrease in effort or variation in attention since at the highest illumination, where the test object was smallest and the task consequently most difficult, the changes in visual acuity in each subject were minimal.

The slight improvement of the final control values, compared with the initial tests in normal air, may be attributed to two factors. First, the practice received by the subject in the interval may have resulted in some improvement of his ability to resolve the test object. Second, it is possible that the inhalation of 100 per cent oxygen from a cylinder may result in a slightly higher degree of visual acuity than normal air, although it is an established fact that even under the latter conditions the oxygen saturation of arterial blood is about 95 per cent of its capacity. Rosenthal (1939) has shown that inhalation of 100 per cent oxygen is associated with a contraction of the retinal angioscotomas as compared with normal air, an effect which is in the opposite direction to that caused by anoxia (Evans and McFarland, 1938). This suggests that the slight additional oxygen content of the arterial blood may produce perceptible sensory changes.
FOVEAL VISUAL ACUITY AND LOW OXYGEN TENSION

As a possible practical application of our results, it might be concluded that, as far as foveal visual acuity is concerned, it is much more important that airplane pilots use oxygen during night flights than during daylight flights. Ferree and Rand (1938) have stressed the importance of a high visual acuity in dim illumination for night flying and night driving.

SUMMARY

1. The foveal visual acuity of eleven subjects was studied in relation to illumination under normal atmospheric conditions and at simulated altitudes of 10,000 feet (14.3 per cent O₂) and 18,000 feet (10.3 per cent O₂). A mask was used to administer the desired mixtures of oxygen and nitrogen. At the end of each experiment, measurements were made while inhaling 100 per cent oxygen from a cylinder. A red filter (No. 70 Wratten) was used so as to study only the behavior of the cones of the retina.

2. The logarithm of illumination was plotted horizontally (abscissa) and the logarithm of visual acuity vertically (ordinate). The reduced oxygen tensions resulted in a shift of the curve to the right, along the intensity axis, the extent of the change being 0.24 of a log unit at 14.3 per cent O₂ and 0.47 of a log unit at 10.3 per cent O₂. These effects were completely counteracted within a few minutes by inhaling oxygen.

3. As a consequence of the shape of the curve, such a shift to the right resulted in a relatively large decrease of visual acuity at low illuminations. At increasing light intensities anoxia produced less and less change, until at very high illuminations the decrease was negligible. Thus with 10.34 per cent O₂ the visual acuity at 0.144 photons decreased an average of 0.344 of a log unit, to 45 per cent of its normal value. At 1320 photons, however, it decreased only 0.026 of a log unit, to 94 per cent of its normal value for that intensity.

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