Vision Research 48 (2008) 2466–2475

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Effect of visual experience on the maturation of ON–OFF direction selective ganglion cells in the rabbit retina

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A R T I C L E I N F O

Article history:
Received 19 March 2008
Received in revised form 11 August 2008

Keywords:
Visual deprivation
Receptive field maturation
Tracer coupling
Direction selective ganglion cells

A B S T R A C T

Activity-dependent neural plasticity is well known in the development of the visual cortical circuitry. However, the role of neural plasticity in the developing retina is less well understood. In the light of recent findings that light deprivation alters the development of synaptic pathway in the mouse and turtle retinas, we studied whether visual experience is required for the maturation of the ON–OFF direction selective ganglion cells (DSGCs) in the rabbit retina. The DSGCs of rabbits raised under a normal light–dark cycle and in the constant darkness were recorded extracellularly at various postnatal stages. Receptive field properties, such as direction selectivity, velocity tuning, classical center–surround interaction and motion-induced surround inhibition were examined. Recorded cells were subsequently injected with Neurobiotin in order to characterize their morphological features and tracer coupling patterns. Our results revealed that visual experience is not critical for the maturation of the classical receptive field properties of the DSGCs, such as direction selectivity and velocity tuning. However, the dark-reared rabbits showed altered surround inhibition, which is mediated by the amacrine cells of the inner retina. In addition, the DSGCs of both normal- and dark-reared rabbits showed similar dendritic features and tracer coupling patterns. Taken together, this study indicates that visual experience plays a less significant role on the DS circuitry maturation in the retina than in the cortex.

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1. Introduction

The ON–OFF direction selective ganglion cells (DSGCs) in the rabbit retina have been characterized for more than 40 years (Barlow & Hill, 1963). DSGCs exhibit vigorous spiking activity when a light or dark object moves in their preferred direction across the receptive field, but show little or no response when the same object sweeps across in the opposite (null) direction (Barlow, Hill, & Levick, 1964). Prevailing evidence indicates that spatially offset inhibition in the null direction is responsible for this robust direction selectivity (Barlow & Levick, 1965; Fried, Munch, & Werblin, 2002; Wyatt & Daw, 1975). In spite of extensive studies on the cellular mechanisms of DSGCs (Demb, 2007; Fried & Masland, 2007; Taylor & Vaney, 2003), little is known about the maturation of this intricate circuit as development progresses (Zhou & Lee, 2005).

Earlier studies on the receptive field properties of retinal ganglion cells (RGCs) in the rabbit retina have shown that the center–surround receptive fields and the direction selectivity can be detected at around the time of eye opening, namely postnatal days 10–11 (P10–11) and reach the adult level at P21 (Bowe-Anders, Miller, & Dacheux, 1975; Masland, 1977). Recent whole-cell patch experiments in the developing rabbit retina also confirm that DSGCs show direction selectivity and that the input currents to the DSGCs are adult-like immediately after eye opening (Zhou & Lee, 2005). However, results from electroretinogram (ERG) studies indicate that mature retinal function is not present until 5 weeks of age (Gorfinkel, Lachapelle, & Molotchnikoff, 1988; Reuter, 1976). In addition, it is known that the DSGCs undergo significant dendritic remodeling in the first 3 weeks after birth (Wong, 1990) and the tracer coupling pattern among DSGCs changes drastically before eye opening (DeBoer & Vaney, 2005). Taken together, the physiological and morphological evidence indicates that the intricate direction selective circuitry seen in the adult rabbit retina may be functional after eye opening, but that the entire receptive field properties may take several more weeks to fully develop.

Numerous studies have shown that visual experience is essential for the normal development of the visual cortex (Cynader, Timney, & Mitchell, 1980; Gordon & Stryker, 1996; Kirkwood, Rioult, & Bear, 1996). Recent studies further suggest that visual deprivation dramatically alters the formation of direction selectivity in the ferret visual cortex (Li, Fitzpatrick, & White, 2006). The presence of an impact by visual experience on the development of pre-cortical regions has also been reported. Dark-rearing prior to natural eye opening has striking effects on the ON–OFF

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doi:10.1016/j.visres.2008.08.010

segregation in the ferret dLGN neurons (Akerman, Smyth, & Thompson, 2002). Furthermore, naturalistic visual stimuli presented through unopened eyelids can significantly activate the dLGN neurons (Akerman et al., 2002). These results imply that visual experience before eye opening has a significant developmental impact.

Although it is well accepted that there is a significant plasticity of synaptic connections and circuit refinements across the higher visual centers of developing vertebrates, it is less certain if the retina itself is also susceptible to visual deprivation during development (Daw, Reid, Wang, & Flavin, 1995). Early evidence has indicated that visual experience does affect the functional and morphological refinement of the retina (Chow, Riesen, & Newell, 1957; Fisher, 1979; Fujikado, Hosohata, & Omoto, 1996; Sernagor & Grzywacz, 1996; Sosula & Glow, 1971; Wingate & Thompson, 1994). Recent studies have further indicated that the development of synaptic function and RGC dendritic stratification does undergo drastic activity-dependent remodeling (Chalupa & Gunhan, 2004; Sernagor, Eglen, & Wong, 2001; Tian, 2004; Wong & Ghosh, 2002). In the mouse and rat retinas, dark rearing reduces the light-evoked responsiveness of the inner retinal neurons (Giovannelli, Di Marco, Maccarone, & Bisti, 2008; Tian & Copenhagen, 2001). Light deprivation also reduces the maturational loss of the ON–OFF responsive RGCs and the pruning of dendrites (Tian & Copenhagen, 2003; Xu & Tian, 2007). Furthermore, an ERG study has shown that the light response of the inner retina in the dark-reared mice is significantly suppressed (Vistamehr & Tian, 2004). In the developing rabbit retina, light deprivation has been shown to delay morphological differentiation of bipolar cells (Wu & Chiao, 2007). In the turtle retina, dark rearing has been demonstrated to modify early spontaneous activity and consequently promotes dendritic growth in developing RGCs (Mehta & Sernagor, 2006). In addition to these visual experience mediated functional and morphological refinements in the vertebrate retinas, light deprivation has also been reported to alter the expression patterns of glutamate receptor subunits in the rat retina (Xue & Cooper, 2001; Xue, Li, Laabich, & Cooper, 2001). Taken together, these different pieces of evidence suggest that maturation of RGCs may be highly susceptible to visual deprivation.

The primary goals of this study are to characterize the maturation of the DSGC receptive field during development and to examine the effect of visual deprivation on DSGC circuitry in the developing rabbit retina. We found that DSCC direction selectivity was present immediately after eye opening in both normal- and dark-reared rabbits, although the maturation of motion surround inhibition was significantly altered. Furthermore, injected DSGCs apparently showed similar dendritic and tracer coupling patterns regardless of the conditions under which they were reared. Our results thus indicate that visual deprivation does not affect the maturation of the DSGC trigger features or dendritic morphologies in the developing rabbit retina, but the development of certain receptive field properties may be delayed or altered when light stimulation after birth is absent. A preliminary account of these findings was present earlier in abstract form (Chan & Chiao, 2006).

2. Materials and methods

2.1. Retina preparation

New Zealand White rabbits raised under a normal light–dark cycle were either bred in our animal facility or purchased from a local breeder. Dark-reared neonates were obtained by transferring pregnant rabbits to a complete dark room before parturition and the pups were kept with mothers in the darkness until experimentation. The day of the pups' birth is termed P0 and the age groups included in this study are P10–14, P15–21 and P22-adult.

The animals used in this study were dark adapted for at least 1 h before dissection. A mixture of ketamine (150 mg/kg) and xylazine (30 mg/kg) were injected intramuscularly to anesthetize rabbits and a few drops of 0.5% proparacaine hydrochloride ophthalmic solution (Alcaine; Alcon-Couvreur, Belgium) was applied topically before enucleation under a dim red light. After hemisection, the lenses and vitreous humors were removed immediately. The posterior eyecups were everted over the round head of a Teflon rod and immersed in the oxygenated Ames' medium (Sigma St. Louis, MO) (Ames & Nesbett, 1981) or the modified Ames' medium (120 mM NaCl, 3.1 mM KCl, 0.5 mM KH_2PO_4, 1.2 mM $MgSO_4$, 1.15 mM $CaCl_2$ and 6.0 mM d-glucose) containing 23 mM $NaHCO_3$. Retinas were carefully detached from the retinal pigment epithelium. Rabbits were then euthanized with an overdose of ketamine. All procedures were approved by the institutional animal care and use committee and were in accordance with the ARVO Statement for Use of Animals in Ophthalmic and Vision Research. To label the nuclei of the neurons, retinas were incubated in 5 μM 4′,6-diamidino-2-phenylindole (DAPI; Sigma) in oxygenated Ames' medium for 1 h. The retina was then placed photoreceptor-side down and adhered on a coverslip coated with the tissue adhesive (Cell-Tak; BD Biosciences, Bedford, MA). The preparation was transferred to a recording chamber mounted on the stage of a fluorescence microscope (Axioskop 2 FS Plus, Zeiss, Germany) and superfused with the oxygenated Ames' medium (1.5–2 ml/min) at 34–37 °C.

2.2. Light stimuli

Visual stimuli generated by the VisionWorks (Vision Research Graphics, Durham, NH) were displayed on a CRT monitor (refresh rate 100 Hz; SyncMaster 757NF; Samsung, Korea) and reflected upward by a mirror positioned beneath the microscope stage. A 20× microscope objective (A-plan, NA 0.45, Zeiss) replaced the condenser was used to focus the stimulus onto the photoreceptor layer of the retina. The DSGCs were identified initially by its signature ON and OFF responses upon a flash light stimulation, and subsequently by their direction selective responses to a bar of light maneuvered manually. A flashing square $180 \times 180\ \mu m^2$ was then used to map the overall receptive field. To characterize the receptive field properties of the DSGCs throughout development, four different visual stimulus paradigms were used in this study. First, the preferred direction of the DSGCs was determined by a moving bar ($540 \times 180\ \mu m^2$, ~900 μm/s) swept across the receptive field center in 12 equally spanned radial directions. Secondly, the velocity tuning was examined by a moving bar ($540 \times 180\ \mu m^2$) swept in the preferred direction at various speeds. Thirdly, the center–surround interaction was studied using a flashing light circle of various diameters (167 ms) centered at the receptive field center. Fourthly, the surround inhibition induced by the preferred direction motion was determined by a moving rectangle (~900 μm/s) extending perpendicularly to the preferred-null axis swept in the preferred direction at various heights. Luminance values on the stage ranged from less than 0.01 cd/m^2 to 18 cd/m^2 and these generally fell within the mesopic range.

2.3. Extracellular recording

Retinal ganglion cells labeled with DAPI were visualized under brief fluorescence illumination (365 nm excitation) using a 40× water immersion objective (Achroplan, NA 0.8, Zeiss) and the DSGCs were targeted with the aid of soma features described previously (Chiao & Masland, 2002; Vaney, 1994; Yang & Masland, 1994). The activity of a single ganglion cell was recorded using a tungsten-in-glass electrode (Levick, 1972). A LabVIEW based data acquisition system (National Instruments, Austin, TX) was used

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