Development and proliferation of the photoreceptor cells in the pineal organ and retina of fish

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INTRODUCTION

During the early development of teleost fish the pineal photoreceptors develop faster prior to the retinal differentiation, thus establishing the light-dark recognition and photoneuroendocrine system to oscillate the circadian rhythm. The retinal differentiation depends rather on the time of hatching and/or feeding, while the retinal photoreceptors continuously increase in number throughout the life of fish.

PINEAL PHOTORECEPTORS DEVELOP PRIOR TO THE RETINAL DIFFERENTIATION

The development of photoreceptor cells in the pineal organ and retina of the embryonic and larval fish, such as ayu Plecoglossus altivelis; lefteye flounder Paralichthys olivaceus; black bream Acanthopagrus schlegelii and rainbow trout Oncorhynchus mykiss was investigated by means of light and electron microscopy.1, 2) In each species, the photoreceptor cells endowed with photo receptive outer segments and signal-transmitting synapses appeared earlier in the pineal organ than in the retina, despite great disparities in their incubation times and behavioral activities. In the ayu, lefteye flounder and black bream the pineal and retinal photoreceptors first appear from 3 to 4 days and 5 to 6 days after fertilization, respectively. In the rainbow trout, the pineal photoreceptors first appear 15 days after fertilization and fully developed by 21 days, while the retinal counterparts appear 27 days after fertilization (one day before hatching). This early development of pineal photoreceptors may be involved in light-dark recognition, establishment of the diel and circadian rhythms, and entrainment to the environmental photoperiod in the embryonic fish.

CONE CELLS APPEAR FIRST IN THE DEVELOPING RETINA

It has been presumed that cone cells are dominant in the retina of prelarval fish, while rod cells appear only after or at metamorphosis. Alternatively, pure-rod retina of the eel leptocephalus, Anguilla anguilla, seemed to be an exceptional case of photoreceptor development.3) We examined the retina of the eel leptocephalus, Anguilla japonica, collected from the Pacific Ocean, close to the spawning area,4) and also from the new born eel larvae cultivated in laboratory aquarium. Subsequently, we revealed that the retina of prelarval eel possesses regular cone-like photoreceptor cells, as found in other fish, e.g. left eye flounder and black bream.5) However, according to recent knowledges from in situ hybridization of retinal opsins, the precocious rods express opsin prior to cone opsin expression in the direct development of fish, such as goldfish and zebrafish.6, 7) The timing of rod and cone appearance during the early development might be examined using both morphological and molecular analyses, although there are many discrepancies of developmental events between direct and indirect developing fish species.

RETINAL PHOTORECEPTORS PROLIFERATE THROUGHOUT THE LIFE

The retinas of many teleost fish grow continuously and add photoreceptor cells throughout their life,8, 9) although in most vertebrates the retina completes
its development during embryogenesis. We revealed that the retinal photoreceptors increased in number throughout the life of two indirect developing fish. In the eel, leptocephalus, elver, adult river, and catadromous marine stages exhibit 1, 2, 3, and 4 layers of outer and inner segments, respectively.\(^{10}\) Ratios of cones vs. nuclei of the outer nuclear layer were 1:1 at leptocephalus stage, 1:6.7 at elver stage, 1:10.9 at adult river stage, and 1:14.0 at catadromous marine stage. In the lefteye flounder, a pure cone retina exists until 2 or 3 weeks after hatching, rods appear around 40 days, and the adult retina consists of single layer of cones and irregularly accumulated, multiple layer of rods.\(^{11}\)

In many species,\(^{12,13}\) proliferating photoreceptor cells were demonstrated by marking PCNA (proliferating cell nuclear antigen) immunoreactive cells, scattered throughout the outer nuclear layer (Omura & Sugiura, unpublished observations). In the pineal organ of teleost fish, so far, few proliferating cells have been demonstrated (Meissl, personal communication). As we revealed before in the ayu,\(^{14}\) the pineal photoreceptors exhibit a sign of degeneration after maturation. Photoreceptive outer segments changed from the regularly lamellar type of juveniles into distorting or swirling lamellar types of adults, and lammellae-isolated type of old fish.

In normal retina of teleost fish rod precursors, scattered throughout the outer nuclear layer, continually generate rod photoreceptors, while multipotent progenitors of the marginal germinal zone continuously produce cone photoreceptors and other neurons of inner nuclear and ganglion cell layers. This remarkable activity of proliferation capacitates to regenerate the injured neural retina following mechanical and chemical trauma.\(^{15}\)

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