Different Visual Deprivations Produce Different Ametropias and Different Eye Shapes

Michael D. Gottlieb, Lisa A. Fugate-Wentzek,* and Josh Wallman

To compare the effects on the postnatal development of the eye of both total and partial form deprivation in diurnally reared chicks and of dark-rearing, chicks were reared with occluders covering one eye from hatching for up to 6 weeks. In diurnally reared birds, both total and partial form deprivation resulted in severe axial myopia and increased eye size. These effects were greatest for the eyes of chicks raised with total form deprivation; they had highly curved corneas and very deep anterior and vitreous chambers. In addition, the amount of myopia produced in eyes with total form deprivation was the same at 2 and 6 weeks, whereas eyes with partial form deprivation showed substantial remission even with the occluders left on. The partially deprived eyes developed a striking shape asymmetry: the posterior globe only became enlarged in the deprived region of the retina. The eyes of dark-reared chicks, regardless of whether or not an occluder was worn, also were enlarged but were hyperopic owing to a severe flattening of the cornea. This hyperopia was slow to develop compared to the myopia produced in the diurnally reared visually restricted eyes. Finally, the shape of the posterior globe of these hyperopic eyes was no different from that of normal eyes. Invest Ophthalmol Vis Sci 28:1225-1235, 1987

In humans, there is evidence that various ocular pathologies in childhood lead to myopia. For example, congenital cataract, lens opacity, soft tissue swelling of periorbital structures, hemangioma of the eyelid and orbit, and retinitis pigmentosa have all been linked to myopia. These conditions have in common an interference with form vision. In studies of ptotic eyes, in which the amount of form vision varies over a considerable range, an increased incidence of myopia is apparent in some investigations but not in others.

While these data from retrospective studies in humans do not prove that the interference with form vision in childhood causes myopia, animal studies indicate that it is the obstruction of form vision and not the physical effect of eyelid closure that produces myopia. For example, in monkeys, total deprivation of form vision by both lid-suture and corneal opacification results in myopia, whereas lid-sutured monkeys reared in the dark do not develop myopia. Similarly, in tree shrews, chickens, and sometimes cats, the interference with form vision by either lid-suture or devices worn over the eye results in myopia. Furthermore, both total and partial deprivation of form vision produces myopia in chicks.

In contrast to the usual association of myopia with visual deprivation, a recent study reported hyperopia in humans in connection with albinism, maculopathies, and rod monochromasy. No doubt these conditions also interfere with form vision, but in a different way. In animal studies too, a different kind of form deprivation, dark-rearing, results in hyperopia in several species. Dark-rearing also protects against the myopia characteristically induced by form deprivation in diurnally reared animals. In chicks, rearing in continuous light as well results in abnormal ocular growth.

In an effort to bring together the results of several studies that have reported ametropias and abnormal eye growth as a consequence of different visual deprivations, we systematically compared the effects of both total and partial deprivation of form vision and
of dark-rearing on refractive status and eye growth in chicks.

A preliminary report of these findings has been presented.22

Materials and Methods

Subjects and Treatments

White Leghorn chicks (Gallus gallus domesticus) were hatched in our laboratory (eggs obtained from Shamrock Poultry Farms, NJ) and raised in temperature controlled brooders under fluorescent lights on a 14:10 hr light:dark cycle (diurnally reared) or in complete darkness (dark-reared). The diurnally reared chicks were raised with one eye either totally deprived of form vision (no-form-vision eyes) or partially deprived of form vision (frontal-vision eyes). The no-form-vision eyes had a white translucent plastic hemisphere (occluder) glued to the feathers surrounding the eye.26 The frontal-vision eyes had a segment from the anterior portion of the occluder removed (Fig. 1, ref. 10); this allowed for unrestricted vision extending horizontally from the front of the head up to approximately 10° anterior to the optic axis. As a result, the nasal retina of these frontal-vision eyes was deprived of form vision. In both groups, the untreated fellow eyes served as controls (normal vision eyes). Treatments started at hatching and lasted for 14, 28, or 42 days. Food (Purina Startena Crumbles, Purina Mills, St. Louis, MO) and water were available ad libitum.

Similarly, dark-reared chicks had either a total or partial occluder over one eye from hatching for 14 or 42 days. In addition to the water and food readily available, these chicks were force-fed, three to four times daily for 1 week, a mash consisting of water and food (pulverized Purina Startena Crumbles). This procedure resulted in a developmental pattern of weight gain for dark-reared chicks that was not significantly different from that for normal chicks. Without force-feeding, dark-reared chicks grew more slowly than normal chicks and had a higher mortality rate. The dark-reared chicks were exposed briefly to a very dim red light during maintenance. The treatment and care of animals in this study was in accordance with the ARVO Resolution on the Use of Animals in Research.

Measurements

In vivo: At the end of each treatment, chicks were anesthetized with chloral hydrate/sodium pentobarbital (Chloropent, Fort Dodge, Albany, NY, approximately 3.3 cc/kg) or 40% urethane (approximately 5 cc/kg), after receiving approximately 0.4 mg of atropine sulfate to reduce salivary secretions. To obtain
of a dissecting microscope or from photographic negatives of the eyes projected onto a digitizing tablet that was interfaced to a computer. The averages of two measures of axial length (one from a top view and one from a side view) and two measures of equatorial diameter (nastotemporal and dorsoventral) were obtained for each eye.

The shape of each eye was assessed by tracing its contour from a projected photographic negative (top view). Each tracing was digitized, and a computer was programmed to calculate the midpoint of a line connecting the nasal and temporal margins of the cornea and the length of "radii" from this midpoint to the back of the eye at 2° intervals. For purposes of averaging within each treatment group, eyes were aligned with one another such that these midpoints coincided and the lines joining the corneal margins were colinear. To permit the averaging of right and left eyes, the data from the left eyes were reversed; thus, our figures present all eyes as right eyes.

**Results**

**Refractions**

The eyes of visually deprived diurnally reared chicks were more myopic than normal eyes (Fig. 1, Mann-Whitney, $P < .01$). The no-form-vision eyes were most severely myopic, having median refractive errors of $-31 \text{ D}$, $-30 \text{ D}$, and $-27 \text{ D}$ after 14, 28, and 42 days of treatment, respectively. The frontal-vision eyes were also myopic, but less so, having median refractive errors of $-14 \text{ D}$, $-11 \text{ D}$, and $-7 \text{ D}$ after 14, 28, and 42 days of treatment, respectively.

The eyes of visually deprived diurnally reared chicks were more variable than normal eyes in refractive error (Fig. 1; F-tests for homogeneity of variance, $P < .01$). Thus, these treatments not only changed the median refractive error but also the shape of the distribution. The variability in refractive error decreased for all groups of diurnally reared chicks from 14 to 42 days.

In diurnally reared chicks, frontal-vision and no-form-vision eyes differed with respect to the retention of myopia with age (Fig. 2). The frontal-vision eyes showed a significant remission in myopia with age (medians: $-14 \text{ D}$ at 2 weeks to $-7 \text{ D}$ at 6 weeks, Mann-Whitney, $P < .01$) whereas no-form-vision eyes did not ($-31 \text{ D}$ to $-27 \text{ D}$ from 2 to 6 weeks, Mann-Whitney, $P > .05$).

In the dark, partially and totally occluded eyes did not become severely myopic (Fig. 1). At 14 days, the unoccluded and partially occluded eyes of dark-reared chicks were each no different from normal eyes of the same age (Mann-Whitney, $P > .05$) while the totally occluded eyes of dark-reared chicks were only slightly myopic compared to normal eyes ($-0.60 \text{ D}$ vs $+3.4 \text{ D}$, Mann-Whitney, $P < .01$). Taken together, the eyes of 14-day-old dark-reared chicks were no different from normal eyes ($+1.6 \text{ D}$ vs $+3.4 \text{ D}$, Mann-Whitney, $P > .05$).

**Fig. 1.** Distributions of the refractive errors in diopters (D) for eyes after 14 (left panel), 28 (middle panel), and 42 (right panel) days of treatment. The arrows indicate the medians. Note the greater variability in refractive error for experimental eyes as compared to normal eyes. The no-form-vision, frontal-vision, and normal-vision eyes were from diurnally-reared chicks.
respectively, Mann-Whitney, \( P > .05 \)). Had we looked only at this age, we would have concluded that dark-rearing protects against the severe myopia characterized by total and partial occluders in diurnally reared chicks. However, by 42 days, the eyes of dark-reared chicks (combined data) were hyperopic compared to normal eyes (+6.1 D vs +3.0 D, respectively, Mann-Whitney, \( P < .01 \)). (In subsequent analyses, we combined the data for the different groups of dark-reared chicks at each age, because these groups did not differ from each other on any of our measurements.)

As Figure 1 shows, the eyes of dark-reared chicks had the greatest variability in refractive error. Even at 14 days, when the median refractive error was not significantly different from that for normal eyes, the eyes of dark-reared chicks were significantly more variable (F-test, \( P < .01 \)); the variability at 42 days was greater still (F-test, \( P < .01 \)).

The hyperopia of dark-reared chicks was slow to develop and became more severe over the period studied (+1.6 D to +6.1 D from 14 to 42 days, Mann-Whitney, \( P < .01 \)).

Eye Size

**Volume:** The eyes of visually deprived diurnally-reared chicks and the eyes of dark-reared chicks became enlarged compared to normal eyes (Table 1). After 14 days, no-form-vision and frontal-vision eyes were 25% and 31% larger, respectively, than normal eyes (Mann-Whitney, \( P < .01 \)). Only the eyes of dark-reared chicks did not differ from normal eyes at 14 days with respect to volume. After 42 days of treatment, all experimental eyes were significantly larger than normal eyes of the same age (Mann-Whitney, \( P < .01 \)). The no-form-vision eyes were the largest, 52% larger than normal eyes, frontal-vision

Table 1. Volume, equatorial diameter, and radius of corneal curvature [mean ± SD (N)]

<table>
<thead>
<tr>
<th></th>
<th>Diurnally reared</th>
<th>Dark-reared</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Normal vision</td>
<td>Frontal vision</td>
</tr>
<tr>
<td>Volume (ml)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 days</td>
<td>.59 ± .08 (25)</td>
<td>.77 ± .09 (7)</td>
</tr>
<tr>
<td>42 days</td>
<td>1.17 ± .12 (21)</td>
<td>1.49 ± .19 (8)</td>
</tr>
<tr>
<td>Equatorial diameter (mm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 days</td>
<td>11.86 ± .41 (27)</td>
<td>12.38 ± .54 (14)</td>
</tr>
<tr>
<td>42 days</td>
<td>14.65 ± .46 (28)</td>
<td>15.80 ± .67 (14)</td>
</tr>
<tr>
<td>Corneal curvature (mm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 days</td>
<td>3.18 ± .09 (45)</td>
<td>3.05 ± .16 (23)</td>
</tr>
<tr>
<td>28 days</td>
<td>3.65 ± .07 (10)</td>
<td>3.49 ± .14 (10)</td>
</tr>
<tr>
<td>42 days</td>
<td>3.97 ± .10 (27)</td>
<td>3.88 ± .14 (14)</td>
</tr>
</tbody>
</table>
Table 2. Ultrasound measurements (mm) [mean ± SD (N)]

<table>
<thead>
<tr>
<th></th>
<th>Diurnally reared</th>
<th>Dark-reared</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Normal vision</td>
<td>Frontal vision</td>
</tr>
<tr>
<td>Axial length</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 days</td>
<td>8.70 ± 0.27 (43)</td>
<td>9.89 ± 0.48 (22)</td>
</tr>
<tr>
<td>28 days</td>
<td>10.09 ± 0.22 (22)</td>
<td>11.52 ± 0.62 (13)</td>
</tr>
<tr>
<td>42 days</td>
<td>10.98 ± 0.40 (27)</td>
<td>12.73 ± 0.91 (12)</td>
</tr>
<tr>
<td>Anterior chamber depth</td>
<td>1.21 ± 0.08 (43)</td>
<td>1.42 ± 0.24 (22)</td>
</tr>
<tr>
<td>28 days</td>
<td>1.50 ± 0.06 (22)</td>
<td>1.78 ± 0.24 (13)</td>
</tr>
<tr>
<td>42 days</td>
<td>1.70 ± 0.15 (27)</td>
<td>1.97 ± 0.52 (12)</td>
</tr>
<tr>
<td>Lens thickness</td>
<td>2.34 ± 0.08 (43)</td>
<td>2.35 ± 0.09 (22)</td>
</tr>
<tr>
<td>28 days</td>
<td>2.70 ± 0.08 (22)</td>
<td>2.72 ± 0.10 (13)</td>
</tr>
<tr>
<td>42 days</td>
<td>2.95 ± 0.14 (27)</td>
<td>2.92 ± 0.12 (12)</td>
</tr>
<tr>
<td>Vitreous chamber depth</td>
<td>5.15 ± 0.23 (43)</td>
<td>6.12 ± 0.36 (22)</td>
</tr>
<tr>
<td>28 days</td>
<td>5.88 ± 0.17 (22)</td>
<td>7.01 ± 0.42 (13)</td>
</tr>
<tr>
<td>42 days</td>
<td>6.33 ± 0.31 (27)</td>
<td>7.85 ± 0.65 (12)</td>
</tr>
</tbody>
</table>

eyes were 27% larger, and the eyes of dark-reared chicks were 28% larger. Thus, both hyperopic and myopic eyes were abnormally enlarged after 42 days of treatment.

Axial length: The axial lengths of no-form-vision and frontal-vision eyes at 14 and 42 days and of the eyes of dark-reared chicks at 42 days were abnormally large (Table 2). At 14 days, eyes with no form vision were 20% longer and those with frontal vision were 14% longer than normal eyes (Mann-Whitney, P < .01). At 28 days, no-form-vision and frontal-vision eyes were 26% and 14% longer, respectively, than normal eyes (Mann-Whitney, P < .01). At 42 days, no-form-vision and frontal-vision eyes were 30% and 16% longer, respectively, than normal eyes (Mann-Whitney, P < .01). The temporal pattern of growth also differed in these two groups: frontal-vision eyes maintained approximately the same degree of elongation at each age vis-à-vis normal eyes (14%, 14%, and 16% longer at 2, 4, and 6 weeks, respectively), whereas no-form-vision eyes became increasingly longer from 14 to 42 days (20%, 26%, and 30% longer at 2, 4, and 6 weeks, respectively). This progressive increase resulted from deepening of the anterior chamber in no-form-vision eyes. The eyes of dark-reared chicks, on the other hand, were the same length as normal eyes at 14 days and were only slightly longer (5%) than normal eyes at 42 days (Mann-Whitney, P < .01). The absence of axial elongation after 14 days of dark-rearing and the small amount after 42 days apparently result from the relatively small increase in anterior chamber depth posthatching (see below).

Vitreous chamber depth: Table 2 shows that eyes in all experimental groups had vitreous chambers that were significantly longer (range 8%–34%) than normal at each age (Mann-Whitney, P < .01). The eyes of no-form-vision chicks always displayed the deepest vitreous chambers, followed by frontal-vision eyes, and eyes of chicks reared in darkness.

Equatorial diameter: The eyes of visually deprived diurnally reared chicks and the eyes of dark-reared chicks exhibited wider than normal equatorial diameters; however, these increases were more modest than those observed for axial length (Table 1). At 14 days, no-form-vision and frontal-vision eyes were each 4% wider than the eyes of normal chicks (Mann-Whitney, P < .01). At 42 days, no-form-vision and frontal-vision eyes were 12% and 8% wider, respectively than normal eyes (Mann-Whitney, P < .01). This increase in equatorial diameter for dark-reared eyes at 14 days contrasts with the lack of a significant increase in axial length during this same period.

Anterior chamber depth: The visually deprived eyes of diurnally reared chicks had deeper than normal
Fig. 3. Anterior chamber depth as a proportion of axial length for each group of eyes as a function of the duration of treatment. The data points are means and the error bars indicate ±1 SEM. The no-form-vision, frontal-vision, and light-reared controls were eyes from diurnally reared chicks. Dark-Reared, all eyes of dark-reared chicks.

If anterior chamber depth is expressed as a proportion of axial length, the same general relationships are seen (Fig. 3). In eyes with no form vision, the anterior chamber grew faster than the eye as a whole and comprised a greater proportion of axial length than in any other condition. This ratio increased from 16% to 21% from 14 to 42 days (Mann-Whitney, P < .01). In contrast, frontal-vision eyes had the same proportion of axial length accounted for by the anterior chamber as normal eyes. In the eyes of dark-reared chicks, the proportion of axial length accounted for by anterior chamber depth decreased from 11% at 14 days to 10% at 42 days (Mann-Whitney, P < .01).

Corneal curvature: Like anterior chamber depth, corneal curvature changes were opposite for no-form-vision and dark-reared chicks (Table 1). The eyes of no-form-vision chicks differed from all other eyes in having corneas that were noticeably more curved (decreased radius of curvature). The corneal curvature for both no-form-vision and frontal-vision eyes was greater than that for normal eyes at all ages sampled (Mann-Whitney, P < .01), although the effect for frontal-vision eyes was less marked. Quite the opposite was true for the corneas of dark-reared chicks, which were flatter than normal at all ages sampled (Mann-Whitney, P < .01).

Lens thickness: Visual deprivation in diurnally reared chicks had no effect on lens thickness (Table 2). Dark-rearing, on the other hand, resulted in a relatively small (approximately 6% and 8% at 14 and 42 days, respectively) but significant reduction in lens thickness as compared to normal eyes (Mann-Whitney, P < .01).
ent from normal eyes, Mann-Whitney, \( P < .01 \)). The frontal-vision eyes were also more elongated than normal eyes at each age, but less so (Mann-Whitney, \( P < .01 \)). Although the eyes of dark-reared chicks had ratios that were slightly greater than those for normal eyes at 2 weeks (Mann-Whitney, \( P < .01 \)), by 6 weeks they did not differ from normal eyes.

Finally, the overall shape of eyes subjected to different treatments was examined. Figure 5 illustrates the dramatic differences in the shape of the posterior globe for the different types of visual deprivation at 42 days. The frontal-vision eyes were strikingly asymmetric, exhibiting a bulge in the posterior globe corresponding to the region of the retina that was deprived of form vision (nasal retina). The part of the frontal-vision eye that had normal vision was essentially the same size as a normal eye. These observations were confirmed statistically by comparing the radii (see Materials and Methods) at 30° to either side of the optic axis for frontal-vision and normal eyes. In the frontal-vision eyes (\( N = 9 \)), the deprived nasal retina was 10% longer than the non-deprived temporal retina (Wilcoxon, \( P < .05 \)) while in the normal eyes (\( N = 9 \)) the difference was less than 2% and not statistically significant (Wilcoxon, \( P > .05 \)). In contrast, the posterior globe of no-form-vision eyes and the eyes of dark-reared chicks was symmetrically enlarged on either side of the optic axis.

**Discussion**

The three different visual deprivations studied here resulted in major differences in refractive status, eye size and eye shape. The no-form-vision eyes have the largest volumes, axial lengths, and the most myopic refractive errors; they have the most highly curved corneas and deepest anterior chambers, even relative to axial length, and their shape is most elongated. Finally, the myopia is essentially stable with age. The frontal-vision eyes are also axially myopic; they display less obvious anterior segment effects, and their myopia remits with age. The frontal-vision eyes exhibit dramatic local shape changes in the posterior globe. The eyes of dark-reared chicks are also enlarged but have markedly shallow anterior chambers, flattened corneas, and slightly thinner lenses; they are...
not different from normal eyes in the shape of the posterior globe.

**Differences in Eye Shape**

The most dramatic difference between no-form-vision and frontal-vision eyes was in their shapes. The frontal-vision eyes exhibited a bulge in the posterior globe in the area overlying the visually deprived retina. We view this shape change as being made up of two components. The first is a general enhancement of ocular growth during restricted vision, especially in the axial direction; the second is a specific restraining of growth in those regions of the retina that have normal vision. The less severe myopia and axial elongation observed in the frontal-vision eyes could be due to the fact that the axis along which both refractive error and axial length were measured was located at the boundary between the visually experienced and visually deprived parts of the retina. We have evidence that in frontal-vision eyes, the visually deprived nasal retina is more myopic than the retina along the optic axis, and the visually experienced temporal retina is hardly myopic at all. Furthermore, selective deprivation of either the nasal or temporal retina results in elongation and myopia only in the deprived region. These findings imply a local control of the growth of different parts of the posterior globe of the eye.

Our results confirm the suggestion of Hodos and Kuenzel that the pattern of eye growth is influenced by visual experience. In our study, compared to frontal-vision eyes, no-form-vision eyes exhibited greater ratios of axial length to equatorial diameter and became increasingly elongated as long as they were completely deprived of form vision. In contrast, in a similar study, Hodos and Kuenzel found a relative flattening in chick eyes subjected to visual degradation. In eyes subjected to total field image degradation, equatorial diameter increased more than axial length, the opposite of the pattern reported here. Perhaps this difference arises from the fact that their occluders distorted form vision, whereas ours eliminated it.

**Fig. 5.** Averaged outlines of eyes from the different experimental treatments. Dashed lines indicate experimental eyes. Solid lines indicate untreated fellow eyes, except in the case of the eyes of dark-reared chicks, where the solid line is the diurnally reared control eyes. Number of eyes in each group from top to bottom is 9, 18, and 9, respectively. Note, in the frontal-vision eyes, the bulge in the nasal sclera corresponding to the region of the retina that was deprived of form vision. All of these eyes are from 6-week-old animals. The figure presents all eyes as right eyes. Note the increased corneal curvature in the no-form-vision eyes and the decreased corneal curvature in the eyes of dark-reared chicks. The no-form-vision and frontal-vision eyes were from diurnally reared chicks.
Differences in Refractive Status

With respect to the greater severity of myopia induced in no-form-vision than in frontal-vision eyes, our results are consistent with those of Hodos et al. who produced myopia (assessed by an electroretinographic method of ocular refraction) with devices that degraded rather than prevented form vision. In their work too, whole visual field interference produced a more severe myopia than partial field interference. The overall degree of myopia was less than that found in the present study, possibly because most of their devices had spontaneously detached by the time of measurement, some as much as 20 days earlier. These factors may well have made their results more variable, since chicks recover quickly from myopia if occluders are removed before 6 weeks of age.

We have shown a greater persistence of myopia in no-form-vision than in frontal-vision eyes when the occluders are left on. Preliminary results from our laboratory indicate that if the occluders are removed, the no-form-vision eyes of diurnally reared chicks show less recovery than frontal-vision eyes.

Differences in Anterior Chamber Depth

Visual restriction in diurnally reared birds and dark-rearing had opposite effects on the anterior chamber. The no-form-vision eyes showed deepening of the anterior chamber, both absolutely and as a proportion of total axial length, whereas dark-reared animals, in our study and those of others, displayed shallower than normal anterior chambers, even though their eyes too were enlarged. Chicks reared in continuous light also have shallow anterior chambers.

These findings suggest to us the possibility that the lack of a daily photoperiod may be involved in producing shallow anterior chambers by disrupting normal circadian rhythms. In support of this possibility are preliminary findings from an experiment in our laboratory designed to reduce the effect of light deprivation on circadian rhythms. In this study, chicks were raised in the dark except for 2 min a day of light distributed in 4 sec pulses every 30 min during the 14-hr “day.” In addition, a radio played only during the “day.” The anterior chambers of these animals were considerably less shallow than those of chicks reared in continuous darkness. We suspect that it was not the 2 min/day of light, per se, that was effective in maintaining normal anterior chamber depth but that for these animals the light and sound were adequate Zeitgebers to maintain normal circadian rhythms.

Our suspicion that dark-rearing and continuous light-rearing are similar, by virtue of their both interfering with normal circadian rhythms, is further reinforced by our data and calculations by us from the data of others showing that the ratio of axial length to equatorial diameter decreases in both dark-reared and continuous light-reared chicks. Likewise, there is little change from normal in the ratio of posterior globe axial length to equatorial diameter as a consequence of rearing either in continuous light or darkness, in agreement with our results.

The possibility exists that the greatly enlarged anterior chambers in the diurnally reared totally restricted eyes were due to factors other than form deprivation, since there are substantial non-visual concomitants of wearing occluders. Without evaporation, an occluded eye most likely experiences an elevation in temperature and humidity. (We often found a buildup of fluid in the immediate vicinity of the cornea upon removal of a total occluder.) In addition, occluders probably compromise the diffusion of atmospheric oxygen to the corneal epithelium. In humans, the mean level of oxygen at the corneal surface beneath closed eyelids in air falls to about 7.7%. The fact that no-form-vision eyes suffer from these non-visual factors to a greater degree than frontal-vision eyes might account for the more extreme anterior chamber effects in the no-form-vision eyes. Still other non-visual factors may account for lid-sutured eyes in chicks having flatter corneas and thicker lenses relative to normal eyes.

Effects of Dark-Rearing

Dark-rearing appears to protect against the severe myopia characteristically induced in diurnally reared chicks with occluders, a finding that is consistent with studies on monkeys. However, we found that longer periods of dark-rearing produced hyperopia, apparently because the corneal flattening exerts a greater effect than the increase in vitreous chamber depth. Hyperopia has also been reported in dark-reared monkeys, cats, and chicks.

We speculate that two mechanisms may be at work in the dark-reared animals: one, responsive to the visual deprivation, causes the eye to enlarge; another, perhaps responsive to the lack of a daily photoperiod, causes the cornea to flatten. At 2 weeks of age, these two effects just balance each other so that the eyes are approximately emmetropic.

The eyes of dark-reared chicks have been described by others as heavier, shallower in anterior chamber, yet longer axially. In addition, we found, as did another recent study, that the eyes of dark-reared chicks have flatter corneas, thinner lenses, and are wider equatorially relative to the eyes of normal chicks. Despite these changes, our eye tracings and ratios of posterior globe axial length to equatorial di-
ameter show that there is no change in the shape of the posterior globe of the eyes of dark-reared chicks. In conclusion, the results of these several deprivations argue that the elimination of form vision interferes with the regulation of normal ocular growth. They further suggest to us the possibility that there exists a local growth-regulatory mechanism that is dependent on pattern vision to produce emmetropia. This mechanism may operate at the level of the retina, since in eyes of diurnally reared chicks that are partially deprived of form vision, the elongation of the posterior globe characteristic of axial myopia is restricted to the visually deprived region of the eye. The fact that dark-rearing and partial or total form deprivation in diurnally reared chicks are associated with a distinct pattern of change in refractive error, eye size and eye shape clearly indicates that a number of separate ocular growth processes must normally be coordinated to produce emmetropic refractions. Understanding how vision influences these processes may well be a key to understanding normal ocular growth.

Key words: chickens, dark-rearing, eyes, hyperopia, myopia, refractive error

Acknowledgments

We thank David Troilo for his critical reading of the manuscript and Gertrude Fisher for her help in preparing the figures.

References


Erratum
Page 930, second column, second line from top, should read as follows: “By 3 months, denervated eyes were becoming less supersensitive to PILO and response to ES was returning. Six months to one year or more after denervation, most of the denervated eyes were indistinguishable from their fellow control eyes in their accommodative responses to both PILO and to ES (Fig. 3).”