Lack of oblique astigmatism in the chicken eye

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ABSTRACT

Primate eyes display considerable oblique off-axis astigmatism which could provide information on the sign of defocus that is needed for emmetropization. The pattern of peripheral astigmatism is not known in the chicken eye, a common model of myopia. Peripheral astigmatism was mapped out over the horizontal visual field in three chickens, 43 days old, and in three near emmetropic human subjects, average age 34.7 years, using infrared photoretinoscopy. There were no differences in astigmatism between humans and chickens in the central visual field (chicks −0.35D, humans −0.65D, n.s.) but large differences in the periphery (i.e. astigmatism at 40° in the temporal visual field: humans −4.21D, chicks −0.63D, $p < 0.001$, unpaired t-test). The lack of peripheral astigmatism in chicks was not due to differences in corneal shape. Perhaps related to their superior peripheral optics, we found that chickens had excellent visual performance also in the far periphery. Using an automated optokinetic nystagmus paradigm, no difference was observed in spatial visual performance with vision restricted to either the central 67° of the visual field or to the periphery beyond 67°. Accommodation was elicited by stimuli presented far out in the visual field. Transscleral images of single infrared LEDs showed no sign of peripheral astigmatism. The chick may be the first terrestrial vertebrate described to lack oblique astigmatism. Since corneal shape cannot account for the difference in astigmatism in humans and chicks, it must trace back to the design of the crystalline lens. The lack of peripheral astigmatism in chicks also excludes a role in emmetropization.

1. Introduction

Newborns tend to be hyperopic with highly variable refractive errors but the process of emmetropization reduces the variability over time so that most of the children are close to emmetropia at the age of 6 years (Schaeffel, Mathis, & Bruggemann, 2007). Experimental work in animal models has shown that emmetropization is largely controlled by the retina (Wallman & Winawer, 2004). The retina can detect image defocus, including its sign, at each position in the visual field and releases biochemical messengers to adjust the growth rates in the posterior part of the globe such that a close match is achieved between retinal shape and the shape of the image shell (Diether & Schaeffel, 1997; Miles & Wallman, 1990). It was demonstrated also in rhesus monkeys that eye shape is adjusted during development to match the image shell. Local myopia can be induced when only parts of the visual field are defocused by hemifield lenses (Smith et al., 2010). Emmetropization can generate irregular eye shapes if

defocus is imposed selectively in local retinal areas (Schippert & Schaeffel, 2006). Emmetropization may also involve reduction of astigmatism (Kisilak et al., 2008, Chu, Kee and Guggenheim, personal communication 2014) although it is not clear how messengers released from the retina can adjust the sphericity of the cornea and lens. At least, astigmatic accommodation was ruled out as a mechanism for later permanent changes in corneal or lenticular astigmatism (Thomas & Schaeffel, 2000).

The retinal image processing underlying the detection of defocus and its sign is largely unknown (Wallman & Winawer, 2004). There were numerous attempts to identify visual cues that provide the retina with information about the sign of defocus. Longitudinal chromatic aberration was extensively studied (Schaeffel & Howland, 1991; Wildsoet et al., 1993), but it is clear that chromatic cues are at least not obligatory although they may interact with emmetropization (Rucker, 2013; Rucker & Wallman, 2009, 2012). Higher order aberrations could provide a sign of defocus-related cues (Wilson, Decker, & Roorda, 2002) but there is no convincing evidence that they are used during emmetropization (Wallman & Winawer, 2004). Interestingly, imposing high amounts of astigmatism by cross-cylinder spectacle

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lenses had little effect on emmetropization to spherical refractive errors in chickens (McLean & Wallman, 2003). Some amount of on-axis astigmatism is present in almost all vertebrate eyes and high amounts of oblique astigmatism were also found in other terrestrial vertebrate eyes (Schaeffel et al., 1994). Oblique astigmatism could therefore provide a cue about the sign of spherical defocus since either its tangential or radial axis is in better focus, depending on spherical refractive error. The peripheral retina controls the growth of the globe in the periphery of the visual field and plays an important role in emmetropization also in foveate animals, like rhesus monkeys (Smith et al., 2005), because the foveal position along the optical axis cannot be independent from the growth of the globe in the periphery. Therefore, Howland proposed such a role of oblique astigmatism (Howland, Proceedings of the 13th International Myopia Conference 2010; further discussed by Charman, 2011). In human eyes, its magnitude was described by a parabolic function (astigmatism relative to the pupil axis = 0.00328 * angle^2; Howland, 2010). However, the pattern of peripheral astigmatism has not yet been studied in the chicken eye. While humans have their best visual acuity in a small region of the retina with a diameter of less than a degree of visual angle, chickens have an area centralis which extends over several degrees, with only a moderate decline in ganglion cell density toward the periphery of the visual field (Ehrlich, 1981; Morris, 1977). Since little is known about spatial visual performance in the periphery, we used an automated optokinetic paradigm to study this question as well. We also tested whether accommodation can be elicited in chicks by presenting a target far out at the margins of the visual field and analyzed peripheral transscleral images in excised eyes to evaluate peripheral image quality.

2. Methods

2.1. Animals

Experiments were conducted in agreement with the ARVO statement for the use of Animals in Ophthalmic and Vision Research and approved by the Commission for Animal Welfare of the Medical Faculty of the University of Tuebingen. White leghorn chicks (Gallus domesticus) were obtained from a local hatchery (Weiss, Kirchberg, Germany) 1 day after hatching and were raised in groups in large cages in the animal facilities of the institute at a 12 h light/dark cycle. Room temperature was kept at 30 °C during the first week post-hatching and at 28 °C afterwards. Water and food were supplied *ad libitum*. Table 1 gives numbers and ages of chicks used in the different experiments. The measurements were approved by the University committee for animal welfare.

2.2. Experimental procedures

2.2.1. Measurement of central and peripheral astigmatism in humans
Refractions over the horizontal visual field were measured with a custom-built "scanning photorefractor" as described by Tabernero and Schaeffel (2009) in three near emmetropic young subjects (spherical equivalent between −0.5 and +0.5D,

Table 1
Number of animals used in the different experiments.

Experiment	Ages [days]	# of chicks
Photorefraction	42	3
Measurement of the chicken Hirschberg ratio	7–43	7
Corneal shape measurements	24	6
OKN measurements	25	2
Peripheral accommodation	21/11	1/2
Transscleral images	21	2

astigmatism <0.5D as measured by subjective refraction by a certified optometrist; average age 34.7 years). In short, photorefraction was performed using a hot mirror that was controlled by two stepping motors such that the camera imaged the eye at a stationary position but from different angles, ranging from −50° to +50° over the central horizontal visual field. One scan took about 3 s. With a video camera frame rate of 62 Hz, the angular resolution was about 1°. The refractor first scanned the refractions in the vertical pupil meridian and, on its way back, the refractions in the horizontal meridian, by switching the orientation of the IR-LED array of the photoretinoscope. During this procedure, it has to be taken into account that the number of pixels that determines the slope of the brightness profile in the pupil is compressed when measuring from an off-axis position. A correction was therefore made by multiplying the slope with the cosine of the angle of measurement (also below, in the measurements in chickens). Refractions were previously calibrated with trial lenses as described by (Schaeffel, Wilhelm, & Zrenner, 1993). Accommodation was controlled by asking the subjects to fixate a target in primary gaze position at one meter distance. The difference between the refractions in the horizontal and vertical meridian was taken as a measure of astigmatism although it is clear that full measurements of astigmatism (sphere, cylinder and axis) requires at least 3 LED segments in the photoretinoscope at different angular positions (Choi et al., 2000). Because we were interested mainly in oblique astigmatism which dominates the periphery and adopts a cylinder axis around 0° in negative cylinder convention, exact measurements of the cylinder axis were not important. The negative cylinder convention was used in all cases. The measurements in human subjects were approved by the Ethics Commission of the University of Tuebingen. They were carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) and informed consent was obtained for experimentation with human subjects.

2.2.2. Measurement of astigmatism in chicks
Three chicks were trained to accept that the operator turned their heads by moving their beaks. The advantage of this trained procedure was that chicks did not close their eyes. Their heads could be rotated in all directions and videos were recorded of the pupils, showing the different brightness profiles that occur during eccentric photorefraction. Photorefraction has been previously calibrated in chickens with trial lenses (Seidemann & Schaeffel, 2002). As above, in the case of refractions of human eyes, the photoretinoscope was oriented either horizontally or vertically and the differences in the measured refractions were taken as a measure of off-axis astigmatism. In total, 22,000 video frames were analyzed. Pupil center, first Purkinje image, and brightness slope were determined frame by frame, using a custom developed macro for ImageJ (US National Institute of Health, Bethesda, Maryland, http://imagej.nih.gov/ij/). Accommodation can be excluded as a confounding factor during our measurements since it is clearly visible as a rapid change in the light distribution in the pupil (flipping over from a bright light crescent in the top to one in the bottom, see Fig. 7A for an example). Chicks accommodate with a speed of about 80D/s and they never display sustained accommodation. Also, there were just too many data collected (>22,000, see above) that a single short accommodation "pulse" could have affected the measurements.

2.2.3. Measurement of the orientation of the eye
The angle of orientation of an eye can be determined from the positions of the first Purkinje image relative to the pupil center, given that the Hirschberg ratio (HQ) is known (= degree of rotation per millimeter displacement of the first Purkinje image). In humans, the HQ is about 12 deg/mm (Barry, 1999; Brodie, 1992;