Diurnal illumination patterns affect the development of the chick eye

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Abstract

Exposure to continuous illumination disrupts normal ocular development in young chicks, causing severe corneal flattening, shallow anterior chambers and progressive hyperopia ('constant light (CL) effects'). We have studied the minimum requirements of a diurnal light cycle to prevent CL effects. (1) Seven groups of 10 chicks were reared under a 0 (constant light, CL), or 1, 2, 3,4, 6, or 12/12 h (normal) light–dark cycles. It was found that CL effects were prevented if the dark period was 4 h or longer. Below 4 h, the effects were dose-dependent and inversely correlated with the amplitude of the Fourier component of illumination at 1 cycle per day (CPD). (2) Three groups of 20 chicks were exposed to 4 h of darkness distributed differently over 24 h to vary the amplitude of the Fourier component at 1 CPD. It was found that complete suppression of the CL effects required that the 4 h of darkness were given in one block and at the same time each day. Our results show that normal ocular development in the chick requires a minimum of 4 h darkness per day, provided at the same time of the day without interruption, and suggest that the light–dark cycle interacts with a linear or weakly nonlinear oscillating system. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The growth of the eye can be altered by exposure to light after hatching. Raising chicks in either darkness or constant light can change the growth pattern of the chicks' eyes (Lauber et al., 1970; Gottlieb, Wentzek & Wallman, 1987; Li, Troilo, Glasser & Howland, 1995). In a previous study we showed that the rearing of chicks under constant light (CL) disrupts normal ocular development, resulting in a shallow anterior chamber and progressive hyperopia, caused principally by corneal flattening. Long term CL is also found to produce a small and thickened cornea, thinned lens, cataracts, and damage to the retina and choroid (Li et al., 1995). These results indicated that photoperiodic experience is very important during chick eye development. Quinn, Shin Maguire and Stone's (1999) study

suggested that the interactions of the diurnal illumination patterns with eye growth may also be important in the development of children's refractions, a finding that adds to the significance of the present study.

We wanted to characterize the influence of the length of the dark phase of the diurnal illumination cycle on the anterior segment and refraction of the chick eye. Two questions should be asked here. First, how much darkness per day is needed to maintain normal eye development and to prevent the eye from exhibiting CL effects? Second, to what extent is CL hyperopia due to the loss or attenuation of the diurnal light–dark cycle? Our approach was to monitor eye growth and refractive state while varying the length and temporal pattern of the dark phase in 24-h periods.

Because chicks showed obvious hyperopia and anterior segment changes after 2 weeks of CL treatment, this was the test period that we used in this study. We found that some process, which depends on the duration of the dark phase of the diurnal light–dark cycle (DLDC), acts in the chick eye to bring about normal

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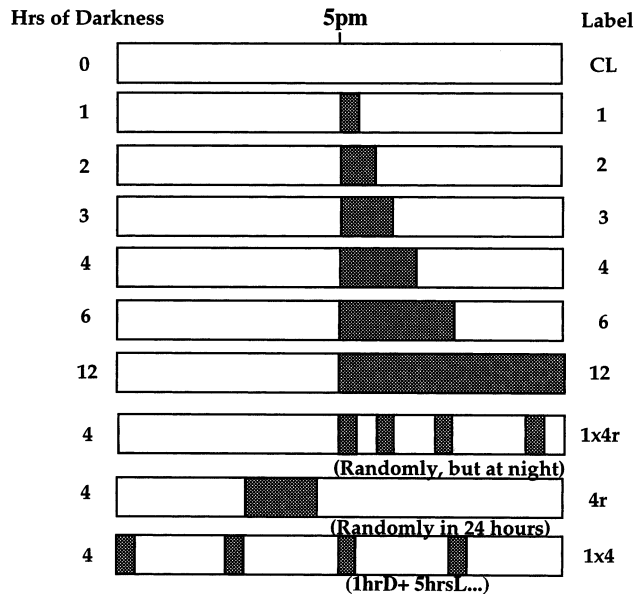*E-mail address:* tl24@cornell.edu (T. Li).

Fig. 1. Illustration of different light–dark distributions for animal groups. The dark blocks indicate the periods of darkness and blank bars present the periods of light. The length of the bars is 24 h.

growth of the eye. By shortening the length of the dark period during the DLDC one is also weakening the strength of the diurnal illumination rhythm, as the Fourier component at 1 cycle per day (CPD) with a single dark period decreases as the dark period shortens according to the equation (Weast & Selby, 1967):

$$\text{Amplitude (DLDC)} = (2/\pi) \sin(\pi d/24) \qquad (1)$$

where d is the length of the dark period in hours.

It is reasonable to expect that the efficacy of entrainment of a 'weakly nonlinear system' (Pavlidis, 1973), such as a van der Pol oscillator, will depend upon the strength of the Fourier component of its natural frequency, because in the, limiting case, a van der Pol oscillator is simply a pendulum.

Another way, however, to decrease the strength of the DLDC without altering the amount of darkness in

the 24-h cycle is to break the dark period into smaller units distributed in various ways in the 24-h cycle. This allows one to separate the effects of amount of darkness from the strength of the DLDC. (For examples of this technique, see Edmonds, 1988.) In this situation the amplitude of the DLDC is most easily computed by numerical methods such as a computer-implemented fast Fourier transform.

Because we found that constant light effects were totally prevented by a DLDC which included a dark period of 4 h or more, we investigated the effect of weakening the amplitude of the DLDC by redistributing 4 h of darkness in various ways throughout the 24 h light–dark cycle.

2. Materials and methods

In the first part of this study, seven groups of ten white leghorn chicks (Cornell K-strain) were randomly divided into several groups and raised respectively under 0 (designated CL), 1, 2, 3, 4, 6, and 12 h of darkness per day (Fig. 1). Treatments began 1 day after hatching. The dark periods always began at 17:00 h and were given in one block each day, with the exception of an ancillary set of two experiments in which the onset of a 4 h period of darkness was at 07:00 or 12:00 h. The ambient illumination level in the aviary, during the light periods, was an average of 700 lux. The illumination was supplied by fluorescent lamps (Sylvania 40 W, cool white). The chicks were raised in temperature controlled brooders ($33 \pm 0.5°C$). Food (Agway), crop gravel, and water were provided ad libitum.

Another three groups of ten newborn Cornell K-strain chicks were raised under a different illumination pattern in order to discover the effect of the amplitude of the DLDC in growing chick eyes. The three groups were raised as follows:

1. Four hours of darkness evenly distributed over a 24-h period — 1 h dark + 5 h light + 1 h dark + ...

Table 1
Rhythm amplitude for different light–dark pattern at 1 CPD[a]

Group designation	Dark–light ratio	Computed rhythm amplitude	Theoretical value
(CL or 0)	0/24	0.000	0.00
(1)	1/23	0.131	$\sin \pi/24$
(2)	2/22	0.259	$\sin \pi/12$
(3)	3/21	0.383	$\sin \pi/8$
(4)	4/20	0.501	$\sin \pi/6$
(6)	6/18	0.707	$\sin \pi/4$
(12)	12/12	1.000	$\sin \pi/2$
($1 \times 4r$)	4/20	0.330	–
(4r)	4/20	0.131	–
(1×4)	4/20	0.000	0.000

[a] The amplitudes of the 1 CPD component of the different diurnal light–dark patterns were computed by using the fast Fourier transform feature of Matlab (Mathworks, Inc., Natick, MA).

This group was set up to have no 24-h diurnal rhythm (relative amplitude at 1 CPD = 0; Table 1). We designate this treatment as '1 × 4'.

2. One block of 4 h of darkness was randomly placed in each 24-h period for every day of the study. Illumination was randomly turned off at different times during the day for a total of 4 h (designated '4r'). This group was set up to have almost no 24-h rhythm but to present the 4 h of darkness in one block. The periods of darkness were chosen by randomly choosing numbers from 1 to 24 (using a computer random number generator) until four different 1-h periods had been selected where no two periods were contiguous.

3. Four 1-h periods of darkness randomly separated in normal night time — each day (1 × 4r). This group was designed to maintain a diurnal rhythm but to separate the 4 h of darkness into four 1-h segments. The same method was employed as in (2) so that there was always at least a 1-h break between two dark blocks.

The amplitudes of the 1 CPD component of the different diurnal light–dark patterns were computed by using the fast Fourier transform feature of Matlab (Mathworks, Inc., Natick, MA). In this procedure, hours of darkness were entered as zeros and hours of light as ones. Thus, each treatment was represented as a vector of 360 values (i.e. 24 h/day times 15 days). These vectors were then transformed to frequency vectors and the amplitude at 1 cycle per 24 h was recorded. Of course, where the light and dark phases occur in a regular fashion, the amplitudes of the 1 CPD rhythm can be computed for an infinite time by Eq. (1). In Table 1 we have normalized all of these amplitudes by dividing every value by the amplitude of a 12/12 light–dark rhythm.

The measurements were made after 2 weeks of different light treatments for all the animals. The chicks were conscious and without cycloplegia. The refractive states and corneal curvatures were measured by IR photoretinoscopy and IR keratometry, respectively. The axial lengths of the ocular components were measured by A-Scan ultrasonography. All the measurements were performed as described in Li et al. (1995).

3. Results

3.1. Refraction

The hyperopic refractive error and ocular changes induced by CL decreases as the period of darkness increases up to 4 h/day (Fig. 2A). When the chicks had 4 h of darkness per day (group 4) or more, given in one block, their eyes developed normally, i.e. they were not significantly different from the chicks raised under 12/

12 h L/D cycles (group 4 versus group 12, $P \leq 0.98$; group 6 versus group 12, $P \leq 0.81$).

But it was necessary for normal development that the darkness had to be given in one block and at the same time every day. This is shown by the fact that the 4 h of darkness in three other 'discontinuous' groups (4r, 1 × 4, and 1 × 4r), could not prevent the CL hyperopia from occurring (Fig. 3A). Although all birds had a total of 4 h of darkness per day, they were all significantly more hyperopic compared with group 4 ($P < 0.001$ for group 4 versus 1 × 4, group 4 versus 1 × 4r, and group 4 versus 4r), and they all had the same hyperopic refractive error (about 8D) as group 2.

3.2. Radius of corneal curvature

Results of the keratometry measurements were similar to the refraction measurements. Four hours or more of darkness in one block at the same time stopped corneal flattening in chicks. Corneal radius decreases as the length of the dark period increases from 0 to 4 h of darkness (Fig. 2B). The other three discontinuous groups of 4 h darkness per day also showed significant corneal flattening compared to 12/12 h eyes ($P < 0.001$ for group 1 × 4 versus group 12; $P < 0.001$ for group 4r versus group 4; $P \leq 0.0025$ for 1 × 4r versus group 12; Fig. 3B).

3.3. Ultrasound

3.3.1. Anterior chamber depth
Four hours or more of darkness per day presented in one block maintained normal anterior chamber depth in the growing chick's eye. In all groups, compared to group 12 eyes, the anterior chamber was shallower with decreasing length of darkness for periods less than 4 h (Fig. 2C). The other three 'discontinuous' groups (1 × 4, 4r, 1 × 4r) receiving 4 h darkness/day showed different degrees of shallow anterior chamber depths. The 1 × 4 group had the shallowest anterior chambers not significantly different from the CL group ($P \leq 0.96$) (Figs. 2C and 3C).

3.3.2. Lens thickness
There were no significant differences in lens thickness among the groups ($P > 0.05$).

3.3.3. Vitreous chamber depth
The depth of the vitreous chamber increased greatly in all groups except those that had continuous 4 h or more darkness per day (Figs. 2D and 3D).

3.3.4. Axial length
Although there were some changes in the anterior segment and vitreous chamber, the axial length of the chicks showed no significant change in any of the groups ($P > 0.05$).
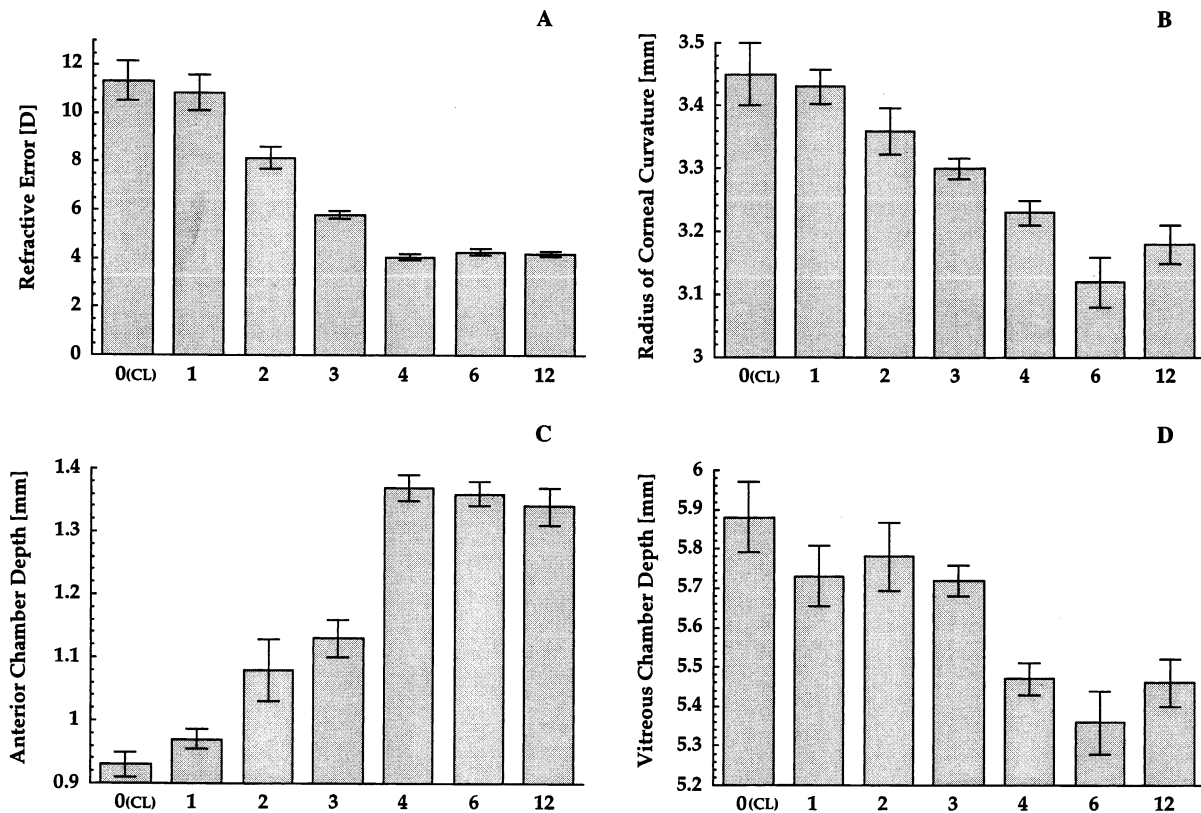
Fig. 2. Comparisons of refractive error (A), radius of corneal curvature (B), anterior chamber (C), and vitreous chamber depth (D) of the chicks exposed to a block of varying lengths of darkness at the same time each day over the first 2 weeks of life. The error bars represent the standard errors. The numbers under each column represent the groups and indicate the time period of darkness for each group. (A) As the period of darkness increases from 0 to 4 h/day, the hyperopic refractive error decreases significantly. When animals had 4 h darkness or more per day, the eyes developed normally with no significant difference between the groups. (B) Results for radius of corneal curvature are similar to the those from the refraction measurements. With 4 h or less of darkness, the corneal power increased as the length of the dark phase increased. The groups with 4 h or more of darkness in one block at the same time did not show significant corneal flattening induced by CL compared with 6 and 12 h of darkness groups. (C) The figure shows that the anterior chamber depth of the chicks with less than 4 h darkness per day had significantly shallower anterior chamber depths, decreasing as the period of darkness decreased. (D) The vitreous chamber depths of animals with 4 h or longer periods of darkness remain normal. All other groups of chicks show significantly deeper vitreous chambers.

3.4. Effect of relative amplitude of the DLDC

When the period of darkness was given as one block every day, the longer the dark time given, the bigger was the relative amplitude of the DLDC, i.e. amplitude at 1 CPD. However, all three discontinuous 4-h darkness designs had much smaller DLDC amplitudes than the continuous 4-h darkness group (Table 1), and they exhibited the CL effects in inverse proportion to the strength of their diurnal rhythm (Fig. 4), even though they all had the same total length of darkness as group 4. Fig. 4 shows that, at the same relative rhythm amplitude, the longer the total darkness the less effect CL has on the radius of corneal curvature (compare group CL versus group 1 × 4 and group 1 versus group 4r).

3.4.1. Time of onset of dark period

In two ancillary experiments we investigated whether or not the time of onset of the dark period influenced the refraction and growth of the eye. We found that there was no difference in the refractive state of the chicks, regardless of when during the day the dark period was initiated, provided only that it was always the same time of day. We did observe minor changes in the corneal curvature and vitreous chamber depth, but these could be attributed to a slightly larger eye and body size of the chicks used in these experiments.

4. Discussion

Our results suggest that there is a general need for some darkness for normal eye development. Shorter periods of darkness reduced CL effects proportionately to their length. However, this period of darkness must be given in one block and at the same time each day. Curiosity as to whether four discontinuous hours of darkness would be as effective as a single continuous period of the same length led us to design three new

'discontinuous' 4-h darkness treatments to test the period of dark phase and the DLDC requirement in the normal ocular growth mechanism.

Among the groups, those with lower DLDC amplitudes showed greater CL effects. This indicates the need for a minimum amplitude of DLDC in the ocular growth mechanism and normal visual function. Figs. 2B, 3B and 4 show that if the darkness is given in one block at the same time every day, the longer the period of darkness given, the greater is the DLDC amplitude and the smaller the CL effect on corneal curvature until reaching more than 4 h. At that point the DLDC amplitude is 0.5 (relative to 1 at a 12 h dark/12 h light rhythm). This is the minimum amplitude required for normal eye development.

Comparing keratometry measurements of all four groups with 4-h darkness treatments, we noticed that the animals showed different degrees of CL effects on corneal curvature changes, corresponding to the diurnal light–dark cycle amplitude (i.e. CL effect: $1 \times 4 > 4r > 1 \times 4r > 4$). The group with virtually no DLDC and no

continuous multi-hour period of darkness (group 1×4) shows the greatest CL effect.

Another interesting observation is that, even with the same DLDC amplitude, the groups that had longer consecutive dark periods exhibited smaller CL effects (e.g. group CL compared with group 1×4 and group 1 compared with group 4r, Fig. 4). This finding suggests that, in addition to the DLDC, the total length of the dark phase is also important for the regulation of eye growth.

Because the amplitude of the DLDC varies inversely with the degree of separation of the dark periods in the groups 1×4 and $1 \times 4r$ where four periods of 1 h of darkness are scattered evenly through the day or restricted to the second half of the 24 h period, one might think that it was not the amplitude of the DLDC, but rather the separation of dark periods which was important for the constant light effects. However, the importance of the amplitude of the DLDC is also demonstrated in the comparison of the effects of the treatments group 4 and group 4r, where the light
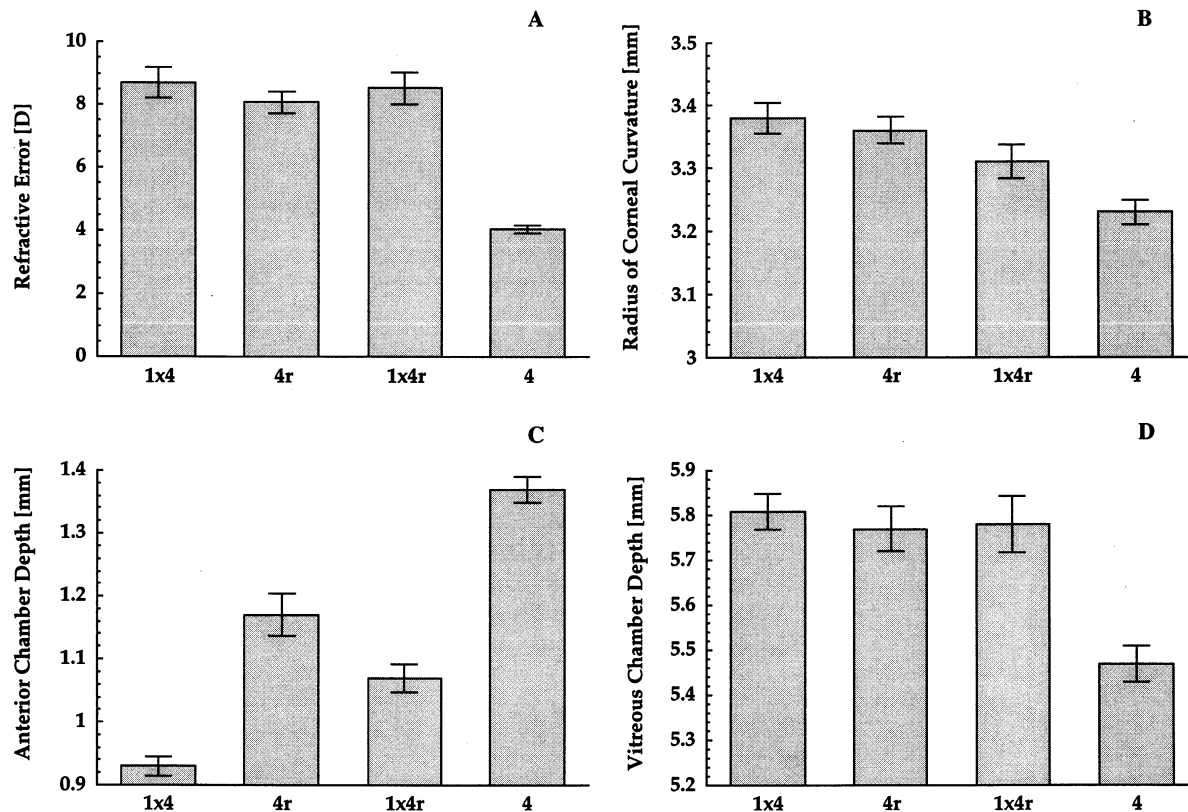

Fig. 3. Comparisons of refractive error (A), radius of corneal curvature (B), anterior chamber (C), and vitreous chamber depth (D) of the chicks' exposed to a total of 4 h darkness per day with different distributions over the first 2 weeks of life. The error bars represent the standard error. The labels under each column represent the groups and indicate the different distributions of dark phase for each group (Table 1). (A) Three 'discontinuous' groups receiving 4 h of darkness a day (4r, 1×4 and $1 \times 4r$) still exhibited the CL hyperopic refractive errors, suggesting that the period of darkness should be given in one block and at the same time every day (i.e. keeping the 24-h diurnal rhythm). (B) The three 'discontinuous' groups receiving 4 h darkness per day still showed different degrees of reduced corneal power compared with those in the group 4. (C) Three 'discontinuous' groups exhibit different degrees of induced shallow anterior chamber depth, while group 4 showed no CL effect on the anterior chamber. (D) The vitreous chamber depths of three 'discontinuous' 4-h groups of chicks were significantly deeper compared with those in group 4.
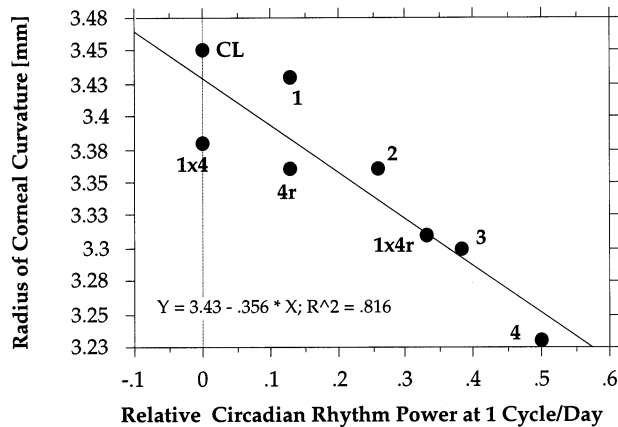
Fig. 4. Comparison of the relationship between CL effect on radius of corneal curvature and relative diurnal rhythm amplitude among different light treated groups for dark intervals of 4 h or less. In this figure we excluded groups 6 and 12 because they did not show the CL effects during the experiment (Figs. 3 and 2). This figure shows that if the darkness is given in one block at the same time every day, the longer period of darkness given, the larger the rhythm amplitude and the smaller the CL effect up to periods of 4 h or more of darkness (i.e. 0.5 rhythm amplitude). Therefore, a relative rhythm amplitude of 0.5 (relative to 1 at a 12 dark/12 light) cycle is the minimum diurnal rhythm amplitude requisite for normal eye development. The figure also shows that with the same rhythm amplitude, the groups which had longer periods of darkness exhibited smaller CL effects, like group CL versus group 1 × 4 and group 1 versus group 4r. Comparing keratometry measurements of all four groups with 4-h darkness treatments, we noticed that the animals showed different CL effects on corneal curvature changes corresponding to the diurnal rhythm amplitude they had (i.e. CL effect: 1 × 4 > 4r > 1 × 4r > 4). Group 1 × 4 which had virtually no rhythm and no continuous, multi-hour period of darkness shows the greatest CL effects.

periods are of identical length, but the amplitudes of the DLDC and the effects of the treatments are very different.

How can we relate these findings to what is known about circadian rhythms and eye growth? Specifically, (1) why is a minimum time of darkness required to prevent constant light effects, and (2) why does increasing the amplitude of a 1 CPD illumination rhythm increase the protection against constant light effects?

4.1. Retinal circadian clocks

An intrinsic circadian clock has been found in photoreceptors of the vertebrate retina that is believed to control the rate of melatonin synthesis and release, which, in turn, influences the melatonin–dopamine reciprocal inhibitory circuit (Cahill & Besharse, 1995). Normally, this clock runs synchronously with diurnal rhythms (Reme, Wirz-Justice & Terman, 1991; Terman, Reme & Wirz-Justice, 1991; Cahill & Besharse, 1993, 1995; Morgan & Boelen, 1996; Tosini, & Menaker, 1996), and can run independently from the central visual system, a result that has been confirmed by optic nerve transection and complete suprachiasmatic nucleus

lesions (Teirstein, Goldman & O'Brien, 1980; Terman et al., 1991). The intrinsic circadian clock has its own free-running rhythm under constant darkness. However, light can override this clock, switching the retinal circuitry from a dark phase to a light one, resulting in a reduction in the melatonin synthesis and release, and an increase in dopamine synthesis. (Bartmann, Schaeffel, Hagel & Zrenner, 1994; Morin, 1994; Cahill & Besharse, 1995; Schaeffel, 1995; Morgan & Boelen, 1996; Tosini & Menaker, 1996).

Weiss and Schaeffel (1993) observed the diurnal growth rhythms in the chicken eye. They found that the eyes grew in length only during the day and even shrank during the night. This diurnal growth rhythm of the eye disappeared under constant light conditions. They also reported that the retinal dopamine level is higher during the day when the eye is growing and is lower during the night when the eye 'shrinks' (Schaeffel, 1995). These data are consistent with a link between dopamine–melatonin rhythms and the growth of the eye.

According to Morgan and Boelen (1996) the effect of illumination on the chick eye is to flip the 'dark–light switch', switching off melatonin production by the photoreceptors and enkephalin, neurotensin and somatostatin production by the ENSLI (encephalin-, neurotensin- and somatosensin-like-immunoreactive) amacrine cells and switching on the production of dopamine by the dopaminergic amacrine cells. Accordingly, constant light should result in low melatonin levels and high dopamine levels. On the other hand, these authors also note that, in contrast to the *switching* of light, '…withdrawal of light in the light phase may not be as potent a drive, and indeed return to the dark phase may be more dependent upon circadian factors'.

These findings could explain the results in this study. A certain length of dark phase may be required for the retina to generate and release melatonin, maintaining a normal melatonin–dopamine reciprocal inhibitory balance in the control of eye growth during development. Presumably a dark period of at least four consecutive hours is required to attain sufficient melatonin levels to prevent CL effects.

Shorter periods of darkness, however may be interacting with the 'well documented circadian rhythm in melatonin synthesis and release in the photoreceptors' (Morgan & Boelen, 1996). Here the synchronization of the clock with the diurnal light–dark rhythm may well depend upon the amplitude of the 1 CPD Fourier component of the photoperiod. As mentioned above, the importance of the one cycle per day Fourier component suggests that the environmental light regime may be interacting with a linear or weakly non-linear oscillating system of the pendulum or van der Pol type. These are systems which have the dynamics of a physical pendulum with mass, a restoring force and little

friction, which in the van der Pol model becomes positive or negative depending upon the amplitude of the swing (Pavlidis, 1973). Such systems exhibit resonance, that is they respond differentially to the frequencies of the driving forces and show a peak sensitivity near their resonant frequency, which we have tacitly assumed to be 1 CPD.

Thus, to return to the chick, if the amplitude of the 1 CPD component is reduced, as in those designated as 4-h 'discontinuous', the normal melatonin–dopamine balance might not be maintained. Thus, CL effects could not be prevented even though a total of 4 h of darkness were presented per 24 h — a darkness period that, if presented in one block at the same time each day (i.e. with a strong enough diurnal light–dark cycle amplitude), would have been sufficient to prevent CL effects.

CL effects exhibited by the $1 \times 4r$ group indicate that the DLDC is not the only factor that should be considered for the normal control of eye development; the length of the darkness given at one time is also very important for maintaining the normal diurnal growth function. In addition, the fact that, with the same relative rhythm amplitude, the longer the period of darkness, the smaller are the CL effects. Again this suggests that normal eye growth during development requires both a DLDC and a certain length of continuous dark phase of that cycle.

Acknowledgements

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