ANOXIA AND BRIGHTNESS DISCRIMINATION*

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I

Nature of Work

It is the commonest of observations both in actual flying and in pressure chamber experiments that lights become dim at high altitudes and then brighten on return to low altitudes. These events are due to the absence and presence of an adequate oxygen supply, as can be shown by their easy elimination when sufficient oxygen is available.

The phenomenon itself has been demonstrated quantitatively as a rise in threshold of the dark-adapted eye during anoxia by McFarland and Evans (1939), by McFarland and Forbes (1940), and by Wald, Harper, Goodman, and Krieger (1942). (Cf. also Bunge, 1936, and Fischer and Jongbloed, 1936.) In addition McFarland and Halperin (1940) found that visual acuity is affected by decreased oxygen tensions.

Brightness discrimination and visual acuity are closely allied visual functions and it is not surprising that Schubert (1932-33) and Gellhorn (1936) detected an influence on brightness discrimination, though they recorded sharply conflicting results. However, McFarland, Halperin, and Niven (1944) have definitely shown that brightness discrimination is impaired by anoxia, and have explored the effect over the significant range of cone vision.

Our own work—completed in 1942 but only now available because of its origins—confirms the findings of McFarland, Halperin, and Niven. Our experiments were made somewhat differently from theirs; theirs cover a greater brightness range, but in most of their work a single low oxygen concentration was compared with room air. We compared seven different oxygen concentrations with room air, at three moderate brightnesses involving cone vision only.

II

Apparatus and Procedure

If $I$ is the light intensity of a uniform field of vision, and $\Delta I$ is the light intensity which needs to be added to a part of this field so that the particular

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shape of the addition may be correctly recognized by an observer, then the fraction \( \Delta I/I \) is a measure of the brightness discrimination of the observer for the prevailing conditions. The larger the fraction \( \Delta I/I \) the greater is the contrast necessary, and the poorer is the brightness discrimination.

In the present experiments the visual field is a large circular area in front of which the observer sits comfortably and becomes adapted to its particular light intensity. By means of a shutter he can project the illuminated image of a broken circle (Landolt Ring or C) on the field for 1/5 of a second. The position of the break in the circle is set by the operator, and it is the task of the subject to discover this position by gradually increasing the brightness of the broken ring.

![Diagram of experimental arrangement](image)

**Fig. 1.** Diagrammatic top view of experimental arrangements. The adapting light \( I \) covers the whole screen; while the added light \( \Delta I \) is in the form of a projected broken circle. Both come from the same lamp, but are separately variable.

The precise arrangements in the dark room may be seen in Fig. 1 which is a diagrammatic top view. The lamp, in a light-tight container, is a 100 watt concentrated filament projection bulb; it is operated through a voltage regulator, and furnishes both the background field illumination \( I \) and the added illumination \( \Delta I \) for the projected C. The background beam, after passing through neutral and color filters, is reflected by a mirror on to the translucent screen composed of a sheet of flashed opal glass and a sheet of ground glass. The background field is 60 cm. in diameter, and since the subject sits 125 cm. in front of it, it subtends a visual angle of 27°.

The added illumination in the form of the Landolt broken ring is projected by two lenses from an opaque slide in which 8 clear rings have been accurately cut, with the break in 8 different positions. The intensity and color of the projected beam is controlled in steps by neutral and color filters, and a neutral wedge and balancer determine the intensity continuously and gradually. The projected Landolt ring subtends 7.5° visual angle, the break being 1.5°. The reason for such a large test object is to place it well over the visual acuity threshold at all illuminations used, and thus confine the study to brightness discrimination alone.
After preliminary experiments we chose three field intensities, approximately 1/1000, 1/100, and 1/10 millilambert, (actually 0.00085, 0.0102, and 0.12 millilambert), thus covering that region of daylight vision in which contrast discrimination varies most rapidly with illumination (Hecht, Peskin, and Patt, 1938). To insure the participation of daylight vision alone even at the lowest intensity, we used red light, secured by inserting Wratten filter No. 29 in both light beams. The light intensities, filters, wedges, etc. were carefully calibrated with the Macbeth illuminometer and a Martens polarization photometer.

Conditions corresponding to high altitudes are achieved by having the subject breathe from tanks containing mixtures of oxygen and nitrogen, whose concentrations vary between 9 and 16 per cent oxygen. The subject breathes through an oxygen-therapy mask, having a 2 liter rubber bag as reservoir. Rebreathing is prevented by a valve between mask and bag, and expiration is through a flutter valve to room air. The rate of flow is controlled by a gauge and varies from 8 to 16 liters a minute, depending on the request of the subject.

After adequate adaptation to the light, five successive determinations of $\Delta I/I$ are usually made with the subject breathing room air without a mask or compressed air from a tank through a mask. A specific oxygen mixture whose concentration is not known by the subject is then supplied to the mask, and an equilibrium period of 15 minutes allowed. Determinations of $\Delta I/I$ are then begun, and continued until five successive measurements show that equilibrium has been reached. This frequently means no more than five or six trials, but occasionally it involves as many as twenty. In succession, various oxygen mixtures are tested in this way, and sometimes the session is concluded with a repetition of room air. We found the latter to agree with the initial reading, and therefore did not make it regularly.

**III**

*Brightness Discrimination*

Seven men and one woman served as subjects. With the exception of S. H. (51 years) their ages were between 17 and 25 years.

The data are given in Table I where for each subject, at each background brightness and each oxygen concentration there is listed the increase in log $\Delta I/I$ required as compared to the room air performance. For easy understanding, the significant aspects of the measurements are shown graphically in Fig. 2. It presents the relation between oxygen concentration and the percentage increase in the contrast fraction $\Delta I/I$ as compared to room air. It is apparent that at all three background illuminations, decreasing the oxygen concentration causes a rapidly accelerated increase in the amount of contrast difference which can just be recognized. Thus at lower oxygen tensions increasingly larger brightness differences between surfaces become necessary before they can be seen as different.

Three aspects of this visual impairment are to be noted. The first relates to altitude. The altitudes corresponding to the oxygen mixtures used in the
experiments have been calculated\(^1\) and are shown in Fig. 2. From this it is apparent that for these brightnesses the deterioration of contrast discrimination begins at fairly low altitudes, and is definite at 8,000 feet. At 15,000 feet elevation, deterioration is marked, especially at the lowest brightness where a contrast must be twice as great as at sea level before it can be recognized. Evidently for achieving maximum visual capacities at these illuminations, it is necessary to supplement with oxygen the air breathed by those flying at even moderate altitudes.

Second, a given increase in altitude causes a greater impairment in contrast recognition at high altitudes than at lower ones. Thus, in going from 12,000 to 15,000 feet the increase in brightness difference required for contrast recognition is twice as great as that in going from 6,000 to 9,000 feet. Above 15,000 feet there is indication of a somewhat less rapid deterioration of brightness discrimination. This may be due to compensation by the body for the anoxia.

\(^1\) In the computations, proper consideration was given to the saturation of the inspired gas mixture with water vapor, a factor which has occasionally been neglected.

### TABLE I

<table>
<thead>
<tr>
<th>Background intensity log (I)</th>
<th>Oxygen breathed</th>
<th>Increment in (\Delta I/I) over room air for</th>
</tr>
</thead>
<tbody>
<tr>
<td>-3.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.6</td>
<td>0.00 0.01</td>
<td>0.04 0.00 0.08 0.01 0.05 0.12 0.038</td>
</tr>
<tr>
<td>14.8</td>
<td>0.16 0.07</td>
<td>-0.01 0.03 0.13 0.17 0.11 0.15 0.106</td>
</tr>
<tr>
<td>13.2</td>
<td>0.12 0.02</td>
<td>0.09 0.14 0.17 0.24 0.20 0.10 0.126</td>
</tr>
<tr>
<td>12.1</td>
<td>0.36 0.15</td>
<td>0.19 0.25 0.22 0.33 0.30 0.21 0.267</td>
</tr>
<tr>
<td>11.2</td>
<td>0.32 0.15</td>
<td>0.24 0.20 0.40 0.33 0.51 0.25 0.302</td>
</tr>
<tr>
<td>10.3</td>
<td>0.35 0.14</td>
<td>0.17 0.19 0.24 0.24 0.98 0.36 0.333</td>
</tr>
<tr>
<td>-1.99</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.6</td>
<td>0.00 0.07</td>
<td>-0.02 0.05 -0.03 0.02 0.00 0.02 0.013</td>
</tr>
<tr>
<td>14.9</td>
<td>0.06 0.07</td>
<td>0.03 0.04 0.16 0.03 0.01 0.03 0.042</td>
</tr>
<tr>
<td>13.2</td>
<td>0.15 0.07</td>
<td>0.06 0.11 0.17 0.27 0.00 0.12 0.119</td>
</tr>
<tr>
<td>12.2</td>
<td>0.13 0.09</td>
<td>0.14 0.16 0.20 0.27 0.33 0.15 0.184</td>
</tr>
<tr>
<td>11.1</td>
<td>0.21 0.08</td>
<td>0.11 0.29 0.21 0.32 0.48 0.07 0.220</td>
</tr>
<tr>
<td>10.3</td>
<td>0.27 0.19</td>
<td>0.14 0.30 0.27 0.32 0.34 0.24 0.260</td>
</tr>
<tr>
<td>-0.92</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.5</td>
<td>0.11 0.02</td>
<td>0.01 0.00 0.00 0.00 0.03 -0.01 0.020</td>
</tr>
<tr>
<td>14.9</td>
<td>0.05 0.04</td>
<td>0.05 0.07 0.01 0.07 0.08 0.04 0.051</td>
</tr>
<tr>
<td>13.2</td>
<td>0.12 0.09</td>
<td>0.07 0.06 0.08 0.09 0.03 0.10 0.080</td>
</tr>
<tr>
<td>12.2</td>
<td>0.17 0.08</td>
<td>0.10 0.16 0.09 0.23 0.09 0.04 0.120</td>
</tr>
<tr>
<td>11.1</td>
<td>0.28 0.15</td>
<td>0.13 0.20 0.12 0.13 0.09 0.04 0.142</td>
</tr>
<tr>
<td>10.3</td>
<td>0.37 0.17</td>
<td>0.17 0.24 0.22 0.23 0.40 0.20 0.250</td>
</tr>
</tbody>
</table>
Third, though the deterioration in brightness discrimination occurs at all three light intensities, the effect decreases as the illumination increases. The brightnesses included in the data cover most of the intensity range within which contrast discrimination varies. They represent the appearance of objects after sunset, and between dawn and sunrise. For a brightness ten times greater than our highest the deterioration is small but definite, whereas at still higher levels it is negligible. The two dotted curves in Fig. 2 are extrapolations from the measurements (cf. section V) and show what would be expected at higher intensities of 1 and 10 millilamberts; these expectations have been realized by McFarland, Halperin, and Niven.
Threshold after Dark Adaptation

Several groups of measurements have been reported on the effect of anoxia on the final dark-adapted threshold of the eye (McFarland and Evans, 1939; McDonald and Adler, 1939; and Wald, Harper, Goodman, and Krieger, 1942). We made similar tests first, to see whether our oxygen mixtures would give comparable results; and second, to compare the effect of anoxia on the dark-adapted cone threshold with that on the rod threshold.

TABLE II
Anoxia and Thresholds after Complete Dark Adaptation

The absolute values at room air are given in parentheses in the first line. The other values are the increments in log \( I \) compared to room air.

<table>
<thead>
<tr>
<th>Oxygen breathed per cent</th>
<th>Increase over room air in threshold intensity, log ( I ), micromicrolamberts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>With violet filter (rod)</td>
</tr>
<tr>
<td></td>
<td>S.F.</td>
</tr>
<tr>
<td>21.0</td>
<td>(3.01)</td>
</tr>
<tr>
<td>16.4</td>
<td>0.00</td>
</tr>
<tr>
<td>14.9</td>
<td>0.12</td>
</tr>
<tr>
<td>13.2</td>
<td>0.18</td>
</tr>
<tr>
<td>12.2</td>
<td>0.35</td>
</tr>
<tr>
<td>11.1</td>
<td>0.20</td>
</tr>
<tr>
<td>10.6</td>
<td>0.30</td>
</tr>
<tr>
<td>9.4</td>
<td>—</td>
</tr>
</tbody>
</table>

For two subjects the thresholds of the completely dark-adapted eye were measured with the Hecht-Shlaer adaptometer (Hecht and Shlaer, 1938). The Corning 511 violet filter was used for the rod threshold; and either the Wratten 88 or 29 red filter for the cone threshold.

The individual measurements are given in Table II. The data refer to a circular 3° retinal field situated 7° nasally. The averages are shown in Fig. 3, which includes as well the results of previous investigators.

From this comparison it follows that our measurements correspond to those of previous workers about as well as they agree with one another. Moreover, it appears that within the limits of experimental error, cone and rod thresholds are affected equally by low oxygen concentrations.

The effects on the absolute cone threshold are slightly larger than for the contrast threshold at the lowest brightness shown in Fig. 2. This is in keeping
with the general trend of the measurements that visual deterioration is more evident at lower than at higher illuminations.

V

Contrast Discrimination, Final Thresholds, and Anoxia

It is possible to show that the quantitative effects of anoxia on contrast discrimination are intimately related to the effects on the final dark-adapted thresholds reported in the preceding section. To bring this out we need to recognize the well established relation between light intensity and contrast discrimination.

For convenience in showing the data in Table I and Fig. 2, we presented the changes in the contrast fraction $\Delta I/I$ during anoxia relative to the normal values in room air. The actual numerical magnitudes of $\Delta I/I$ in room air for eight subjects are given in Table III, so that from them the numerical values may be derived for all other altitudes in Table I for each subject.

Our interest here lies only in the average results, and in Fig. 4 these are plotted against the background intensities. Through the data has been drawn the theoretical curve for the dependence of the intensity discrimination, $\Delta I/I$,
on the light intensity, \( I \) (Hecht, 1935). It is to the point that McFarland, Halperin, and Niven (1944) found their measurements, which cover a greater range of illuminations than ours, to be described with fine precision by this same theoretical equation.

We have shown in the preceding section that the cone threshold is increased during anoxia. What this means is that the top of the curve in Fig. 4 is shifted to the right to higher and higher intensity levels. It is reasonable to suppose that not merely the top of the curve, but the curve as a whole is

<table>
<thead>
<tr>
<th>Background intensity ( \log I )</th>
<th>log ( \Delta I/I ) for</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \text{millilamberts} )</td>
<td>( \text{S.H.} )</td>
</tr>
<tr>
<td>(-3.07)</td>
<td>(-0.29)</td>
</tr>
<tr>
<td>(-1.99)</td>
<td>(-1.07)</td>
</tr>
<tr>
<td>(-0.92)</td>
<td>(-1.70)</td>
</tr>
</tbody>
</table>

**TABLE III**

Contrast Discrimination in Room Air

**Fig. 4.** The relation between just perceptible contrast \( \Delta I/I \) and the prevailing \( I \). The curves are theoretical and are from equation (9). The effect of altitude (or oxygen lack) is merely to translate the curve along the abscissas.
shifted and that this is the basic visual effect of anoxia. Such a shift of the whole visual function along the intensity axis has already been found by McFarland and Halperin for visual acuity, and by McFarland, Halperin, and Niven for brightness discrimination. In fact, they were able to show that for a given oxygen concentration the intensity shift for brightness discrimination is exactly the same size as the shift in cone threshold during dark adaptation.

In Fig. 4 we have drawn these shifted curves for three altitudes, using the average threshold measurements of Fig. 3. It is apparent that though the horizontal intensity distance is the same between any two curves, the vertical distance becomes less as the intensity increases. In other words, though anoxia actually affects the whole intensity discrimination function at all levels, the effect is considerably more apparent at lower intensities than at high.

One can find the precise horizontal displacement of the curves from the measurements of contrast discrimination themselves. The data in Table I and in Fig. 2 give the vertical displacement of the \( \Delta I/I \) curves at different oxygen concentrations for the three light intensities. These vertical displacements can be converted into horizontal displacements by dividing the vertical increment at any intensity by the slope of the curve at that particular intensity. On a large scale plot of Fig. 4 we measured the slopes of the curve at the three experimental intensities. They are 0.752, 0.588, and 0.465 going from the low to the high intensity.

For each oxygen concentration we have in Table I a vertical displacement at each intensity. Dividing each displacement by the appropriate slope, and averaging the three we get the horizontal displacement for each oxygen concentration. These averages are given in Table IV and thus form the basic description of the effect of oxygen lack on brightness discrimination. From them one can determine the horizontal shift of the \( \Delta I/I \) curve for any altitude, after which one can then easily determine the vertical shift in order to get the change in \( \Delta I/I \) at any value of the intensity. Note that in Table IV the hori-

---

### Table IV

<table>
<thead>
<tr>
<th>Oxygen concentration (per cent)</th>
<th>Shift in ( \log I )</th>
</tr>
</thead>
<tbody>
<tr>
<td>21.0</td>
<td>0.000</td>
</tr>
<tr>
<td>16.6</td>
<td>0.037</td>
</tr>
<tr>
<td>14.8</td>
<td>0.107</td>
</tr>
<tr>
<td>13.2</td>
<td>0.181</td>
</tr>
<tr>
<td>12.1</td>
<td>0.309</td>
</tr>
<tr>
<td>11.1</td>
<td>0.360</td>
</tr>
<tr>
<td>10.3</td>
<td>0.474</td>
</tr>
</tbody>
</table>
zontal shift for 11.1 per cent oxygen is 0.360 log unit. This agrees well enough with the value of 0.356 log unit for 10.8 per cent oxygen found by McFarland, Halperin, and Niven to serve as independent corroboration of the measurements.

VI

Oxygen Lack and Retinal Chemistry

The dislocation of the visual system during oxygen lack is most likely an indication of the similar impairment of many other parts of the nervous system. Indeed it has been the common supposition (Gellhorn, 1942) that the changes in visual function are merely an index of the impairment of the central nervous system. While this may be true, it has not been established; and there are some indications that the retina itself may be the seat of the anoxic changes shown in vision.

One such sign is the high oxygen requirement of the retina. The rat retina consumes 31 c. mm. O₂ per mg. per hour. This is the highest rate of oxygen consumption of any tissue recorded by Warburg (1927), the nearest competitor being kidney with an oxygen consumption of 21 c. mm. per mg. per hour.

A related piece of evidence is that when flyers are subjected to centrifugal forces several times gravity they become temporarily blind before they become unconscious. It is thus likely that the retina is more sensitive to oxygen lack than the cortex. Actually Craik and Vernon (1941) have shown that the visual threshold can be changed markedly merely by cutting off the oxygen supply to the retina.

Whether the effects of anoxia on the retina depend on the impairment of its specifically nervous elements like bipolar and ganglion cells, or of the rods and cones themselves cannot now be decided. Any consideration of the effect of anoxia, however, needs to begin with the theoretical formulation of visual chemistry which has served as an accurate description of brightness discrimination, visual acuity, and other visual phenomena (Hecht, 1937).

We start with two established facts. One is that the rods contain a light-sensitive substance, visual purple, and the cones contain a similar substance, visual violet, both of which absorb light and are changed chemically by it. The other fact is that these photosensitive substances are constantly replenished, probably by the combination of some of their photoproducts with additional materials like vitamin A supplied by the retina and ultimately by the circulation.

Let the concentration of photosensitive material in the cones in the dark be a. Let a-x be its concentration at the intensity I after the eye has become adapted to the light; therefore x is the concentration of photoproducts formed
which remain in the cones to be used for the regeneration of the sensitive material. The rate of photochemical change is

$$\frac{dx}{dt} = k_1(a - x)^m$$

(1)

where $k_1$ is the combined absorption and velocity constant and $m$ represents the order of the reaction, and may be 1, 2, etc. The rate of regeneration from the photoproducts is

$$-\frac{dx}{dt} = k_2x^n$$

(2)

where $k_2$ is a velocity constant and $n$ is the order of the reaction. At light adaptation to the intensity $I$ the two rates become equal, and a photostationary state is reached. Setting equation (1) equal to equation (2) and solving for $I$, we get

$$k_1 I / k_2 = x^n / (a - x)^m$$

(3)

which represents the relations between light intensity and the concentrations of photosensitive substance and photoproducts at the stationary state.

The photostationary state during light adaptation appears superficially like an equilibrium, in that its components remain constant. However, it is not a true equilibrium because it can be maintained only by the continuous addition of light. Without the light, the back-reaction would at once increase the concentration of sensitive material. And without the back-reaction the light would destroy all the photosensitive material and vision would disappear. The balance between the action of light and the regeneration reaction insures a steady concentration of sensitive material which thus absorbs light at a regular pace and converts it into chemical action at a rate set by $k_1 I (a - x)^m$, so that we continue to see the light as long as it shines.

Equation (3) of the photostationary state in the retina has served as a quantitative description for a variety of visual functions as they vary with the adapting intensity of the light. Intensity discrimination, visual acuity, flicker perception, instantaneous threshold, all vary in a similar way with brightness and all fall into a comparable pattern when expressed as functions of concentration at the stationary state (Hecht, 1937).

In setting up equations (1) and (2) we introduced the fewest components required for quantitative description and explanation. The result is that equation (3) involves light intensity and concentration with only the most necessary constants to connect them with known chemical and physical laws. However, in making visual experiments one does not measure concentrations of sensitive materials; instead, one has to measure some physiological property like brightness discrimination or visual acuity which is the expression of nerve impulses resulting from the chemical transformation of the sensitive pigments.
by light. Therefore there is needed an explicit formulation for the conversion of photochemically effective light into magnitude of visual function. In the past this relation has usually been assumed as one-to-one and has been implicitly included in the constant $k_1$. This procedure has been adequate because the physiological conditions of the organism as a whole have been maintained constant during such measurements, and therefore the relation between chemical change and physiological magnitude has been assumed constant.

The situation during oxygen deficiency, however, demands a more explicit recognition of this relation because there is every likelihood that the physiological conditions inside the organism are changed, and the magnitude of the change may well affect the transformation of chemical change into physiological function. Let us still assume a simple relation between the two but let us merely designate a factor for it. Let the conversion of chemically effective light into visual function be governed by the factor $\alpha$. This factor must then be included in equations (1) and (3) whenever these represent visual properties rather than merely concentrations. The simplest meaning to attach to $\alpha$ is that of a linear conversion factor from light absorbed to number of impulses leaving the particular sense organ, or ultimately reaching the cortex. One may then write

$$\frac{di}{dt} = \alpha \frac{dx}{dt} = \alpha k_1 I(a-x)^m$$ \hspace{1cm} (1a)

as representing the rate of impulse production $i$ during the stationary state, or more generally the magnitude of any physiological counterpart of the photochemical change. In the same visual terms the stationary state equation becomes

$$\frac{ak_1 I}{k_2} = \frac{x^m}{(a-x)^m}.$$ \hspace{1cm} (3a)

Under normal physiological conditions the conversion factor $\alpha$ is constant and merges with $k_1$ to form one constant. But under changed physiological conditions such as oxygen deficiency $\alpha$ is bound to change, even though both $k_1$ and $k_2$ probably remain constant. With lack of oxygen the conversion factor is surely smaller than normal, and $\alpha$ decreases. Thus the same chemical change $k_1 I(a-x)^m$ will produce less visual effect when multiplied by a smaller $\alpha$, which is why light appears dimmer under diminished oxygen.

Let us now add light to a part of the visual field to which the eye is adapted. The intensity which needs to be added before its presence is recognized as extra brightness is $\Delta I$. The increase in photochemical change produced by this added light $\Delta I$ is $dx/dt = k_2 \Delta I(a-x)^m$; but since we are interested in the final visual effect we must include the conversion factor $\alpha$ and consider

$$\frac{di}{dt} = \alpha k_1 \Delta I(a-x)^m$$ \hspace{1cm} (4)

as describing the burst of impulses produced by the added light and photochemical change.
Suppose that we recognize an increase in brightness when the number of impulses leaving the retina (or reaching the cortex) is increased by a constant amount \( c \). This makes equation (4) equal to \( c \) and yields

\[
\Delta I = \frac{c}{\alpha k_l(a - x)^m}
\]

on solving for \( \Delta I \). Similarly in (3a) one can solve for \( I \) and get

\[
I = \frac{k_2 x^n}{\alpha b(a - x)^n}
\]

and as a result derive \( \Delta I/I \) by dividing (5) by (6). This yields

\[
\frac{\Delta I}{I} = \frac{c}{k_2 a^n}
\]

from which \( x \) can be eliminated only in terms of equation (3a) when \( m \) and \( n \) are given specific values. Previous work (Hecht, 1937) has shown that for cone vision both \( m \) and \( n \) equal 2. As a result, equation (3a) yields

\[
x = \frac{a}{1 + 1/(\alpha K I)^{1/2}}
\]

where \( K = k_l/k_2 \) for convenience. If we now substitute this value of \( x \) from (8) into (7) we get

\[
\frac{\Delta I}{I} = C \left[ 1 + \frac{1}{(\alpha K I)^{1/2}} \right]^g
\]

where \( C = c/\alpha^2 k_2 \).

Under constant physiological conditions the conversion factor \( \alpha \) is constant and cannot be separated from the combined constant \( K \) which is merely the ratio \( k_l/k_2 \). Therefore the relation between \( \Delta I/I \) and the brightness \( I \) should be described by equation (9) with or without \( \alpha \); and as a matter of history, that equation does fit all brightness discrimination data from the earliest by Aubert (1865) to the most recent by McFarland, Halperin, and Niven (1944).

When equation (9) is plotted on a double logarithmic grid as in Fig. 4 the shape of its curve is constant and independent of the parameters \( C \), and \( \alpha K \). These merely locate the position of the curve on the axes: \( C \) on the ordinates and \( \alpha K \) on the abscissas. The measurements in Fig. 4 as well as those of McFarland, Halperin, and Niven show that oxygen lack does not change the shape of the curve, nor does it change its position on the ordinates. This means that \( C \) remains unchanged. But oxygen lack does displace the curve to higher intensities, which means that either \( \alpha \) or \( K \) is altered.

The constant \( C \) stands for \( c/\alpha^2 k_2 \), and since \( C \) is not altered by oxygen lack, its components are also not altered, unless we make the extremely unlikely assumption that the change in the numerator is balanced by a precisely similar change in the denominator. The data, however, say that either \( \alpha \) or \( K \) or both
are altered, and become smaller the lower the oxygen concentration. The constant $K$ equals $k_1/k_2$, and we have just seen that $k_2$ is unaltered. It is also very unlikely that $k_1$ is altered by oxygen lack, because $k_1$ has the dimensions of light absorption (Hecht, 1924) and does not change with temperature or oxygen (Hecht, 1921; Bruner and Kleinau, 1936; Chase and Hagan, 1943). Therefore $K$ is probably uninfluenced by lack of oxygen, and leaves the conversion factor $\alpha$ as the only parameter to be changed under the circumstances.

This seems sensible because the conversion probably involves the action of bipolar and ganglion cells which are sensitive to oxygen lack.

From the measurements one can find precisely how $\alpha$ varies with oxygen concentration. Table IV gives the horizontal displacement along the log $I$ axis which the curves suffer at different oxygen concentrations. According to equation (9) a constant $\Delta I/I$ requires $\alpha K I$ to be constant. Since oxygen lack shifts the curve, and thus increases $I$, this means that $\alpha$ varies inversely with the intensity increment. If we assume that $\alpha$ is 1 at sea level, we can compute its value for any other oxygen concentration from the numbers in Table IV by remembering that log $\alpha$ will be 0 minus the increase in log $I$ for that oxygen concentration.
The computed values of α are shown in Fig. 5 against the oxygen concentration. The relation between the two seems reasonable; the curve is steep at low oxygen concentrations and flattens off at normal oxygen values of air at sea level. The shape of the curve is reminiscent of the upper part of the oxygen saturation curve of blood. Its vertical extent, however, is much greater than the saturation curve for the same oxygen concentrations.

There is actually a simple relation between α (or its equivalent, the shift in light intensity) and the arterial saturation at different oxygen concentrations. From Chart B3 of the Handbook of respiratory data in aviation we have taken the average arterial saturation corresponding to the oxygen concentrations used in our experiments. In Fig. 6 these arterial saturations are plotted as abscissas against the intensity shift of the ΔI/I curve, both on a log scale. The straight line through the points has a slope of 4, which means that the log I shift or its equivalent α varies as the fourth power of the arterial saturation. Considerably more knowledge about oxygen action will be necessary before such a fourth power relation can have meaning but its presence indicates that relatively slight changes in oxygen saturation produce large changes in vision.

SUMMARY

1. Brightness discrimination has been studied with individuals breathing oxygen concentrations corresponding to 7 altitudes between sea level and 17,000 feet. The brightnesses were 0.1, 0.01, and 0.001 millilambert involving only daylight (cone) vision.

2. At these light intensities, brightness discrimination begins to deteriorate at fairly low altitudes. The deterioration is obvious at 8,000 feet, and becomes marked at 15,000 feet, where at low brightness, the contrast must be increased 100 per cent over the sea level value before it can be recognized.

3. The impairment of brightness discrimination with increase in altitude is greater at higher altitudes than at lower. The impairment starts slowly and becomes increasingly rapid the higher the altitude.

4. Impairment of brightness discrimination varies inversely with the light intensity. It is most evident under the lowest light intensities studied, but

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*Added in proof. The essentials of these ideas were communicated by letter to Dr. R. A. McFarland and have been so reported in a recent paper by McFarland, Halperin, and Niven on Visual thresholds as an index of physiological imbalance during insulin hypoglycemia (Am. J. Physiol., 1946, 145, 299). Apparently insulin hypoglycemia affects brightness discrimination much as does anoxia, and our formulation of the basis for the shift of the ΔI/I curve along the log I axis holds for this as well as for anoxia.
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shows in all of them. However, it decreases in such a way that the deterioration is negligible in full daylight and sunlight.

5. The thresholds of night (rod) vision and day (cone) vision are equally affected by anoxia.

6. The quantitative form of the relation between brightness discrimination $\Delta I/I$ and the prevailing brightness $I$ remains the same at all oxygen concentrations. The curve merely shifts along the log $I$ axis, and the extent of the shift indicates the visual deterioration.

7. The data are described in terms of retinal chemistry. Since anoxia causes only a shift in log $I$ it is shown that the photochemical receptor system cannot be affected. Instead the conversion of photochemical change into visual function is impaired in such a way that the conversion factor varies as the fourth power of the arterial oxygen saturation.

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