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Müller cell alignment in bird fovea: possible role in vision

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Abstract

Birds which possess high visual acuity, such as eagles and falcons, are known to have retinas with a deep conically curved central foveal pit. There have been different attempts to explain the importance of this particular shape of the fovea in visual resolution. Recently, the function of Müller cells as “light fibers” was discovered, showing how the endfeet of Müller cells trap the light and then transfer it to a single cone photoreceptor. Here we describe how the endfeet of Müller cells line the walls of the foveal pit in the Pied Flycatcher, and how the Müller cell body extends its processes towards individual cones, forming machinery that could allow for light transfer from the pit wall to the photoreceptor layer alongside the pit. We describe how this construction may send an image from the fovea to the cones, and also, how the angular positioning of Müller cells, being optical extensions of the cones, has the advantage of being much denser than on a flat or slightly curved fovea. We, therefore, suggest that this type of optic fiber alignment can be used as a novel type of “amplifying array” that simply increases the amount of megapixels at the photoreceptor cell layer.

Introduction

It is known that eagles have a visual acuity of about 8 to 10 times greater than that of the average human (Reymond, 1985). In part, the visual sharpness of eagles can be attributed to their eye optics consisting of a multi-lens construction similar to that of a telephoto objective lens system (Snyder, Miller, 1978). This is similar to cameras, whose acquired image quality depends on (i) the optics of their objectives and (ii) the amount of megapixels in the sensor chip. In addition, the eagle's retina is characterized by having a higher density of

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photoreceptors than other birds, and a deep and sharp conical foveal pit also typical in falconiformes birds (Wood, 1917; Snyder, Miller, 1978; Reymond, 1985).

The density of photoreceptors in the retina is crucial for visual acuity or resolving power. The retina is a thick layer of neural tissue lining the back of the eye responsible for transducing visual information. The photoreceptor cells located on the outer surface of the retina are sensory elements that absorb the photons of light. Therefore, light should cross all scattering tissue to reach cones which then transfer light energy into the biochemical c-GMP cascade and to electrical signals that pass through a network of neurons, the optic nerve, and then finally to the brain. Photoreceptors are not uniformly organized across the retina; there are specialized regions, such as the fovea, areae, and visual streaks, possessing different densities of these cells (Collin, 1999; 2008; Moore et al., 2012). The fovea is the part of the inner retinal tissue with an invagination and that part that possesses the highest density of cone photoreceptor cells, thus having the highest resolution and preeminent color vision (Fite, Rosenfield-Wessels, 1975; Collin, 1999; 2008).

In birds and some reptilians the central fovea is a deep funnel- or whirlpool-shaped pit (Walls, 1937; 1942; Fite, Rosenfield-Wessels, 1975; Collin, 1999; 2008), while in mammals (humans included) the fovea is just a shallow saucer-shaped depression in the retina. The pit is particularly deep and sharp in eagles (Reymond, 1985), and in smaller birds that need extremely sharp eyesight to help fulfill their hunting needs (Khokhlova et al., 2000; Zueva et al., 2003). Therefore, it is important to explain the possible functional significance of the shape of the foveal pit in relation to visual acuity.

Previously, the reason for the radial displacement of the neural layers away from the center of the foveal pit was described as allowing a clear and uninterrupted optical path between the pupil and the cones (Wood, 1917). Walls (1937) criticized this opinion, based on the data known at that time, and suggested that the vitreous body behind the lens and anterior to the foveal pit can give up to an 8X additional magnification, thus augmenting the acuity. Walls suggested this additional *"concave lens"* and argued that this cannot be contradicted by the fact that the fovea in the living retina can be observed by ophthalmoscopic inspection, without needing additional magnification (Walls, 1937; 1942). The crucial hypothesis of the "concave lens" theory is that the retina should have a higher than vitreal liquid refractive index and, therefore, light can be bent at the retinal surface to bring images aside from their axial projection to the pit but toward para-foveal area (to the periphery) and this does not require any additional light fiber elements (rev. Reichenbach et al., 2014).

Moreover, R. Pumphrey (1948) criticized the "additional lens" theory by pointing out that in a golden eagle (Aquila chrysaetus) the vitreous body anterior to the foveal pit cannot work as an additional lens because it will give massive optical aberrations and would substantially diminish the potential acuity in the central retina. Instead, he suggested that these aberrations that "have the remarkable property of transforming symmetrical image into an asymmetrical one" can be what eagles use for the "sensitive appreciation" of the angular movements of objects. So, his theory can be described as a modified Walls theory of an additional lens, where special aberrations emphasize angular movements. As we mentioned, this contradicts

the simple fact that the fovea in the living retina can be observed by ophthalmoscopic inspection to be very well optically focused without additional magnification or distortions.

In this article, we explain how the presence of an extremely sharp and deep pit in the *convexiclivate* fovea of birds with high visual acuity could be crucial. The light images are focused first on the inner surface of the foveal pit (endfeet of Müller cells) and not directly onto photoreceptors and then photoreceptors get the light by special light transmission fibers that transfer the light energy from the inner retina to the outer retina. This mechanism was recently described for thick Müller cells and in the peripheral guinea pig retina, in which Müller cells were shown to play the role of specialized "light cables", similar to fiber optic cables (Franze et al., 2007; Agte et al., 2011; Reichenbach et al., 2012). The surface of the fovea pit is covered by the endings of the Müller cells, called endfeet, which may serve as the entrance for light. It is known that in whole retina, Müller cells form a "cone–vitreous body interface" with a one-to-one ratio between Müller cells and cones (Labin et al., 2014).

We show here that in case of birds, the presence of a pit gives the advantage of an increased retinal surface (and therefore an increased density of Müller cells endfeet), that is described as $1/(\sin\alpha)$, where α is the angle of the pit. If in the adult Pied Flycatcher retina (similarly to adult Aguila), the angle of the foveal pit is near 20° (Zueva et al., 2003), that therefore gives about 1/0.3, approximately 3.33-times of increased surface. This can allow more light fibers to be packed into the area than in a flat retina, subsequently increasing visual acuity in this zone by projection of the visual image to a large para-foveal area using the "optical plate" formed by Müller cells.

2. Methods

Histological tissues used were collected at the Prioksk-Terrace natural reserve (Russia) during a study about the growth and maturation of the bifoveal retina of the pied flycatcher (*Ficedula hypoleuca)* (Khokhlova et al., 2000). The eyeballs of flycatcher chicks were collected 27 days after hatching and subsequently fixed in 3% gluteraldehyde with 2% paraformaldehyde in 0.15 M cacodylate buffer and postfixed with 1% OsO(4) in the same buffer. The eyeballs were oriented relative to the position of the pecten and embedded in Epon-812 epoxy resin. Semi-thin sections of 1μm were cut serially on an LKB Bromma Ultratome Ultra Microtome (L.K.B. Instruments Ltd., Northampton, UK), stained with 0.1 % Toluidine Blue and examined with a BH-2 light microscope (Olympus, Japan). Ultrathin sections of 60 nm were made using the same LKB Ultratome and examined with a JEM 100B electron microscope (JEOL Ltd., Japan) as previously described (Kondrashev et al., 2012).

3. Results

The Müller cell columnar position and alignment in the retina is important to keep the tissue structure (Reichenbach and Robinson, 1995) and for light energy transfer (Franze et al., 2007). Therefore, we studied Müller cells in the foveal pit area on transverse sections of the retina of Pied Flycatchers (Fig.1). We used both conventional optics (Fig. 1A) and electron microscopy (Fig. 1B, C) in order to evaluate the fine structure of the foveal pit.

3.1 Müller cell endfeet (inverted taper-shaped endings of the Müller cells) form the inner limiting membrane (ILM) in the foveal pit of the Pied Flycatcher

The toluidine blue stained retinal section from a 27-day old Pied Flycatcher (Fig. 1A) has a well pronounced foveal pit. The angle of the pit depression (about 30 degrees) is not as sharp as in adult birds (20 degrees, Zueva et al., 2003); however, in retinas of young birds the staining of both neurons (light cells) and of Müller cells (dark cells) is clearly visible (Fig. 1A). In other aspects, this retina has all the principal features of an adult Flycatcher retina (Zueva et al., 2003). Figure 1 clearly demonstrates that Müller cell endfeet cover the entire inner surface of the retina in the foveal area, including the slopes of the pit (Fig. 1A), thus forming the inner limiting membrane of the retina. Another important feature of such alignment is that the tapered-like Müller cell endfeet turn to the stalks that spread to the far periphery from the foveal pit. This structural alignment suggests that light images are projected to the pit and then the images can be propagated to the wider (para-foveal) area using Müller cells as light fibers. This was confirmed also by electron microscopy (Fig. 1B-blue arrow). Also, Müller cells extends perpendicularly to the inner surface in all points of the inner membrane (Fig. 1A, Fig. 1B), and thus may serve as inlets for light energy as shown before in guinea pig retina (Franze et al., 2007; Agte et al., 2011) where they serve as tapered light traps or focons (Putilin, 2012).

3.2. Long processes of Müller cells form a cap structure around cone photoreceptors thus forming the outer limiting membrane (OLM)

The Müller cells of many species extend their endfoot processes towards the vitreous body, while they extend their basal (called distal) processes to the cone photoreceptors, thus forming a cone–vitreous body interface (Reichenbach and Robinson, 1995). This is important for (i) light cable function (Franze et al., 2007) and (ii) tandem-cell (Müller cell-to-cone) potassium homeostasis (Zayas-Santiago et al., 2014). In the fovea centralis zone the Müller cell-cone ratio is generally one-to-one. Consistent with these findings, the retina of the Pied Flycatcher (Fig. 1C) has Müller cells that form the outer limiting membrane, in which the outer segments of cones are radiating outwardly from the outer limiting membrane onto the Müller cell distal processes, thus forming a kind of cap structure (Fig. 2). As observed in other species (see. Reichenbach and Robinson, 1995), the surface of the Müller cell facing the pigment epithelium and subretinal space is expanded by many projections of the Müller cell membrane known typically as apical villi. Therefore, the Müller cell structure in the bird foveal pit is similar to the peripheral retina of most studied vertebrates.

3.3. Hypothetic scheme of light propagation and photosensitivity in retinas with a deep foveal pit

In summary, according to our observations discussed in sections 3.1 and 3.2, all the inner retinal surface of the Pied Flycatcher, which includes the foveal pit, is covered by Müller cell endfeet that form the inner limiting membrane (ILM) (Fig. 2, Müller cells colored yellow). From the opposite side, Müller cells are forming the outer limiting membrane (OLM), surrounding individual cone photoreceptor inner segments and forming a kind of cup around the cones (Fig. 1C, red arrow; Fig. 2, central panel). The cell body of cones, their

nuclei and synaptic terminals are inclined away from the center of the fovea, forming a visible angle (Fig. 1 C, cone compartments are white; Fig. 2, cones are colored blue). So, the light pathway (via Müller cell alignment) and the electrical pathway (via cone synapses) are aligned in different directions in the fovea (Fig. 2, central panel), while in the periphery both pathways are axially aligned (Fig. 2, right panel).

Since Franze et al. (2007) described that the endfeet serve as light traps, the endfeet catch photons regardless of the angle of light coming to the retinal surface (Franze et al., 2007; Reichenbach et al., 2012; 2014). We, therefore, hypothesize that the light can enter each individual Müller cell endfoot and be further propagated to an individual cone into the parafoveal zone. Therefore, each Müller cell serves as an "optical extension" of the cone photoreceptor, similar to what was observed in the guinea pig peripheral retina (Labin et al., 2014). However, unlike in the flat peripheral retina of guinea pig, Müller cells from the Pied Flycatcher are curved in the foveal pit wall, allowing light propagation to the larger area (Fig. 2).

If light enters through the endfeet situated on the wall of the pit, and assuming all endfeet have about the same dimensions, as is observed in Fig. 1B, the surface size of the endfeet (let it be $\boldsymbol{b}$) will be inclined at the angle α in the fovea (Fig. 2 and Fig. 3). Due to this angle, the total surface for the light entrance through the endfeet in fovea will be reduced by the factor $\boldsymbol{b}\cdot\sin(\alpha)$, and the density of the endfeet (as light cables) will be augmented as $1/\sin(\alpha)$. In the Pied Flycatcher chick eye, as observed in Fig. 1 the angle is near 45°, and the increase in density will be about 2 times. In sharp pits like that of an adult Pied Flycatcher or an adult Eagle retina which posses a 20° pit (Snyder, Miller, 1978) the formula and simple computational analysis will give a 3 times higher density of "light inputs" (endfeet) when compared with a flat retina. Such foveal organization in bird central pit can serve as an advantage to bring a projected image from the narrow pit to the larger para-foveal area.

3.4. Calculation of the criteria for image focusing at the foveal pit area

It is well known that the foveal pit of an eagle can be observed with an ophthalmoscope and that the dip of the pit appears in focus with the rest of the retina (Wood, 1917; Wells, 1937). This phenomenon should be explained as it will help to understand the depth of field (depth of focusing) of the eagle eye. According to a standard definition, "depth of field" of the optical system is determined by the distance from the nearest object plane in acceptable focus to that of the farthest plane also simultaneously in acceptable focus. In simple words, the lens system of the eye is projecting the image on the retina. Then the image appears in focus not only in the focal plane, but also nearby, at some depth (in our Fig. 4 this is called $\boldsymbol{h}$). The "*acceptable defocusing*" or "*circle of confusion*" criteria can be different, but we will use terms used by Von Rohr (1899) for a simple optical objective. Simply, "acceptable defocusing" can be determined as 10% of the size of the sensory element $\boldsymbol{b}$ (Figs. 3,4); in our case $\boldsymbol{b}$ can be determined as a single Müller cell endfoot (about 2-8 μm). Using geometrical optics, we have calculated in Appendix 2 (Fig.4) that $\boldsymbol{h}$ can be approximated as: $h=\frac{\Delta b}{b}f$. As observed in Fig. 1, the optical sensor dimension (Müller cell endfoot) is about 2-8 μm (Fig.1 B). The "acceptable distortion" $\boldsymbol{\Delta b}$ will be ~10% of 2 μm ≈ 0.2 μm ($\lambda/2$ of the wavelength of blue light, or 0.8 μm for larger endfoot size). It is known that the focal

distance of the Pied Flycatcher eye is about 5000 μm (Zueva et al., 2003). In this case, the depth of focusing for a flycatcher eye will be: 5000/10 = 500 μm.

Interestingly, the depth of the foveal pit is very close to 300 μm in adult or about 150 μm in chicks (See Fig. 1A), therefore the images will be well focused in the whole pit and all Müller cell endfeet there can be used for image reception (Appendix 2).

4. Discussion

Müller cells are not simply support elements in the retina, but a key element of retinal organization during development. It is known that during retinal development Müller cells direct the migration of other cells (neurons) to their final positions in the retina and also direct neurite differentiation (Reichenbach and Robinson, 1995). Similarly, during age-related macular disease, the first event is Müller cell degeneration, which leads to the destruction of nearby neurons and the retraction of the photoreceptor cones, thus forming a macular hole (Koizumi et al., 2007). Recently, it was found that Müller cells also form an optical extension to cone photoreceptors, providing a low-scattering passage for light from the retinal surface to the photoreceptor cells (Franze et al., 2007; Agte et al., 2011). Using computational analysis, Labin et al. (2014) showed that an individual Müller cell can direct red light to an individual cone which leads to a significant gain, by a factor of 7.5 of photon absorption. This makes the “glia-to-cone tandem” very attractive for further study because according to these data Müller cells mediate the light transfer through the vertebrate retina with minimal distortion and low loss, acting like an “optical fibers”.

The idea of Müller cells being “light cables” was initially rejected, on the basis that the processes of Müller cells were too thin to transfer light. However, it was finally proved in 2007 with strong evidence (Franze et al., 2007). While the exact mechanisms of light energy transfer from top to bottom in Müller cells through their three major compartments (endfoot, stalk, distal processes) is still unknown and must be investigated, it may be related to the newly discovered physical principles of nano-optics. Recently, a visible light energy transfer through fibers of less than 10 nm (much less the λ of the visible light) with plasmons was developed for technical purposes (see for review: Gramotnev, Bozhevolnyi, 2010; Berini, DeLeon, 2011) and the principles of nano-focusing of conventional light into waveguide nano-fibers were formulated (Vedantam et al., 2009).

While technical devices cannot be directly compared to biological light fibers, it has long been appreciated that the deep conical foveal pit in the central retina of birds that possess extremely sharp eyesight is somehow related to visual acuity. Previously, scientists tried to explain the importance of the pit by suggesting special optical properties of the vitreous body protruding inside the pit forming an additional perfect lens (Walls, 1937) or forming a kind of specialized prism inside the pit (Pumphrey, 1948). Both theories (“prism” or “concave lens”) use the slight difference in refractive indices of “retina” and “vitreous” (the ratio is about 1.0063 according to Walls, 1937) to explain additional optical effects. However (i) there is still no data about the refractive indices of the liquid filling the pit, and (ii) Franze et al. (2007) showed that the differences in refractive indices between endfeet and vitreal liquid will be harmful for light trapping by endfeet and propagation to cones because

it can induce reflection of the light back from the retina. Therefore, the refractive indices of vitreous and glial endfoot should be about equal (Franze et al., 2007). Indeed, the behavior and hunting of nocturnal animals is correlated with only a few photons coming to retina which supports the idea that Müller cells are nearly ideal light catchers (trapping the light) and cables (conducting photons to cones and rods). In this context, the idea of the "concave lens" becomes less relevant.

Müller cells as an optical extension of cones, which form a kind of "light cable" from the inner retina to the photoreceptors (Franze et al, 2007), provides a different point of view to explain the importance of the conical tapered pit to provide high resolution. We have found that the walls of the foveal pit are covered by Müller cell endfeet, which could serve as the entrance of the light cable. Therefore, the Müller cell projects to a specific cone at the photoreceptor layer, and the light could be transferred from the pit wall, through the Müller cell body, to a cone photoreceptor (Fig. 2).

We also have shown that there is no need for an image to be focused on the photoreceptor layer: it is well enough to focus the image on the pit area. With depth of field (see Results Part 3.4) in the Pied Flycatcher eye being about 500 μm (see Part 3.4 and Fig. 4), all endfeet on the pit wall will be simultaneously in focus if the image plane will be in the middle the pit depth. On the other hand, in adult eagles the retina is about 400 μm, the eye is bigger as well and the focal distance is about the dimension of the eye (Wood, 1917). This gives give a much bigger depth of field and all the depth of the retina as well will be simultaneously in focus. And most notably, if a Müller cell transduces the light intensity individually and specifically to a photoreceptor, (i) the refraction between vitreous body and "retina" has no importance in forming the image on photoreceptor layer and (ii) such Müller cell alignment can bring images far from the fovea. Therefore, the angular positioning of "light cable's" entrances at the wall of the fovea pit gives the advantage of $1/(\sin\alpha)$ (there α is an angle of the pit wall) ~2 times in Pied flycatcher chicks and ~3 times in adult, thereby, increasing the number of Müller cells (and thus cones) involved (see Results Part 3.3).

In conclusion, the light propagation function of Müller cells allows us to suggest a new explanation for the shape of the foveal pit in birds: the deep conical shape of the pit is an advantage, and not an obstacle, for the formation of an image. We can suggest also that the same optical principles can be used for new photo-equipment, because their objectives usually have relatively large depth of field for image formation as in birds.

Appendix

Apendix 1 Calculation of the visual resolution and the sensory element (endfoot) density in a flat retina and a retina with the pit (See Fig. 3)

Let the detector system consist of (i) the optical lens with diaphragm, and (ii) a 2D array of sensory elements (Fig. 3, red triangles). This optical sensor array determines the number of pixels and thus optical resolution. Let the diaphragm have a hole in the center with radius ***r*** (eye iris size) and let ***a*** be the smallest object (Fig. 3, red arrow) that can be resolved by a detector placed in the image plane. Note: if the size ***a*** of a physical object is smaller than

radius ***r*** of the input aperture of the detector diaphragm, we have to use in all relations shown below the symbol ***a*** (but if we have inverse conditions, symbol ***a*** should be substituted everywhere by symbol ***r*** as a limit of input aperture).

Distance from the focus point to the top of sensor array is determined as follows:

$$tg\,(\beta)=\frac{a}{f}$$

$$x=\frac{b}{tg\,(\beta)}=\frac{bf}{a}$$

Here ***b*** is the size of sensor unit (pixel), ***f*** is a focal distance of the lens.

Distance S_2 from the center of the lens to the surface of sensor array is determined as follows (Fig. 3):

$$S_2=f+x=f+\frac{bf}{a}$$

Using basic relationship for the lens, we determined S_1, the distance from the lens center to the object ***a***

$$\frac{1}{S_1}+\frac{1}{S_2}=\frac{1}{f}$$
$$\frac{1}{S_1}=\frac{1}{f}-\frac{1}{S_2}=\frac{1}{f}-\frac{1}{f+\frac{bf}{a}}=\frac{1}{f}\frac{b}{a\left(1+\frac{b}{a}\right)}=\frac{1}{f}\frac{b}{a+b}$$
$$S_1=f\frac{a+b}{b}\approx f\frac{a}{b}$$

The next step is to determine how the form of the sensor's array (flat) versus deep conical plays a role in optical resolution. As Fig. 2 shows, for a sensor unit (in our case for a single endfoot of a Müller cell) with size ***b*** placed on the surface of a conical pit, inclined by angle α to the optical axis (Fig. 2), the last relation can be presented as follows:

$$S_1'=\quad f\frac{a+b\cdot Sin(\alpha)}{b\cdot Sin(\alpha)}\approx f\frac{a}{b\cdot Sin(\alpha)}$$
$$\chi=\quad \frac{S_1'}{S_1}=\frac{1}{Sin(\alpha)}$$

i.e. the distance S'_1 at which an eagle can see the same object increases according to a factor X: Similarly, the amount of endfeet ("sensor units" in the optical array) will be increased when the pit surface is compared with the surface of the flat fovea: if the length of the pit side is *L*, then the ratio of the overall amount of sensor units and the density (of pixels) per image is:

$$\chi=\frac{S_1'}{S_1}=\frac{1}{Sin\,(\alpha)},\quad i.e.,\quad \text{about 3 times for a } 20^\circ \text{ fovea pit.}$$

$$Density'=\frac{D'}{D}=\frac{\pi rL}{\pi r^2}=\frac{L}{r}=\frac{1}{Sin\,(\alpha)}=3 \quad \text{times larger at a conical surface than at a flat surface.}$$

Apendix.2 Calculation of the distortion of the image out of the focal plane (Fig. 4)

Let ***x*** be the length from object to focal point. Then:

$$tg\,(\alpha)=\frac{b}{f}$$

$$x=\frac{a}{tg\,(\alpha)}=a\frac{f}{b}$$

The distance S_1 from the object ***a*** to the lens center can be determined as follows:

$$s_1=f+x=f\left(\frac{a}{b}+1\right)$$

The ***tg β*** can be determined as follows:

$$tg\,(\beta)=\frac{a}{s_1}=\frac{a}{f\left(\frac{a}{b}+1\right)}=\frac{ab}{f\,(a+b)}$$

At the foveal pit, the distance S_2 between the lens and the object image (thin red arrow, ***b***) can be determined as follows:

$$s_2=\frac{b}{tg\,(\beta)}=\frac{f\,(a+b)}{a}$$

A distance (y_1) between the lens and the top of the pit *(b')* and the distance (y_2) between the lens and the pit bottom *(b'')* can be determined as follows:

$$\begin{aligned} y_1&= s_2-\tfrac{h}{2}=\tfrac{f(a+b)}{a}-\tfrac{h}{2}\\ y_2&= s_2+\tfrac{h}{2}=\tfrac{f(a+b)}{a}+\tfrac{h}{2}\end{aligned}$$

Image sizes related to these distances can be determined as follows:

$$b' = y_1 tg(\beta) = \left[\frac{f(a+b)}{a} - \frac{h}{2}\right] \frac{ab}{f(a+b)} = b - \frac{abh}{2f(a+b)}$$
$$b'' = y_2 tg(\beta) = \left[\frac{f(a+b)}{a} + \frac{h}{2}\right] \frac{ab}{f(a+b)} = b + \frac{abh}{2f(a+b)}$$

Thus, image will be distorted by a value of **Δ*b***:

$$\Delta b = \frac{abh}{f(a+b)}$$

and

$$\frac{\Delta b}{b} = \frac{ab}{f(a+b)}$$

Because ***b*** is negligibly smaller than ***a***,

$$a >> b$$
$$\frac{\Delta b}{b} = \frac{h}{f}$$

Thus, the calculations show that the distance ***h*** (green line) between focal planes ***b'*** and ***b''*** with distortion **Δ*b*** will be:

$$h = \frac{\Delta b}{b} f$$

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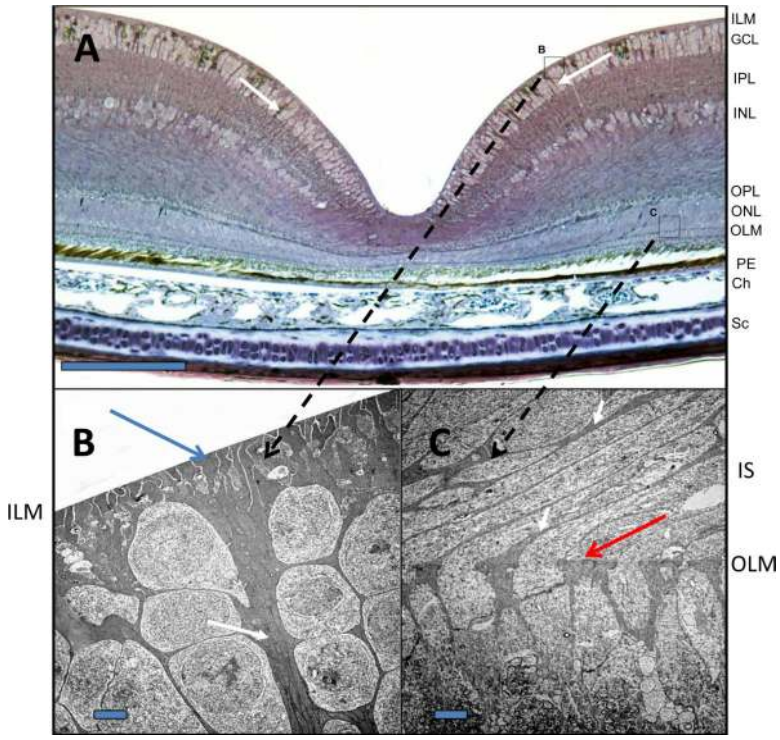

Figure 1. Retina of a Pied Flycatcher

A: Central foveal pit is shown. Toluidine blue staining of 27 day old Pied Flycatcher retina reveals Müller cells (dark) in the foveal pit (white arrows point Müller cell stalks). **B:** The insert from **A** with electron microphotography showing Müller cell endfeet (blue arrow) that form the inner limiting membrane (ILM). The endfeet are coming to the stalks of the cells (white arrow). The stalks are spanning the internal retina. **C:** The insert from **A**, showing Müller cell distal processes (grey, pointed by white arrows) that surround and enwrap cone inner segments (IS). At the layer between inner segments and outer segments of photoreceptors, Müller cells form a border (red arrow) and outline a cap like structure around cone photoreceptors thus forming the outer limiting membrane (OLM). Scale bar: 100 micrometers in **A**, 2 micrometers in **B** and **C**. Abbreviations: **ILM**-inner limiting membrane, **GCL**-ganglion cell layer, **IPL**-inner plexiform layer, **INL**-inner nuclear layer, **ONL**-outer nuclear layer, **OLM**-outer limiting membrane, **IS**-inner segments of photoreceptors, **PE**-pigment epithelium, **Ch**-choroid, **Sc**- sclera.

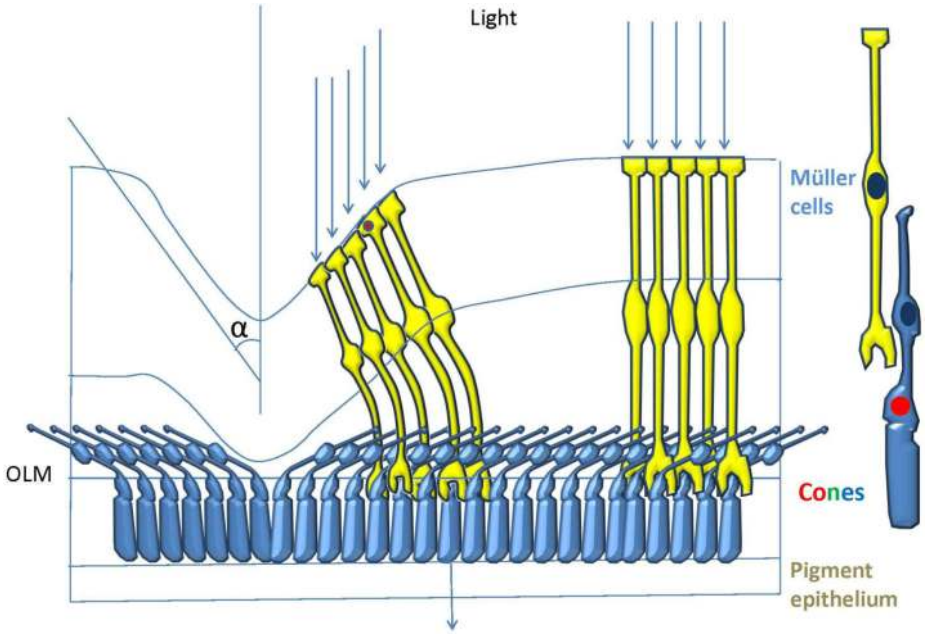

Figure 2. Proposed scheme of Müller cell organization in the foveal pit of Pied Flycatcher

Müller cells (yellow fibers) serve as "light cables" with properties to project a foveal image on the para-foveal cones (blue cells). Therefore, Müller cells can propagate an image (projected to central fovea) far outside the center and thus serving an extended and enlarged amount of photoreceptors (details in Results and Appendix).

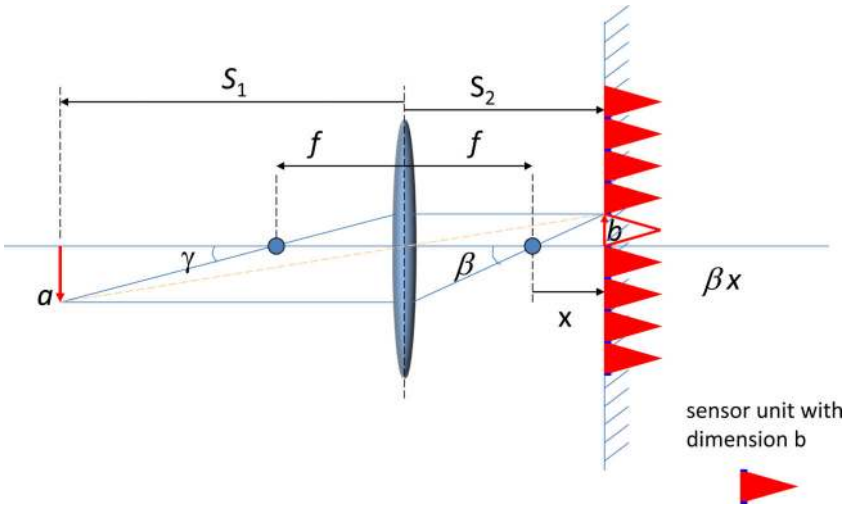

Figure 3. Calculation of the visual resolution in a flat retina (peripheral retina) compared with the central foveal pit

The detector system consists of the optical lens with diaphragm, and a plane detector with discrete sensory units (red triangles) making a sensor array. We suggest that this 2D array represents endfeet of Müller cells to which an image (red arrow) is projected. In this scheme, ***a*** is the smallest object that can be resolved by a sensory array placed at the image plane; ***b*** is the size of the sensor unit (single endfoot size); ***f*** is the focal distance of the lens. Details in text and in Appendix 1.

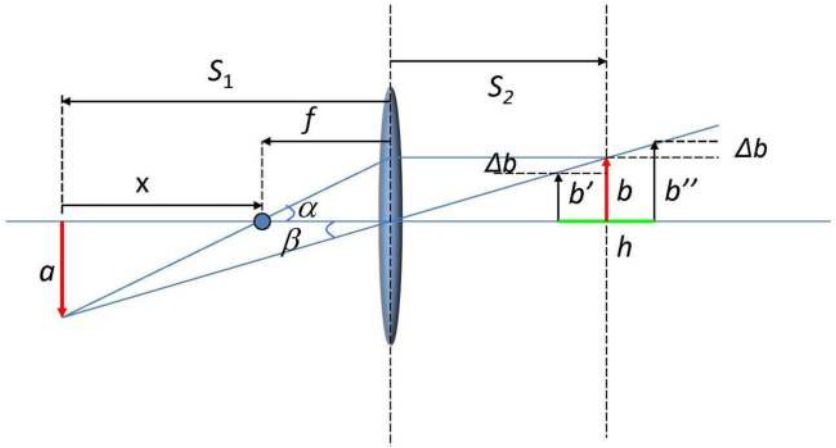

Figure 4.

Calculations of acceptable focal distortion (**Δ*b***) of an image (***b***) near the focal plane. The distance ***h*** represents the *"depth of field"* (green line). We suggest that the depth of field is bigger than the depth of the foveal pit (Fig. 1A). For details see Appendix 2.