Distribution of the α -Type Ganglion Cells in the Chicken Retina

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ABSTRACT. The distribution of retinal ganglion cells, particularly the α -type ganglion cells, in the chicken retinae was studied with whole mount preparations stained with cresyl violet. The density maps of all the cells including the glial cells and the displaced amacrine cells in the retinal ganglion cell layer showed that the area centralis was the region of the highest cell density. There was a drop in density about the circumference of the area centralis in all directions without the formation of the visual streak. However, the decrease in cell density was not so remarkable toward the superior-temporal region. The α -type ganglion cells in the area centralis were less numerous than those in the peripheral regions. The density of the α -type ganglion cells was higher in the inferior-temporal, inferior, inferior-nasal, nasal and superior-nasal regions compared with that in the other regions. The distribution of the α -type ganglion cells in the chicken retina differed considerably from that in mammals.

In bird's retinae, the distribution of retinal ganglion cells has been reported only in the pigeon [1] and chick [6].

The retinal ganglion cell populations were morphologically classified into large-, medium- and small-sized cell types and designated as α -, β - and γ -type ganglion cells, respectively. The different functional roles and central projections of these distinct types of ganglion cells have been demonstrated [10, 11, 16, 21, 22, 26]. The dendritic branching patterns of these cells have been shown by the Golgi impregnation method and the significance of their morphological differences has been discussed from a physiological standpoint [2, 22]. It is suggested that the α -type ganglion cells correspond to the brisk-transient units [3], subserve such peripheral vision function as detection of fast-moving images [26], and project to both the midbrain and the forebrain [10, 11, 16, 21, 22, 26]. The distribution of the α -type ganglion cells in the retina, however, has been

described only in the cat [24, 32], owl monkey [33] and pigmented rabbit [18].

The present paper describes for the first time the distribution of α -type ganglion cells in whole mount preparations of the chicken retina.

MATERIALS AND METHODS

Seven White Leghorn chickens, 10, 15, 30, 40, 60, 80 and 400 days old, were used in this study. The eyes were removed immediately after sacrifice. The anterior portion was discarded and the vitreous humor was removed as much as possible, and the pecten and optic nerves were cut off at the positions close to the retina. After removal of the underlying pigment epithelium, the retinae were cut radially and laid on a gelatinized slide. The slides were stored for 30 min in formalin vapor to fix retinae. The retinae were then stained with 0.1% cresyl violet. The areas of the flat mounts were measured with a planimeter on the photomicrographs taken at a magnifica-

tion of $\times 132$. Cell counts were made at 1-mm intervals on the retinal surface. In the whole mount preparations stained with cresyl violet, the displaced amacrine cells were difficult to discriminate from the ganglion cell populations, so that they were included in the cell count. The cells were counted in the retinal area of 0.023 mm^2 at a magnification of $\times 132$ of a photomicrograph in two cases (60 and 80 days old chickens). Maps of the retinal ganglion cell distribution over the retina were then drawn with isodensity lines.

The α -type ganglion cells were $10 \mu\text{m}$ or more in mean diameter and could easily be distinguished from the other types of cells. The count of the α -type ganglion cells was made in all cases and the distribution of these cells on the retinae was plotted on the map.

RESULTS

The retinal ganglion cell layer is composed of ganglion, glial and displaced amacrine cells. The displaced amacrine cells are hardly distinguished from the

ganglion cells. The glial cells, which have small perikarya with darkly stained nuclei and lack Nissl substance in the cytoplasm, could be distinguished from the other components. However, these cells were also counted in this experiment to avoid error in measurement. In the 60 and 80 days old chickens, the areas of the retinae were 393 and 459 mm^2 and the total cell numbers $1,570,000$ and $1,660,000$, respectively. The densities of all the cells contained in the ganglion cell layer of these two retinae are shown in Fig. 1. The highest density was observed in the area centralis and in the oval-shaped isodensity lines encircling the area centralis in all directions; the density decreased though not so remarkably in the superior-temporal region (Fig. 2).

In various retinal regions, the large cells rich in Nissl substance were identified as the α -type ganglion cells and such cells were counted in the retinal area of 0.023 mm^2 at 1-mm intervals on the retinal surface in all the retinae. The diameter of the perikarya of these cells was longer than $10 \mu\text{m}$ on the average.

Fig. 1. Light micrographs of the ganglion cell layer in a whole mounted retina (80 days old chicken) stained with cresyl violet. Note the regional difference in cell size and cell density of the α -type (large) ganglion cells. A: Area centralis. B: Peripheral region. $\times 400$.

Fig. 2. Isodensity map of the cell populations in the retinal ganglion cell layer in the retina (right eye, 80 days old chicken). The figure on each line represents the number of cells. $\times 10^3/\text{mm}^2$. Scale, 1.0 cm.

Fig. 3. The density distribution of the α -type ganglion cells in the retina (80 days old chicken). Scale, 1.0 cm.

Table 1. Areas of the retinae and numbers of the α -type ganglion cells

Age (days)	Area of retina (mm ²)	Number of α -type ganglion cells
400	412.2	39,826
80	459.3	38,087
60	392.9	32,913
40	346.8	30,652
30	322.6	31,783
15	269.5	20,870
10	204.3	19,609

The diameter of α -type ganglion cells in the area centralis was short and tended to elongate toward the peripheral regions of the retina (Fig. 1). The number of α -type ganglion cells was from 30,000 to 40,000 in the retinae of chickens older than 30 days, but less than 30,000 in younger specimens of younger chickens (Table 1). The α -type ganglion cells constituted 2.1 and 2.3% of the total cells in the retinal ganglion cell layer in the 60 and 80 days old chickens, respectively.

The density of the α -type ganglion cells throughout the retinal surface is numerically expressed per mm² in Fig. 3. This figure showed the characteristic pattern of the distribution of this type of ganglion cells. The density was lower in the area centralis than in the peripheral regions. However, higher densities were noted in the inferior-temporal, inferior, inferior-nasal, nasal and superior-nasal regions, than in the other regions.

DISCUSSION

Morphological observations of the retinal ganglion cell layer in birds have been reported only in the pigeon [1] and chick [6].

Two retinae (60 and 80 days old) having surface areas of 393 mm² and 459 mm² of were used for the total cell counts in the retinal ganglion cell layer. The total numbers of cells, including glial and

displaced amacrine cells, were 1,570,000 and 1,660,000, respectively. These values differ greatly from those reported for the pigeon (2,380,000 excluding glial cells) [1] and the chick retina (2,600,000 excluding glial cells and amacrine cells) [6]. The distribution of the ganglion cells in the bird retina was also reported in the pigeon [1] and chick [6]. In the pigeon retina [1], there were two high density areas, namely, a minor posterior fovea and an area of increased density in the superior-posterior quadrant. Ehrlich [6] stated in the chick retina that the high density region extended from the central area into the superior-temporal retina and that the high density region corresponded to the position in the lateral visual field extending into the inferior-frontal fields. The gradual areal increase throughout the entire ganglion cell populations from the high-density to low-density regions reported [6] was similar to that in the present observations (Fig. 2). The two high-density regions described in the pigeon retina [1] were not recognized in the chicken retina, nor was found the formation of the visual streak in this observation.

Ganglion cell populations are composed of small- (γ), medium- (β) and large-sized cells (α). The large-sized cells are easily distinguished from the other two types of neurons as shown in the some size histograms drawn in previous reports [1, 7–9, 12, 14, 15, 18–21, 23, 26, 29–33]. The α -type ganglion cells having perikaryon diameters longer than 10 μ m were 30,000 to 40,000 in number in the adult retina and less in younger retina, possibly as a result of mis-identification of the immature α -type ganglion cells. The α -type ganglion cells occupied 3 to 10% of total ganglion cell population in the cat [13, 15, 24, 32] and 7% in the albino rat [23]. In the present observa-

tions, the percentages of the α -type ganglion cells to the total cells in the retinal ganglion cell layer were 2.1 and 2.3% in 60 and 80 days old chickens, respectively. However, the values to the ganglion cell populations excluding the glial cells and the displaced amacrine cells could have been more highly estimated. These α -type ganglion cells have not found in the area centralis in the pigeon [1], nor could have been distinguished from the remainders of the ganglion cell types in the chick retina [6]. These cells of this type in the area centralis were not distinguishable by areal measurement. In contrast to these descriptions [1, 6], the α -type large ganglion cells were recognized in the area centralis and there was a definite increase in the mean size eccentrically from the area centralis as reported for mammals [5]. The cell density of α -type ganglion cells was different from that of total ganglion cell populations; the number of these cells was smaller in the area centralis and larger in the periphery. The differences in cell density among quadrants, however, were quite evident with high density at the inferior-temporal, inferior, inferior-nasal, nasal and superior-nasal regions and comparatively low density in the other regions (Fig. 3). In the cat, the isodensity lines of α -type ganglion cells had the form of a 4-pointed star with rather blunt points corresponding to the horizontal and vertical ridge of augmented density [32] or the narrow annulus centered on the area centralis [24]. A physiological investigation [9], however, showed that the density of α -type ganglion cells actually decreased at the area centralis. The absolute density of the α -type ganglion cells in the hooded rat showed a relatively flat distribution over the retina [8]. In the pigmented rabbit, the region of high density

of α -type ganglion cells was recognized at the temporal end of the visual streak as a large cell node [18]. Such a large cell node in the pigmented rabbit was considered to be a better candidate for subserving an area centralis-like function in the rabbit than either the visual streak as a whole or the region of the peak ganglion count. The distribution of α -type ganglion cells in the chicken seemed to differ from that in mammals. The dendritic field diameter and the dendritic branching pattern of the three ganglion cell types in mammals were different from each other [2, 13, 17, 25, 28]. Boycott and Wässle [2] suggested a correlation between the morphological class and the physiological units of the ganglion cells. Cleland and Levick [3] and Cleland *et al.* [4] also compared their results with the morphological data of Boycott and Wässle [2] and suggested that the brisk-transient units corresponded to α -type ganglion cells, the brisk-sustained to β -type ganglion cells and the sluggish units were included among the γ -type ganglion cells. In mammals, the different central projections of different ganglion cell types were evidence for their distinct functions [10, 11, 16, 21, 26, 27], the β -type ganglion cells project to the lateral geniculate nucleus, the γ -type ganglion cells project principally to the superior colliculus and also to the lateral geniculate nucleus, and the α -type ganglion cells project to both of these centers. The α -type ganglion cells, as mentioned perviously [26], subserve such peripheral vision function as the detection of fast-moving images, being important to both the midbrain and forebrain visual processing.

The retinal distribution of α -type ganglion cells in the chicken characterized by the morphological features was entirely different from those in mam-

mals. This difference may be explained on the basis of the dissimilar visual behaviors of birds and mammals.

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要 約

鶏網膜における α 型視神経細胞の分布: 上嶋俊彦・上原正人 (鳥取大学農学部家畜解剖学教室)——
鶏網膜視神経細胞層の視神経細胞, とくに α 型細胞の分布について, cresyl violet で染色した whole mount preparation によって, 観察した。視神経細胞は, もっとも高い密度をしめす中心野を中心として superior-temporal の方向にひろがる卵円形の同心円性の等密度線を書いて分布しており, 線状中心野の形成はなかった。生理学的に brisk-transient unit に相当し, 速かに動く像を知覚する機能をもつとされている α 型細胞は, 数的に少数ながら中心野にも存在し, 周辺に向うに従って多かった。とくに inferior-temporal, inferior, inferior-nasal, nasal および superior-nasal の部でより多く, その他の部では比較的少数で, ほ乳類の分布とは異なっていた。