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Differences in Eye Growth and the Response to Visual Deprivation in Different Strains of Chicken

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Several laboratories studying visual deprivation myopia in the domestic chick report varying degrees of axial elongation and myopia induced by similar visual deprivation techniques. In this study we tested the hypothesis that in different strains of chick the eyes respond differently to visual deprivation. We compared under identical conditions two strains of White Leghorn chick commonly used in ocular development research—the Cornell-K strain (K) and Washington H & N Strain (H/N). The normal development of the eye was found to vary significantly between these strains of White Leghorn chicks. The K strain normally develops flatter corneas, thicker lenses, and larger eyes than the H/N strain. The response to visual deprivation also varies significantly between strains. For example, we find that 2 weeks of visual deprivation in the K strain results in less elongation of the vitreous chamber and flattening of the cornea yielding lower levels of induced myopia compared to the H/N strain. Our results show that while visual experience clearly affects normal ocular development in both strains of chick, the nature of the effect depends upon not only the type and duration of the experience but the genetics of the subject population as well.

Chicken Eye growth Experimental myopia Refraction

INTRODUCTION

Many investigations concerning the development of refractive state and myopia have used the domestic chicken as experimental subjects (e.g. Gottlieb, Fugate-Wentzek & Wallman, 1987; Hodos & Kuenzel, 1984; Irving, Callender & Sivak, 1991; Lauber & Oishi, 1987; Miles & Wallman, 1990; Oishi, Lauber & Vriend, 1987; Pickett-Seltner, Weerheim, Sivak & Pasternak, 1987; Rohrer, Spira & Stell, 1993; Schaeffel & Howland, 1991; Sivak, Barrie, Callender, Doughty, Seltner & West, 1990; Stone, Lin, Laties & Iuvone, 1989; Troilo & Wallman, 1991; Wallman, Gottlieb, Rajaram & Fugate-Wentzek, 1987; Yinon, Koslowe, Lobel, Landshman & Barishak, 1982/83). Deprivation of form vision by a variety of methods consistently disrupts the normal development of the eye and results in significant ocular enlargement and myopia. There are, however, considerable differences in the magnitude of the effects obtained in different laboratories using similar visual manipulations on White Leghorn chickens (for examples see Fig. 1). In this study we asked whether these differences are primarily the result of different rearing, experimental and measurement techniques, or whether they might be due to the use of different strains of White Leghorn chicken.

There are several breeds of Leghorn chicken stemming from a southern European ancestry. The White Leghorn breed is the most commonly used in today's egg industry, and includes many different strains. Commercial breeders typically develop and maintain several of their own highly inbred strains for traits such as egg quality, productivity, and resistance to disease. These strains are crossed and back-crossed to produce chickens optimized for egg production and resistance to disease.

We compared under identical conditions the normal growth of the eye and the development of visual deprivation myopia in two different strains of White Leghorn chick currently used in developmental eye research. The Cornell-K strain is a very pure strain developed for resistance to lymphoid leukemia and Mareck's disease (Cole & Hutt, 1973). The other strain used is a hybrid developed for egg production at the Heisdorf and Nelson farms (Washington), and was obtained from Truslow Hatcheries (Maryland).

METHODS

111 chicks from the Cornell-K strain (K) and 25 chicks from the Heisdorf and Nelson hybrid (H/N) were used. K strain chicks were obtained locally from Cornell's

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poultry science development. One-day-old H/N chicks were transported overnight from Truslow Hatcheries in Maryland. Subjects from both strains were housed under identical conditions starting at 2 days of age. Illumination was provided on a 12 hr light/dark cycle using a combination of fluorescent and incandescent lamps. The average ambient illumination in the room was 700 lx. Brooders were fitted with transparent plexiglas tops to allow full illumination.

Form vision was blocked in one eye of each subject with a white translucent plastic occluder glued around the eye with collodion (Wallman, LeDoux & Friedman, 1978a; Wallman, Turkel & Trachtman, 1978b). The contralateral eye remained untreated and served as a paired control. Strain effects (K or H/N) on the response to visual deprivation were tested in four different experimental groups based on the type of deprivation (full or partial visual field deprivation) and its duration (2 or 4 weeks). In the "partial" group the visual deprivation was restricted to the lateral visual field leaving normal form vision in the frontal visual field. In the "full" group the entire visual field was occluded from view. Chicks were raised with the occluders in place for either 2 or 4 weeks. The experimental eyes were measured at the time of occluder removal. The untreated control eyes were measured at 2, 4, 5, and 7 weeks of age.

Infrared (IR) video-retinoscopy, IR video-keratometry, and a-scan ultrasonography were used to measure refractive state, corneal curvature, and the axial dimensions of the eye respectively (for details see Schaeffel, Farkas & Howland, 1987; Schaeffel & Howland, 1987; Troilo & Wallman, 1991). For each eye 3–5 readings of each measure were made and averaged. All eyes were measured in fully conscious birds without cycloplegia. Corneal curvatures are given as radii of curvature; a larger radius indicates a flatter cornea. Where experimental–control differences (x–c: control value subtracted from experimental value) are given, a negative value indicates a more curved experimental cornea and a positive value indicates a flatter experimental cornea.

Strain differences during normal ocular development were examined using a two-factor ANOVA on strain and age. Significant differences between strains over time were further examined using *post-hoc* t-tests with a Bonferroni adjustment.

Within an individual strain, the effect of a visual deprivation condition was examined by testing the differences between the experimental and control eyes using paired t-tests. Strain differences in the induced change in refractive state, vitreous chamber depth, and corneal radius of curvature within a visual deprivation treatment group were examined using two-sample t-tests where t-values and degrees of freedom were adjusted for unequal sample sizes by using the separate variances of the two groups (Brownlee, 1965). From knowledge of the refractive state we could predict the direction of change in ocular morphology and, therefore, used one-tailed significance levels for vitreous chamber depth and corneal radius of curvature comparisons.

RESULTS

Differences in normal development

The development of the untreated control eyes of the K and H/N strains of White Leghorn differ significantly in several respects (Figs 2 and 3). The largest and most consistent difference is that the K strain develops significantly flatter corneas than the H/N strain by 4 weeks of age [Fig. 2(c); two-factor ANOVA, $P < 0.01$]. The eyes of K strain are also significantly longer, have deeper vitreous chambers, and thicker lenses (Fig. 3; two-factor ANOVAs, $P < 0.01$). Body weight, refractive state, and anterior chamber depth do not differ between the strains across the ages examined.

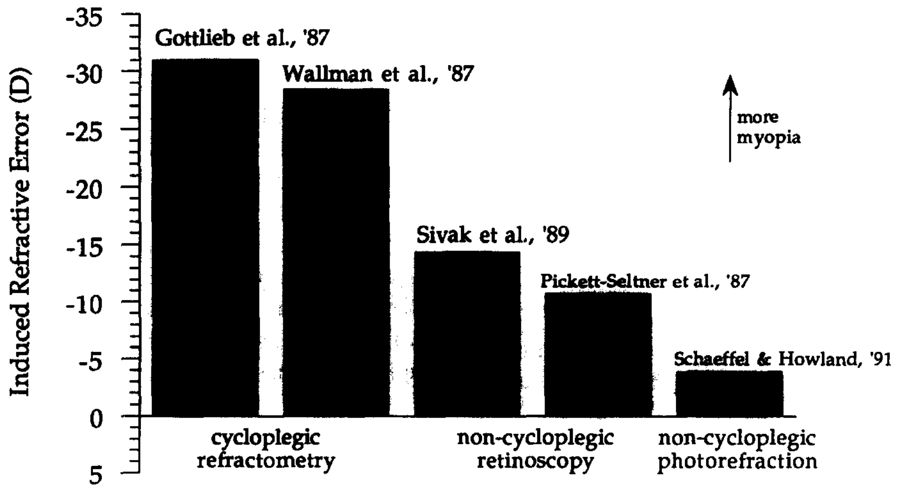

FIGURE 1. Different studies using White Leghorn chicks report varying degrees of myopia produced by similar visual deprivation techniques. Except for Schaeffel and Howland (1991), who used the Cornell-K strain, the strains of White Leghorn used were not reported. In each of these studies visual deprivation took place from hatching to 2 weeks of age. The techniques used to measure the induced refractive changes are indicated below each bar. Cycloplegia would reduce any apparent myopia due to accommodation, and its use does not explain the observed differences. There are also no obvious reasons why the different measures of refractive state used should bias the reported results.

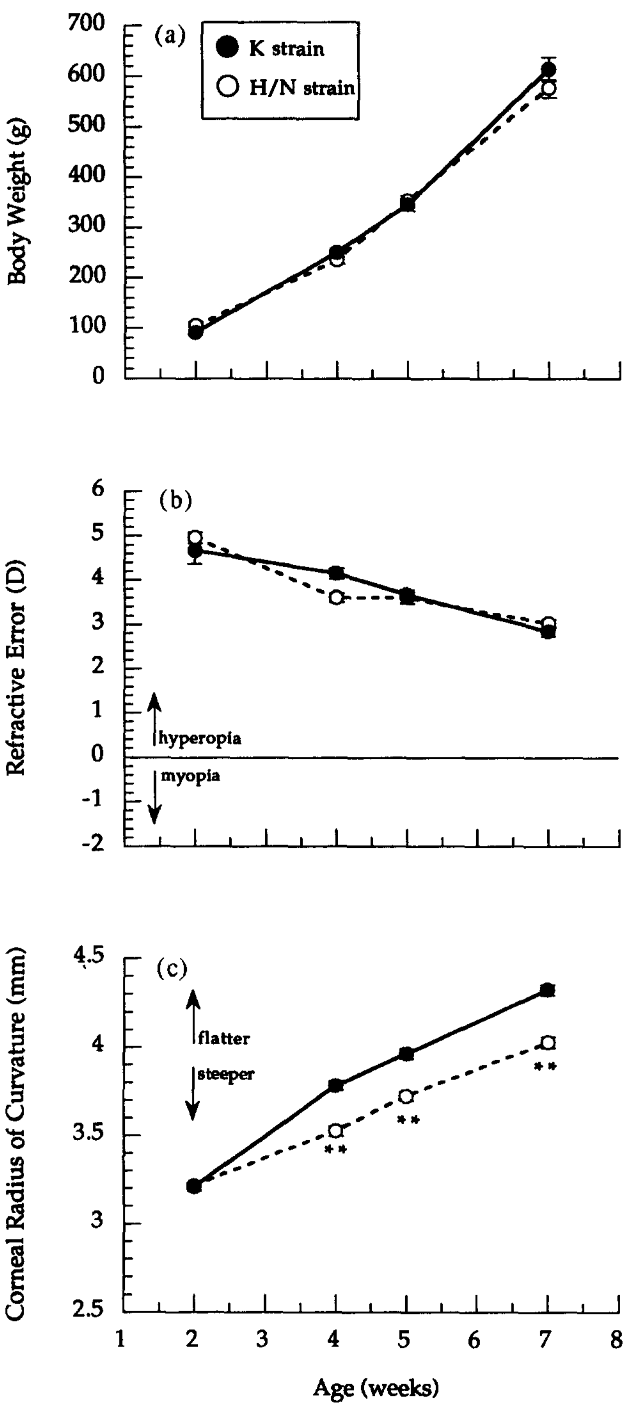

FIGURE 2. Comparison of the normal postnatal development of K and H/N strains of White Leghorn chick. Solid circles represent mean values for K strain, open circles for H/N strain. Standard errors are smaller than the symbol unless indicated. Here, and in Fig. 3, the statistical analysis was a two-factor ANOVA with *post hoc* t-tests and Bonferroni adjustment. Double asterisks indicate significance at $P<0.01$. (a) Change in weight; (b) change in refractive error; (c) development of corneal radius of curvature. The corneas of K strain chicks normally become flatter relative to H/N strain by 4 weeks of age.

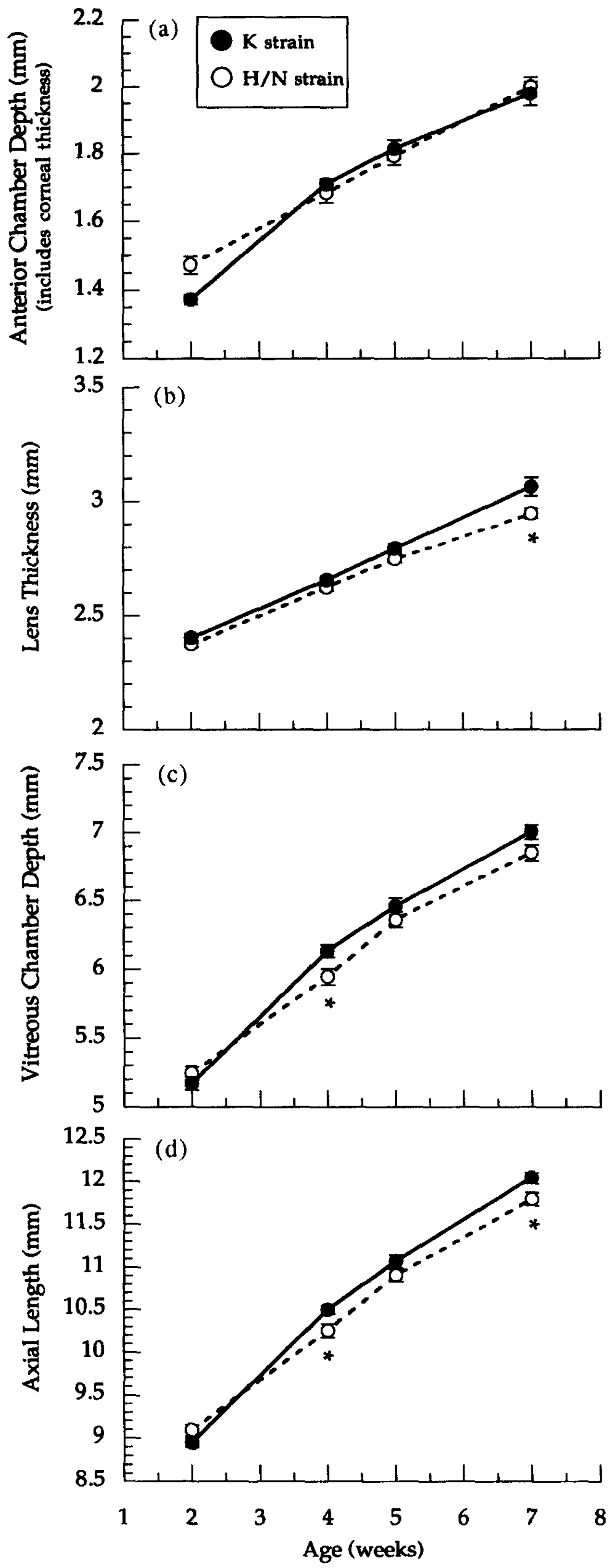

FIGURE 3. Normal development of ocular axial dimensions measured by a-scan ultrasound. There were significant differences between strains in the normal development of lens thickness, vitreous chamber depth, and axial length. The conventions and statistical analysis used here are the same as in Fig. 2. Single asterisks indicate significance of *post hoc* t-tests at $P<0.05$.

Differences in response to visual deprivation

Table 1 gives the means and standard deviations for all measures on experimental and control eyes by age and group. We did not find any strain differences in the effects of visual deprivation on either anterior chamber depth or lens thickness. There were, however, significant strain

TABLE 1. Mean values [±SD (*n*)] of refractive state, radius of corneal curvature, and axial ultrasonography measures for H/N and K strains after either 2 or 4 weeks of full or partial visual field deprivation

	Refractive error (D)		Corneal radius of curvature (mm)		Anterior chamber (mm)		Lens thickness (mm)		Vitreous chamber (mm)	
	E	C	E	C	E	C	E	C	E	C
2 weeks										
H/N-full	−16.8±4.6 (5)	5.0±0.45 (5)	3.16±0.13 (5)	3.19±0.01 (5)	1.53±0.23 (5)	1.42±0.09 (5)	2.39±0.05 (5)	2.36±0.11 (5)	6.42±0.60 (5)	5.2±0.20 (5)
K-full	−3.1±7.6 (19)	3.7±1.4 (19)	3.27±0.19 (29)	3.13±0.16 (29)	1.25±0.20 (26)	1.36±0.10 (26)	2.36±0.07 (26)	2.38±0.08 (26)	6.22±0.34 (26)	5.25±0.18 (26)
H/N partial	−13.8±6.2 (6)	4.9±0.5 (6)	3.26±0.11 (6)	3.23±0.07 (6)	1.49±0.13 (6)	1.52±0.05 (6)	2.36±0.05 (6)	2.39±0.07 (6)	6.20±0.41 (6)	5.28±0.15 (6)
K-partial	−6.1±6.1 (26)	4.4±0.8 (26)	3.15±0.12 (41)	3.15±0.09 (41)	1.32±0.16 (27)	1.30±0.10 (27)	2.36±0.10 (27)	2.39±0.07 (27)	5.77±0.26 (27)	5.19±0.18 (27)
4 weeks										
H/N-full	−18.5±8.0 (9)	3.5±0.3 (9)	3.64±0.20 (9)	3.52±0.11 (9)	1.63±0.19 (9)	1.68±0.06 (9)	2.60±0.08 (9)	2.55±0.13 (9)	8.06±0.44 (9)	5.94±0.17 (9)
K-full	−16.2±15.0 (12)	3.2±1.3 (12)	3.81±0.34 (16)	3.69±0.12 (16)	1.70±0.59 (33)	1.71±0.08 (33)	2.66±0.09 (33)	2.69±0.09 (33)	7.74±0.51 (35)	6.12±0.26 (35)
H/N-partial	−5.5±5.5 (5)	3.4±0.3 (5)	3.49±0.15 (5)	3.53±0.12 (5)	1.65±0.13 (5)	1.62±0.17 (5)	2.66±0.04 (5)	2.60±0.10 (5)	6.28±0.36 (5)	5.83±0.32 (5)
K-partial	−15.8±2.6 (6)	4.3±0.26 (6)	3.62±0.17 (6)	3.79±0.07 (6)	1.93±0.15 (6)	1.71±0.09 (6)	2.67±0.07 (6)	2.67±0.05 (6)	7.17±0.33 (6)	6.17±0.20 (6)

E = experimental; C = control.

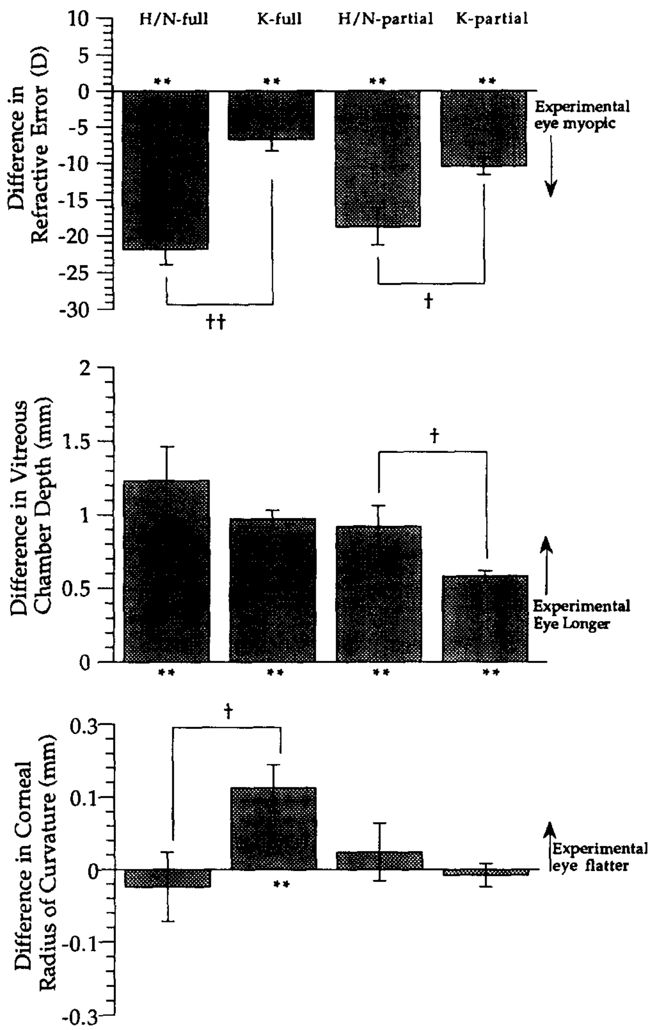

FIGURE 4. Bars indicate the mean difference between experimental and control eyes (x–c) in refractive error, vitreous chamber depth, and corneal radius of curvature, for both strains (K & H/N) and both deprivations (full & partial) after 2 weeks. Error bars represent standard errors. Paired *t*-tests were used to examine differences between experimental and control eyes within a group. Significance at $P<0.01$ is indicated by double asterisks. Differences between strains for a given deprivation condition were tested by independent two-sample *t*-tests adjusted for different sample sizes. Double daggers show significance at $P<0.01$. Single daggers show significance at $P<0.05$.

differences in the effects of visual deprivation on refractive state, corneal radius of curvature, and vitreous chamber depth. In all chicks raised with either full or partial visual field deprivation we find that vitreous chamber depth (VC, in mm) together with corneal radius of curvature (CC, in mm) are excellent predictors of refractive state (RE, in D) (multiple regression: $RE = 14.5 + 26.1\,(CC) - 12.7\,(VC)$; $r = 0.817$, $P<0.01$). Our analyses shown below are, therefore, restricted to these parameters. Figures 4 and 5 compare the mean values of the differences between the experimental and control eyes separated by strain, visual deprivation, and duration.

After 2 weeks of either full or partial visual deprivation, there were considerable differences between strains in the relative (x–c) effects on refractive state, vitreous chamber depth, and corneal radius of curvature (Fig. 4). Full deprivation of the visual field for 2 weeks results in significantly less myopia in the K strain compared to the H & N strain (x–c difference, K vs H/N: −6.74 vs −21.80 D; $t=-5.67$, d.f. = 8.8, $P<0.001$). This is apparently due to significantly flattening of the cornea in the K strain but not in the H/N strain (x–c difference in radius of curvature: 0.14 vs −0.03 mm; $t=-2.32$, d.f. = 8.0, one-tailed $P<0.025$). There is no significant difference in vitreous chamber elongation between strains (0.97 vs 1.23 mm, $t=1.09$, d.f. = 4.5, one-tailed $P=0.165$).

Partial deprivation restricted to the lateral visual field also results in less myopia in the K strain (−10.46 vs −18.75 D; $t=-2.94$, d.f. = 7.2, $P<0.02$). The lower myopia in this case, however, is due to significantly less vitreous chamber enlargement in partially deprived K strain eyes (0.58 vs 0.92 mm; $t=2.39$, d.f. = 5.7, one-tailed $P<0.03$). There is no significant strain difference in corneal radius of curvature after partial deprivation (−0.01 vs 0.03; $t=0.68$, d.f. = 6.0, one-tailed $P=0.26$).

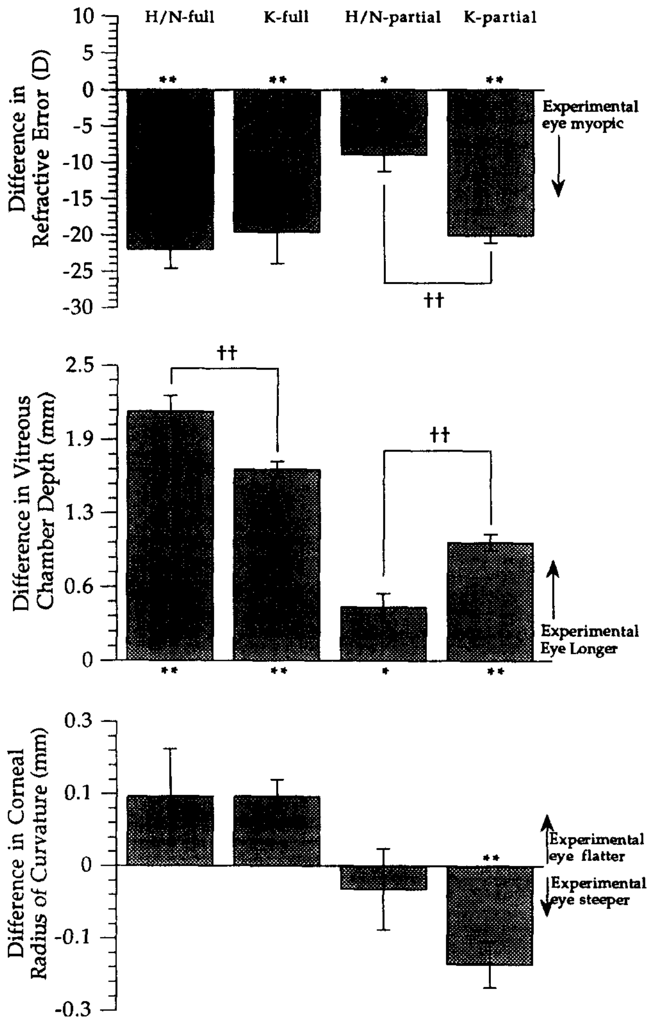

FIGURE 5. Bars indicate the mean difference between experimental and control eyes (x–c) in refractive error, vitreous chamber depth, and corneal radius of curvature, for both strains (K & H/N) and both deprivations (full & partial) after 4 weeks. The conventions and statistical tests are the same as in Fig. 4. A significant difference between experimental and control eyes within a group is indicated by asterisks. Single asterisks show significance at $P<0.05$. Double asterisks show significance at $P<0.01$. Significant differences between strains for a given deprivation condition are indicated by daggers. Double daggers show significance at $P<0.01$.

After 4 weeks of visual deprivation there are significant strain differences (Fig. 5) that differ from those observed after 2 weeks. Full deprivation of the visual field does not result in significant differences in refractive state (−19.65 vs −22.03; $t=-0.47$, d.f. = 7.3, $P=0.32$) although there is significantly less vitreous chamber elongation in the K strain (1.62 vs 2.11 mm; $t=3.34$, d.f. = 12.6, one-tailed $P<0.005$). Difference in corneal radius of curvature does not appear to account for the lack of a difference in refraction; corneal radius of curvature is not significantly different between strains (0.12 vs 0.12, $t=0.02$, d.f. = 19.8, one-tailed $P=0.50$).

Partial visual field deprivation for 4 weeks results in significantly more myopia (−20.08 vs −8.90; $t=4.36$, d.f. = 5.5, $P<0.01$) and greater vitreous chamber elongation (1.0 vs 0.45 mm; $t=3.87$, d.f. = 6.6, one-tailed $P<0.005$) in the visually deprived K strain eyes. Corneal radius of curvature changes did not differ significantly between strains (−0.17 vs −0.04 mm; $t=1.62$, d.f. = 7.0, one-tailed $P=0.075$).

DISCUSSION

To date, the domestic chick has been the most commonly used species in the study of experimentally induced myopia and the postnatal development of the eye. The breeds of chicks used in these studies vary (e.g. Broilers, Plymouth rocks, White Leghorns). Furthermore, breed hybrids and different strains within a breed have been used.

In this paper we have shown significant differences in normal ocular development and the response to visual deprivation myopia between different strains within a single breed of chick, the White Leghorn. Compared to the H/N strain of White Leghorn, the eyes of K strain chicks are normally larger and possess significantly flatter corneas. In response to visual deprivation, strain differences depend upon the type of deprivation and its duration. In general, visual deprivation in the K strain results in flattening of the cornea and less elongation of the vitreous chamber, and consequently lower levels of induced myopia compared to the H/N strain. The notable exception is following 4 weeks of partial deprivation where we observed corneal steepening and significantly greater vitreous elongation and myopia in the K strain. At present we cannot explain the differences between 2 and 4 weeks of visual deprivation.

Our finding that there are significant differences in the normal development and the ocular growth response to visual deprivation in two strains of White Leghorn reared under identical conditions is important for the following reasons: (1) Genetic differences in the visual control of eye growth may exist. Through selective breeding techniques the genes involved in the control of ocular development in chicks can be isolated, and their relationship to the visual control of eye growth can be fully explored. (2) The results emphasize the need for more detailed consideration of strain characteristics in avian models of eye growth and myopia. Differing degrees of myopia produced by similar visual deprivation paradigms in different labs may be accounted for by breed or strain differences. For example, the generally lower myopia induced in the K strain as shown in this study explains the low myopia reported by Schaeffel and Howland (1991) who also used the K strain (see Fig. 1). (3) Different corneal radius of curvature changes can be induced in the K strain by different visual deprivation conditions. This may be used to examine the regulation of corneal and anterior segment shape during development.

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