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FULL PAPER

Anatomy

Morphological analyses of the retinal photoreceptor cells in the nocturnally adapted owl monkeys

Nobue KUNIYOSHI[1)], Yuji YOSHIDA[2)], Yoshiki ITOH[3)], Shin-ichi YOKOTA[4)], Takeshi KURAISHI[4,7)], Shosaku HATTORI[4)], Tomohiro KONDO[5)], Midori YOSHIZAWA[6)], Chieko KAI[4)], Yasuo KISO[1,2)] and Ken Takeshi KUSAKABE[1,2)]*

[1)]Laboratory of Basic Veterinary Science, The United Graduate School of Veterinary Science, Yamaguchi University, Yamaguchi 753-8515, Japan
[2)]Laboratory of Veterinary Anatomy, Joint Faculty of Veterinary Medicine, Yamaguchi University, Yamaguchi 753-8515, Japan
[3)]Laboratory of Veterinary Radiology, Joint Faculty of Veterinary Medicine, Yamaguchi University, Yamaguchi 753-8515, Japan
[4)]Amami Laboratory of Injurious Animals, Institute of Medical Science, The University of Tokyo, Kagoshima 894-1531, Japan
[5)]Laboratory of Laboratory Animal Science, Division of Veterinary Science, Graduate School of Life and Environmental Science, Osaka Prefecture University, Osaka 598-8531, Japan
[6)]Graduate School of Agricultural Science, Utsunomiya University, Tochigi 321-8505, Japan
[7)]Present affiliation: HAMURI Co., Ltd., Ibaraki 306-0101, Japan

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ABSTRACT. Owl monkeys are the only one species possessing the nocturnal lifestyles among the simian monkeys. Their eyes and retinas have been interested associating with the nocturnal adaptation. We examined the cellular specificity and electroretinogram (ERG) reactivity in the retina of the owl monkeys by comparison with the squirrel monkeys, taxonomically close-species and expressing diurnal behavior. Owl monkeys did not have clear structure of the foveal pit by the funduscope, whereas the retinal wholemount specimens indicated a small-condensed spot of the ganglion cells. There were abundant numbers of the rod photoreceptor cells in owl monkeys than those of the squirrel monkeys. However, the owl monkeys' retina did not possess superiority for rod cell-reactivity in the scotopic ERG responses. Scanning electron microscopic observation revealed that the rod cells in owl monkeys' retina had very small-sized inner and outer segments as compared with squirrel monkeys. Owl monkeys showed typical nocturnal traits such as rod-cell dominance. However, the individual photoreceptor cells seemed to be functionally weak for visual capacity, caused from the morphological immaturity at the inner and outer segments.

KEY WORDS: evolution, owl monkey, photoreceptor cell, retina, squirrel monkey

Aotus genus, known as one type of the New World monkeys, are classified in the Simiiformes infraorder, Platyrrhini parvorder, Aotidae family and inhabit at the Central and South American areas, commonly called as "owl monkeys" or "night monkeys", believed as the only one group possessing nocturnal life styles among the simian primates. It is estimated about 15 million years ago the owl monkeys were segregated from the common diurnal ancestors, and passed the transit process from the diurnal to the nocturnal life styles [12]. The retinas of owl monkeys contain the only type of photosensitive pigment, having peak sensitivity around 543 nm in the spectrum curve [8]. They lost the short wavelength pigment (peak sensitivity; around 430 nm), preserving in the retina of the squirrel monkeys, which are taxonomically close species to the owl monkeys [7]. The dual light spectrum reactivity to the short and middle wavelengths is equipped normally in the retinas of Platyrrhine monkeys without the owl monkeys [1].

There are wide diversities of eye structures among animals, and it is believed that most of eyes have adapted to demonstrate excellent visual capacity in their living environment. The eye structures are developed for collection of light, and the retina is specific tissue to receive the photon and evoke the visual image signals. In general, the eye structure is conserved commonly in each species and the retinal morphogenesis looks stable. It is rare to find the intermediate traits to prove acquisition of new functional structure and gradual grades in the eye evolution. Signs of the eye evolution processes are considered to be included in cellular dynamics and molecular basis in the retinas. Dyer *et al.* (2009) examined retinas of the owl monkeys and diurnal capuchin

*Correspondence to: Kusakabe, T. K.: kusakabe@yamaguchi-u.ac.jp

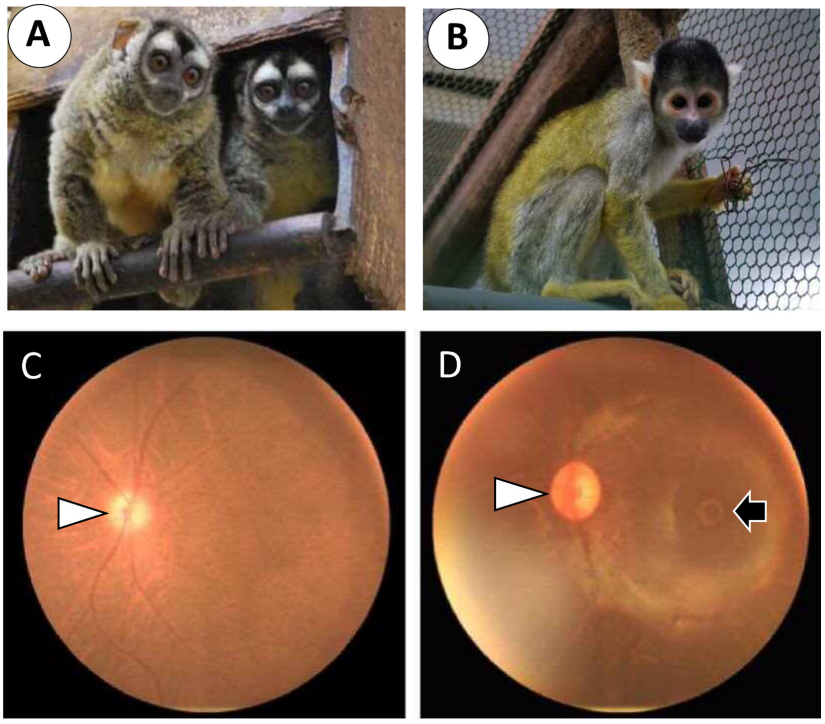

Fig. 1. Visual appearances of the owl monkey (A) and the squirrel monkey (B). Note the larger palpebral fissures in owl monkeys than squirrel monkeys. C, D: Eye fundus photographs (left eyes). The optic disc (white arrowheads) is seen in the retina of owl monkey (C) and the squirrel monkey (D), characterized by the extending vascular arches. The central fovea (black arrow) is clearly seen only in the fundus of squirrel monkeys.

monkeys, and found differences in the velocity of retinal cell mitosis [5]. Also, they suggested that cellular appearance in retinas depend on the differentiation process from the retinal progenitor cells.

The retina of the owl monkeys has been examined and revealed that the photoreceptor cells were biased to the dominancy of the rod cells [15]. The tendency is analogous to the retina of the nocturnal bushbaby and on the other hand, the numbers of the rod and cone photoreceptor cells are the comparable level in the diurnal rhesus monkeys and human [13]. We examined the cellular appearance of the rod, cone and ganglion cells in the owl monkeys precisely and compared to the squirrel monkeys, the close and diurnal species. Furthermore, the morphology of the outer and inner segments of photoreceptor cells was compared. Measurements of the electrophysiologic reactivity were conducted for evaluation of retinal function in both monkeys, and the consistency with the data of appearance and morphology of the retinal cells was analyzed. We found unique retinal profiles in the retina of owl monkeys, and evaluated the morphology of photoreceptor cells for the reflection of visual capacity and the process of evolutional adaptation.

MATERIALS AND METHODS

Animals

The owl monkeys (*Aotus lemurinus*, Fig. 1A) and the squirrel monkeys (*Saimiri boliviensis*, Fig. 1B), bred at the under the laboratory facilities (Amami Laboratory of Injurious Animals, Institute of Medical Science, The University of Tokyo), were used. All monkeys grew under controlled conditions; illumination was basically dependent on the natural light/dark cycles tracked by local sunrise and sunset. Animals were divided along gender lines for the application to each experiment (Table 1), because of the numerical and collectible restriction of sexually matured animals and consideration for the sexual difference of chromatic visual capacity.

Animals for funduscopic observation and electroretinogram analysis were stabilized by enough sedation and deep anesthesia with i.m. 0.05 mg/kg body weight of medetomidine and 15 mg/m*l* body weight of ketamine. After confirmation of deep anesthesia, some monkeys were euthanized by i.v. sodium pentobarbital. Eyeballs were collected and scaled. Animal welfare was preserved following the guideline of the care and use of laboratory animals at The University of Tokyo, and experimental protocols were approved from the experimental animal committee (experimental No. 2013-328).

Funduscope observation

Some monkeys were deeply anesthetized by the methods mentioned above. Observation of the eyegrounds were conducted using the Clear View funduscope (Optibrand, Fort Collins, CO, U.S.A.).

Table1. Animal data and applied experiments

	Identification No.	Sex	Age (Year)	Analysis application
Owl monkeys	Ow001	Male	3	ERG
	Ow002	Male	3	ERG
	Ow003	Female	4	Eyeball measurement
				SEM
	Ow004	Female	4	Eyeball measurement
	Ow005	Female	4	SEM
	Ow006	Female	5	ERG
	Ow007	Male	6	ERG
				Eyeball measurement
				Wholemounts
	Ow008	Male	7	Eyeball measurement
				Wholemounts
	Ow009	Female	>11	SEM
	Ow010	Female	>14	Eyeball measurement
	Ow011	Male	>15	Eyeball measurement
Squirrel monkeys	Sq001	Male	4	ERG
	Sq002	Female	4	ERG
	Sq003	Female	4	Eyeball measurement
				SEM
	Sq004	Male	5	ERG
	Sq005	Female	5	SEM
	Sq006	Female	5	Eyeball measurement
				SEM
	Sq007	Male	9	Eyeball measurement
	Sq008			Wholemounts
	Sq009	Male	13	Eyeball measurement
	Sq010			Wholemounts
	Sq011	Female	13	Eyeball measurement

ERG: electroreytinogram, SEM: scanning electron microscope.

Retinal wholemounts

Eyeballs were cut and divided at the half line of the frontal face. From the posterior halves, retinas were carefully separated with recording the orientation information, cut into some pieces, and fixed with 4% paraformaldehyde during overnight. The retinal wholemount specimens were observed using the differential interference contrast microscope (Olympus, Tokyo, Japan). The specimens were observed again following with Nissl staining. Morphometric assays were conducted using the cellSens imaging software (Olympus).

Scanning electron microscope (SEM)

From the fixed eyeground samples, retinal specimens were trimmed out from the regions of the temporal side on the level line passing through the optic disc, estimated as the central visual area and the around regions. Specimens were treated continuously with 2.5% glutaraldehyde, 1% tannic acid, and 2% osmium tetroxide. Following dehydration with upgraded ethanol series, specimens were freeze-dried using t-butanol and the VFD-21S equipment (Vacuum Device, Mito, Japan). Specimens were coated with platinum using the magnetron-ion spatter (Vacuum Device), and observed using Miniscope TM 3000 (Hitachi High-Technologies, Tokyo, Japan). Morphometric assays were conducted for the rods and cones, measuring the longest width of the inner segments at the 2 points of each cell and data were collected form more than 3 cells in each animal. Also, the combined height length of inner and outer segment was measured from the outer limiting layer to the top of outer segments on more than 3 rod cells.

Eelectroretinogram (ERG)

Following funduscope observation, monkeys were continuously anesthetized and laid on the shield mattress (Japan GE Marquette Medical Systems, Tokyo, Japan) for cutting off electric noises. Needle electrodes were positioned under the auricle skin and the middle of forehead (the indifferent and earthed electrode respectively). The small combined devices for LED light stimulation and eyeball contact electrode (MAYO, Nagoya, Japan) were set on the surface of cornea after treatments of 0.4% oxybuprocaine hydrochloride and 1.5% hydroxyethyl cellulose for corneal anesthesia and protection. Following acclimation in the dark room for 30 min, the scotopic ERGs were measured by the light stimulation of 80 cd/m^2 and 0.12 msec. Then, next acclimation in the bright room for 10 min, the photopic ERGs were measured by the light stimulation of 6,000 cd/m^2(background: 25 cd/m^2) and 0.5 msec. Responses to the flicker signals were measured following the 30 hertz short light stimulations (6,000 cd/m^2 and 0.5 msec). The scotopic ERG reflects the potential response for the rod cells, and both the photopic ERG and the 30 Hz

Table 2. Comparison of eyeball and cornea sizes (female monkeys)

	Body weight (kg)	Eyeball		Cornea width (mm)
		Transversal length (mm)	Anteroposterior length (mm)	
Owl monkeys	0.968 ± 0.122[a)]	19.8 ± 0.52[b)]	19.8 ± 0.98[b)]	13.2 ± 0.17[b)]
Squirrel monkeys	0.678 ± 0.328	14.3 ± 0.68	14.4 ± 1.43	8.13 ± 0.31
Human[c)]		24.22	23.81	11.52

Mean ± S.D. a) $P<0.05$ and b) $P<0.01$ vs. Squirrel monkeys. c) Data of adult Japanese (men and women), cited from reference [11].

flicker ERG reflect the cone cell potentials. Latent times for each ERG after the time point of light stimulation and the peaks of response amplitudes were measured.

Statistical analyses

The data obtained from the measurements of eyeballs, cornea, retinal cells, and the sizes of inner and outer segments were statistically compared between squirrel monkeys and owl monkeys using two-sided Student's *t*-test. Significant differences were considered when *P* values were under 0.05. For the eyeball measurements, statistical analysis was conducted on the female data alone (Table 2) because of inadequacy of the male data numbers (The sizes of male eyeball and cornea were slightly larger than those of females in both monkeys). For the analysis of ERG, all data were mixed following confirmation of non-predominant differences between male and female ERG data in each monkey.

RESULTS

Owl monkeys had the large eyeballs and cornea sizes as compared with squirrel monkeys (Table 2). Same as human, in the retina of squirrel monkeys, the central fovea was observed at the temporal area from the optic disc (Fig. 1D). Retinal topographies prepared by retinal wholemount observation showed the high-density areas for ganglion cells in squirrel monkeys (Fig. 2B), which were corresponded with the position of the central fovea. On the other hand, exploration with funduscope could not find clear structure of central fovea in owl monkeys (Fig. 1C). Observation of the retinal wholemount actualized small dense area of ganglion cells (Fig. 2A).

Measurement of cell density showed wide deviation of the cone photoreceptor cells in squirrel monkeys (Fig. 2C), and the dense area was biased at the region of central fovea (inset of Fig. 3B). Retinas of owl monkeys were composed by few numbers of cone cells and abundant numbers of rod cells as compared with squirrel monkeys (Figs. 2C, 2D and 3A). The averages of cell density in the owl and squirrel monkeys were 346,602 and 100,895 cells/mm^2 (rod), 2,907 and 8,672 cells/mm^2 (cone), and 2,464 and 3,454 cells/mm^2 (ganglion), respectively. Ratios of rod/cone cells also revealed dominance of rod cells in the retina of owl monkeys (Table 3).

Sizes of cellular diameter measured in the wholemount specimens were 2.19 ± 0.33 μm (rod) and 4.74 ± 0.69 μm (cone) in the owl monkeys (Fig. 3A); 4.91 ± 0.91 μm (rod) and 29.1 ± 5.10 μm (cone) in the squirrel monkeys (Fig. 3B). The diameter sizes were significantly small in both of rod and cone cells of owl monkeys. Nissl staining on the wholemounts showed various sizes and shapes of ganglion cells in both monkeys (Fig. 3C and 3D). Measurement of ganglion cell density did not show statistical difference between both monkeys, but the rates of cone/ganglion were significantly higher in the squirrel monkey (Table 3), suspected due to dominance of the cone cells.

SEM observation revealed differences of the size of photoreceptor cells between both monkeys, especially the morphology of the inner and outer segments (IS and OS; Fig. 4A–F). Width of IS of the owl monkeys was smaller about 0.49 and 0.60 times (cone and rod cells, respectively) than those of squirrel monkeys (Fig. 4G and 4H). Combined length of IS and OS (IS+OS) were shorter in owl monkeys about 0.38 times than those of squirrel monkeys (Fig. 4I). Concerning nuclear sizes of the photoreceptor cells (at the outer granular layer of retinal tissue), the major axes were shorter in the owl monkeys (mean length: 4.5 μm, squirrel monkeys: 6.1 μm) and the minor axes were almost same in the length (mean length: 4.4 and 4.6 μm in owl and squirrel monkeys, respectively).

ERG analyses revealed the comparable for the scotopic ERGs level between two monkeys (Fig. 5A and 5D). Superiority of the scotopic ERGs in the owl monkeys compared to the squirrel monkeys did not observed (Fig. 5G and 5H), regardless numerical advantage of the rod cells (Fig. 2D). Stronger reactivity was detected at the photopic ERGs in squirrel monkeys than those of owl monkeys (Fig. 5B, 5E and 5H). Flicker ERGs also showed strong reactivity in the retina of squirrel monkeys as compared with owl monkeys (Fig. 5C, 5F and 5H).

DISCUSSION

Funduscope observation could not find obvious structure of the central fovea in the retinas of owl monkeys. Previous cytological studies reported that there were small or no concentrate area for high cell densities of photoreceptor cells in the owl monkeys'

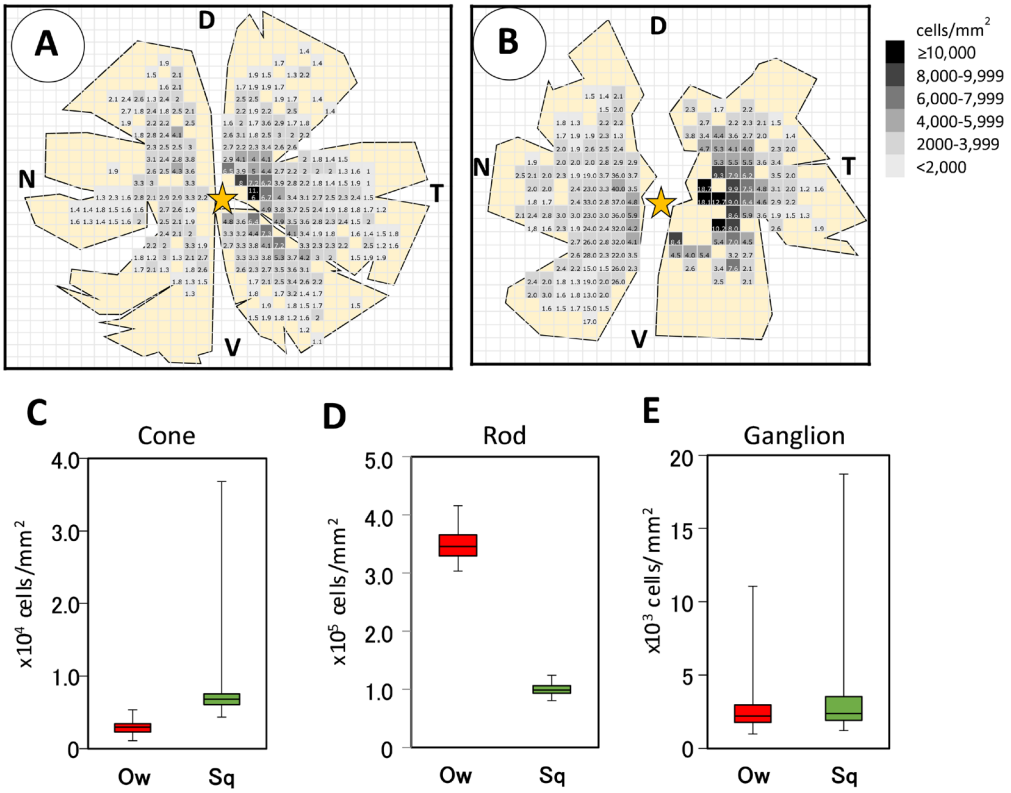

Fig. 2. Retinal topographies of the ganglion cells of owl monkeys (A) and squirrel monkeys (B), measured by the left side of the wholemount specimens. Numbers in the figures represent the density ($\times 10^3$ cells/mm^2). The star figures mean the position of the optic discs. D: distal, V: ventral, N: nasal, T: temporal directions. C–E: Cell densities of cone (C), rod (D) and ganglion cells (E) measured on the wholemount specimens. Ow: owl monkeys; Sq: squirrel monkeys. The lines in each box in graphs mean the 1st, 2nd (median) and 3rd quartile values, respectively. Vertical lines present the range between the maximum and minimum values.

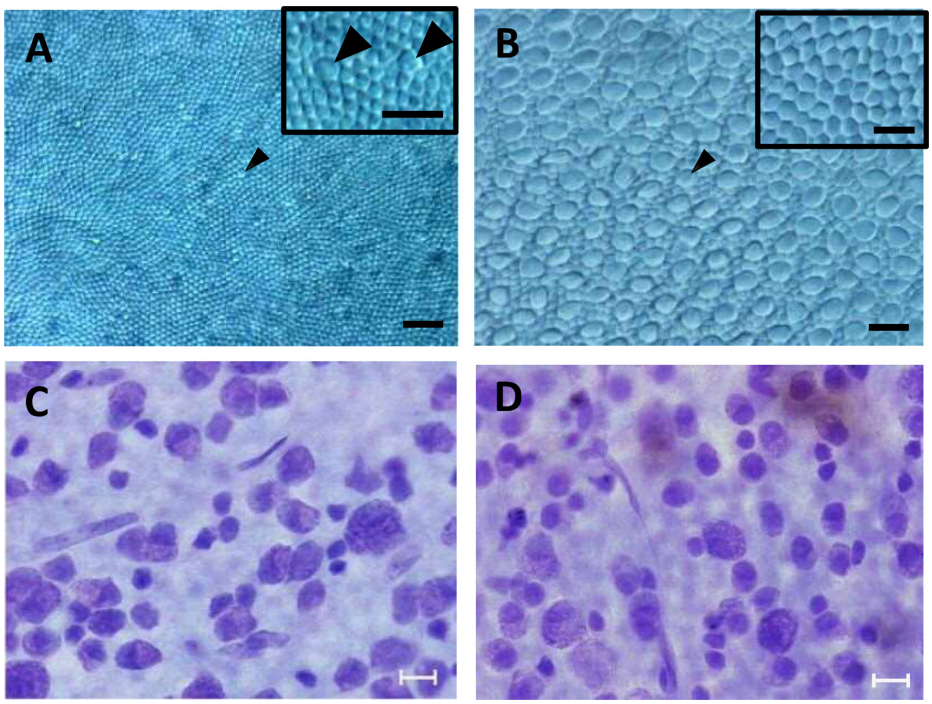

Fig. 3. Retinal wholemounts. Note the very small photoreceptor cells in the owl monkeys (A) than those of the squirrel monkeys (B). Two types of cells are discriminated as the large cone cells (arrowheads) and the surrounding small rod cells. Inset of A: magnified view of cone and rod cells in the owl monkey. Inset of B: the area of the central fovea in the squirrel monkey. Almost all cells are recognized as cone cells. C, D: Nissl staining of wholemounts can visualize ganglion cells composed by various sizes. Bar scales=20 μm (A, B and inset of B) and 10 μm (C, D and inset of A).

Table 3. Ratio of retinal cell numbers measured on the wholemounts

		Owl monkeys	Squirrel monkeys
Rod/Cone	Mean ± SD	115 ± 27.5	14.4 ± 3.08[a)]
	Maximum	188	20.4
	Minimum	72.6	3.47
Cone/Ganglion	Mean ± SD	1.42 ± 0.60	2.94 ± 1.04[a)]
	Maximum	2.70	5.21
	Minimum	0.61	1.13

a) $P<0.01$ vs. owl monkeys.

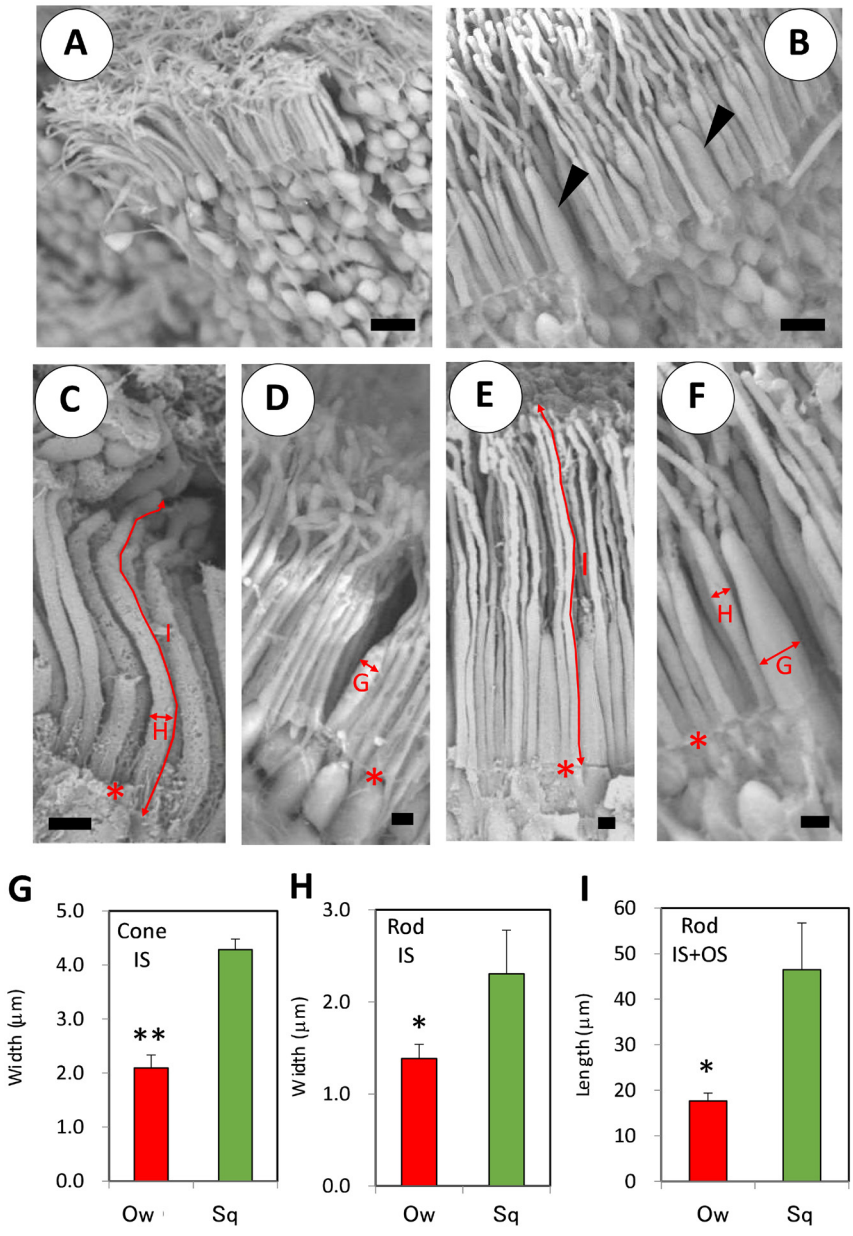

Fig. 4. SEM photographs of the photoreceptor cells from the retinas of owl monkeys (A, C, D) and squirrel monkeys (B, E, F). Scale bars indicate 100 μm (A, B) and 25 μm (C–F). Arrowheads indicate the inner segments of cone cells (B). C–F: Higher magnification of inner and outer segments of photoreceptor cells. Red lines indicate representative sites for measurements. Asterisks indicate positions of the outer limiting layer. G–I: Results of morphometry for the width of inner segments (IS) of cone (G) and rod cells (H), and combined length of the inner and outer segments (IS+OS) of rod cells (I) in the retinas of owl monkeys (Ow) and squirrel monkeys (Sq). *: $P<0.05$ and **: $P<0.01$, vs. squirrel monkeys.

retina [16]. Alnert *et al.* described those retinal characters in the owl monkey as "foveal degradation" [1]. We found the small high-density spot for the ganglion cells in the retina of owl monkeys, but the spot size was not consistent with the size of large owl monkeys' pupils as compared with squirrel monkeys. Our observation of the behavior revealed that the owl monkeys possess single-phase sleep duration and keep certain nighttime activities also under the laboratory facility (data not shown). The wide pupils and large volume eyeballs seem to be beneficial for the nocturnal lifestyle of owl monkeys. High density of rod photoreceptor cells may be applicable for the wide scotopic vision and elevation of small light collection. Defective central fovea

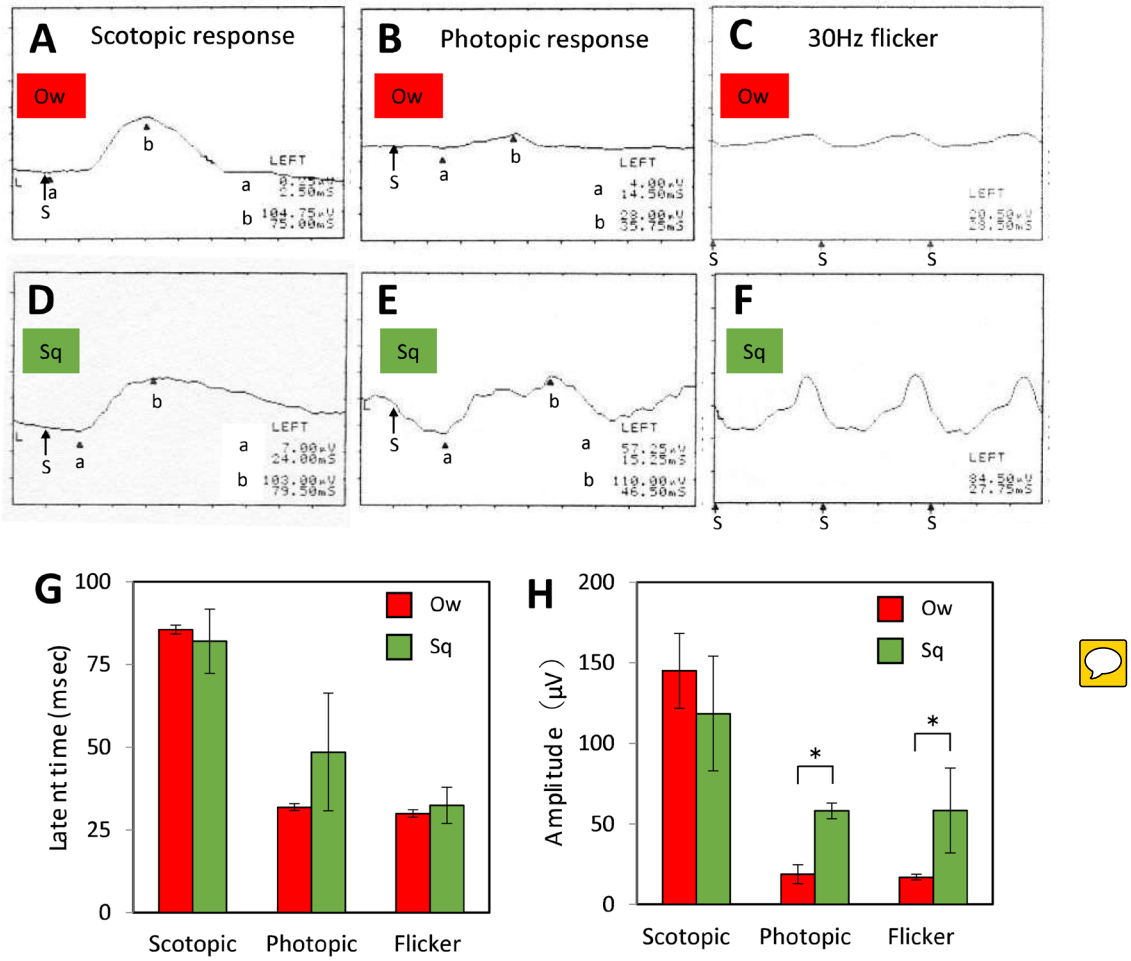

Fig. 5. Measurements of electroretinogram (ERG) in the owl (Ow) and squirrel (Sq) monkeys. A-F: Representative results for the scotopic (A, D), photopic (B, E), and 30 Hz flicker ERGs (C, F). Arrows and points S indicate the timings of light stimulation. Triangles and characters (a and b) indicate the measurement points. Horizontal axes: time progression (A, D: 25 msec/scale, B, C, E, F: 10 msec/scale). Vertical axis: amplitude (50 μV/scale). Measurements of the latent time (G) and signal amplitudes (H) were compared between both monkeys regarding the scotopic, photopic, and 30 Hz flicker ERGs. *P<0.05.

seen at the owl monkeys may have an aptitude for arrangement of the light sensation area distributed equally and broadly on the eye fundus.

On the other hand, squirrel monkeys had clear structure of the central fovea, and cone and ganglion cells were biased to accumulate around the area of central fovea. These deflections resemble human retinas [2, 3], and the rate of rod/cone in squirrel monkeys was comparable to the data of human retina (around 17–21) [3]. The cone cell density of owl monkeys was same level with the bushbaby (*Galago garnetti*) [15], which is belonged to Strepsirrhini and shows nocturnal lifestyles. Beyond the phylogenic relationship, the owl monkeys and the bushbaby shared the retinal specificities for cellular composition and monochronic colored vision [1]. Although the owl and squirrel monkeys share biological and histological backgrounds in the same group of Platyrrhine monkeys, the cone and rod cellular dominancy was quite different, suspected due to nocturnal and diurnal differences. On the other hand, the rates of cone/ganglion cells were resembled among owl monkeys, squirrel monkeys and human (around 2–7) [2]. The rate of cone/ganglion means the convergence efficiency for chromatic visual signals. It means that ganglion cell appearance can be corresponded with the cone cell variation and the visual convergence efficiency may be kept within a certain area in the primate retinas.

Dyer *et al.* proposed a potential for the high growth velocity in the retinal cells of owl monkeys, as compared with *Cebus apella*, diurnal and related species [5]. In the morphogenesis of vertebral retinas, the rod cells appear at the terminal stages developed from the retinal progenitor cells; sequentially differentiated via ganglion, cone, bipolar, and rod cells [5, 9]. The sine oculis homeobox homolog 7 (six7) has been proposed as an essentially responsible gene in the zebrafishes retinas for rod cell development [14]. Hiramatsu *et al.* emphasized a visual importance of the rod-cell function in the feeding behavior of primates. They found superiority of the brightness recognition than the color detection for the processes of fruits finding in the wild black-handed spider monkeys, concretely on the collecting approaches, finding strictness, and ingestion efficiency [6]. Retinal tissue morphogenesis

toward rod-cell dominancy may be required for nocturnal adaptation to enhance foraging and survival activities.

On the other hands, results of ERG did not support functional superiority for the crepuscular vision of owl monkeys. The results of scotopic ERGs actualized a discrepancy against the rod-cell dominant retina acquired at the cytological studies. We found a clue for resolution in the SEM analysis such as the short and narrow sizes of outer and inner segments (OS and IS) at the photoreceptor cells of owl monkeys. It is well known that the OS contains the optic discs equipping the photon receptors composed by opsin protein and 11-cis-retinal. The IS possess the sodium-potassium pumps that is crucial for the membrane polarization and signal transduction. Small OS and IS in the owl monkey were suggested as a reflection of the underperforming reactivity for scotopic ERG signals at the individual photoreceptor cells. It is known that there are wide variations in the eutherian and marsupial regarding the sizes of OS and IS [1]. Especially, the cone cells in the nocturnal animals have the very narrow and elongated shapes of OS and IS than those of the diurnal animals. These shapes are speculated to be an adapted trait for gain of light sensation. Moreover, if the shapes of OS and IS are transformable, these morphologies will become a representative phenotype for the current evolutional adaptation. The elongation of OS and IS may reflect the improvement for light sensitivity and the plasticity of OS and IS means a niche of potential for the environmental adaptation.

Genome size is considered as a critical factor for determination of animal cell size. For instance, the sizes of kidney tubule cells are larger in the polyploid salamanders than the haploid [10]. The normal diploid mammals of rat and pig sustain genome volume commonly around 3 *p*g/cell (animal genome size database, http://www.genomesize.com). Our investigation revealed same level of the cell height in the hepatocytes (rat 19.9 ± 3.46; pig 18.5 ± 1.06 μm, unpublished data). Diversity of mammal erythrocytes, size variation of the diameter in the range of 3–10 μm and shape heterogeneity such as spindle, pear, rod, and triangle [4], are suggested due to an adaptation to the oxygen concentration at the habitat environment and animal activities. Diversity of OS and IS morphology may become a measurable index for cellular plasticity and adaptation relating with visual capacity.

Our study revealed that the owl monkeys, the only one nocturnal species in the simian primates, have typical traits for the nocturnal lifestyles, such as large pupil and eyeball sizes and the retina of rod-cell dominancy. However, the ability for scotopic vision was not developed enough. The size of OS and IS in the retinal photoreceptor cells was small and seemed to be immature, and these morphologies can be a limiting trait for exertion of visual potency. The retina of owl monkeys seemed to have an evolutional potency for elongation of OS and IS and progression for the further nocturnal adaptation.

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REFERENCES

1. Ahnelt, P. K. and Kolb, H. 2000. The mammalian photoreceptor mosaic-adaptive design. *Prog. Retin. Eye Res.* **19**: 711–777. [Medline] [CrossRef]
2. Curcio, C. A. and Allen, K. A. 1990. Topography of ganglion cells in human retina. *J. Comp. Neurol.* **300**: 5–25. [Medline] [CrossRef]
3. Curcio, C. A., Sloan, K. R., Kalina, R. E. and Hendrickson, A. E. 1990. Human photoreceptor topography. *J. Comp. Neurol.* **292**: 497–523. [Medline] [CrossRef]
4. Deldar, A. 1998. Blood and bone marrow. pp. 62–79. *In*: Textbook of Veterinary Histology, 5th ed. (Dellmann, H. D. and Eurell, J. A. eds). Williams and Wilkins, Baltimore.
5. Dyer, M. A., Martins, R., da Silva Filho, M., Muniz, J. A. P. C., Silveira, L. C. L., Cepko, C. L. and Finlay, B. L. 2009. Developmental sources of conservation and variation in the evolution of the primate eye. *Proc. Natl. Acad. Sci. U.S.A.* **106**: 8963–8968. [Medline] [CrossRef]
6. Hiramatsu, C., Melin, A. D., Aureli, F., Schaffner, C. M., Vorobyev, M., Matsumoto, Y. and Kawamura, S. 2008. Importance of achromatic contrast in short-range fruit foraging of primates. *PLoS One* **3**: e3356. [Medline] [CrossRef]
7. Jacobs, G. H. 1977. Visual capacities of the owl monkey (Aotus trivirgatus)--I. Spectral sensitivity and color vision. *Vision Res.* **17**: 811–820. [Medline] [CrossRef]
8. Jacobs, G. H., Deegan, J. F. 2nd., Neitz, J., Crognale, M. A. and Neitz, M. 1993. Photopigments and color vision in the nocturnal monkey, Aotus. *Vision Res.* **33**: 1773–1783. [Medline] [CrossRef]
9. Livesey, F. J. and Cepko, C. L. 2001. Vertebrate neural cell-fate determination: lessons from the retina. *Nat. Rev. Neurosci.* **2**: 109–118. [Medline] [CrossRef]
10. Morgan, D. and Desal, A. Edgar. B., Glotzer, M., Karsenti, E., Nasmyth, K., Pines, J. and Sherr, C. The cell cycle. pp. 1053–1113. *In*: Molecular Biology of the Cell, 5th ed. (Alberts, B., Johnson, A., Lewis, J., Eaff, M., Roberts, K. and Walter, P. eds.), Garland Science, New York.
11. Ogawa, T., Yamada, E. and Yoro, T. 1982. Textbook of anatomy, Volume 3: Esthematology and splanchnology. 11th ed., Kanehara Shuppan, Tokyo.
12. Ross, C. F. 2000. Into the light: The origin of anthropoidea. *Annu. Rev. Anthropol.* **29**: 147–194. [CrossRef]
13. Shinozaki, A., Hosaka, Y., Imagawa, T. and Uehara, M. 2010. Topography of ganglion cells and photoreceptors in the sheep retina. *J. Comp. Neurol.* **518**: 2305–2315. [Medline] [CrossRef]
14. Sotolongo-Lopez, M., Alvarez-Delfin, K., Saade, C. J., Vera, D. L. and Fadool, J. M. 2016. Genetic dissection of dual roles for the transcription factor six7 in photoreceptor development and patterning in zebrafish. *PLoS Genet.* **12**: e1005968–e27. [Medline] [CrossRef]
15. Wikler, K. C. and Rakic, P. 1990. Distribution of photoreceptor subtypes in the retina of diurnal and nocturnal primates. *J. Neurosci.* **10**: 3390–3401. [Medline]
16. Yamada, E. S., Silveira, L. C., Perry, V. H. and Franco, E. C. 2001. M and P retinal ganglion cells of the owl monkey: morphology, size and photoreceptor convergence. *Vision Res.* **41**: 119–131. [Medline] [CrossRef]