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Retinal parallel pathways: Seeing with our inner fish

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ABSTRACT

The general organization of the vertebrate retina is highly conserved, in spite of structural variations that occur in different animal classes. The retinas of cyprinid fish, for example, differ in many aspects from those of primates. However, these differences are in the same order of magnitude as those found among mammalian species. Therefore, it is important to consider whether these changes are minor variations on the same theme or whether they lead to fundamentally different functions. In this light, we compare the retinal organization of teleost fish and mammals as regards parallel processing and discuss their many similarities.

1. Introduction

The first intracellular recordings of vertebrate retinal neurons were performed in teleosts (Svaetichin, 1953, 1956). Paramount discoveries about the organization of the visual system of vertebrates, such as the existence of multiple retinal channels, resulted from such studies in fish and other cold-blooded animals. Since then, many differences were described between fish and mammalian retinas. One can however ask how much these structural differences are functionally significant, as even within the mammalian class there is a large variation as far as retinal structure and wiring are concerned. This review compares the information coding schemes and transmission pathways in the fish and mammal and discusses that, despite species-specific architectural adaptations, the function of various retinal circuits is in principle very similar.

2. Why have multiple pathways?

Why does the retina use parallel streams to convey information to higher areas? It seems intuitively simpler to have a one-to-one connection from the photoreceptors to the brain and leave the processing of information to the latter, such as in the auditory system. However tempting, this reasoning has caveats, as discussed briefly below and in detail elsewhere (Barlow, 1981; Laughlin, 2001; Sterling, 2004).

First, exclusive lines from the retina to the brain would imply a very thick optic nerve, which would increase the size of the blind spot. Second, it would also impair eye movements, which are crucial for retinal fixation and to avoid photoreceptor adaptation (Barlow, 1952; Martinez-Conde, Macknik, & Hubel, 2004). Third, the total ganglion cell population and consequently the retinal energy consumption would increase, since generating spikes in ganglion cells has metabolic costs (Laughlin, 2001; Lennie, 2003).

2.1. The need for retinal convergence raises problems

In order to diminish the absolute cell number, the visual system makes photoreceptor signals *converge* onto second-order neurons. Convergence, in turn, has both advantages and disadvantages. It can have negative effects on many visual aspects such as sensitivity and acuity, as well as spectral and temporal resolution, because different visual functions have conflicting needs in terms of signal transmission (Ashmore & Falk, 1980b; Falk, 1988; Sterling, 2004; Warrant, 2004).

For example, motion detection needs fast transmission but does not rely on spatial detail, whereas visual acuity has exactly the opposite needs (Koch et al., 2006; Sterling, 2004). Vision at different light levels has also multiple requirements. The visual system needs to perform well both at night time and day time, even though photon levels differ enormously from one condition to the other (Barlow, 1981; Sterling, 2004). This requires transmission with high gain at scotopic levels and with low gain at photopic levels. If all photoreceptors would converge onto a single pathway, these needs would not be entirely met and, as a result, visual perception would suffer.

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2.2. Divergence offers solutions

A solution to this design dilemma implies the concomitant use of a second strategy: *divergence*. By having photoreceptor signals travel to the brain via multiple channels with different absolute and spectral sensitivities, as well as spatial and temporal resolutions, the visual system makes sure that relevant information does not get lost due to the convergence necessary to keep the retina economically and functionally viable.

Another advantage of signal divergence is efficient coding. Because a spiking neuron has a limited bandwidth (i.e. it can only transmit a finite amount of information per unit time), dividing signals into different channels with slightly distinct properties might increase both the rate of transmission and the total amount of transmissible information (Barlow, 1981; Koch et al., 2006; Laughlin, 2001). This would, for instance, favor contrast sensitivity and increase the amount of discriminable gray levels (Barlow, 1981).

Finally, the existence of several retinal pathways might create a sort of "neural backup" and prevent large deficits when one particular system is compromised (Heiligenberg, 1987). One such example can be found in the autosomal recessive form of congenital stationary night blindness. This disease results from a defect in the glutamate receptor of ON bipolar cells, which renders the whole ON pathway silent (Dryja et al., 2005; Zeitz et al., 2005). One would expect affected individuals to show major deficits not only at scotopic levels, when all rod-driven signals are conveyed to the inner retina by an ON bipolar cell (discussed in Sterling, 2004 and in the next sections), but also at mesopic and photopic levels, since cone-driven ON bipolar cells also use the same receptor (Vardi et al., 2002). However decreased, mesopic and photopic visual functions in these patients are consistent with the existence of alternative pathways from both rods and cones to the inner retina (Dryja et al., 2005; Zeitz et al., 2005).

Similarly, mice lacking the ON bipolar cell receptor perform as well as wild-type animals in tests of visually-guided behavior (Masu et al., 1995). Together, these results suggest that other retinal pathways compensate for the absence of ON bipolar cell activity. Parallel retinal pathways seem to be a need shared by all vertebrate species, fish and mammals included.

3. Are fish and mammalian channels that different?

The overall architecture of the vertebrate retina is very similar among species (Cajal, 1893), which reflects the fact that the tasks performed by their visual systems are in many ways alike. There are nonetheless differences between fish and mammals as regards retinal structure. In the next sections, we will show that these anatomical variations are in fact quite comparable to the ones found among mammalian species, leaving however the function of the retinal subsystems involved more or less unchanged. This indicates that, as far as the functional organization of the retina is concerned, fish and primates are not so far apart.

But how many retinal channels are there? This is not a straightforward question, because it depends on the criteria used to analyze retinal organization. Although it is tempting to directly relate visual percepts such as motion, form, texture, color and brightness to the activity of individual neurons or pathways (Livingstone & Hubel, 1988), the diversity of retinal cell types indicates that, at this level, more than one channel might be involved in each of these sensations.

At the same time, at each retinal stratum and beyond neurons converge and diverge, making the adjective "parallel" somewhat inappropriate (Merigan & Maunsell, 1993). Evidence of this is the fact that the number of cell types changes with retinal level. Although one might find about 10–12 bipolar cell types in the primate (Fig. 1C, Boycott & Wässle, 1999; Wässle, 2004), at the ganglion cell level the number of channels is already 17–18 (Field & Chichilnisky, 2007; Kolb, Linberg, & Fisher, 1992).

The same mismatch between the number of cell types at each retinal level apparently also holds for the fish retina, although the morphology of fish retinal neurons has not been completely elucidated yet. The zebrafish, for example, seems to have at least 17 distinct bipolar cell types (Connaughton, Graham, & Nelson, 2004), but only about 11 ganglion cell types have been identified (Mangrum, Dowling, & Cohen, 2002) so far. In the closely related goldfish, about 14–15 bipolar cell types (Fig. 1A, Sherry & Yazulla, 1993) and 15 ganglion cell subtypes were described (Hitchcock & Easter, 1986).

Since the physiology of most of the mammalian retinal neurons—and also of their fish counterparts—is still largely unknown, we will concentrate on those pathways whose properties are reasonably well understood: rod and cone, ON and OFF and broadband and opponent channels.

4. Rods use both ON and OFF channels

Fish and mammals with duplex retinas have chosen apparently different strategies to convey rod and cone signals to second-order neurons. As discussed in the next paragraphs, however, these strategies are, functionally speaking, quite similar. The classical picture is that rod signals flow from the outer to the inner retina via different structures in mammals and fish.

These pathways are summarized in Fig. 1A for the goldfish, in Fig. 1B for the mouse and in Fig. 1C for the monkey. Mammals have an exclusive rod-driven channel comprised by an ON bipolar cell, shown in green (Boycott, Dowling, & Kolb, 1969; Cajal, 1893). Fish, on the other hand, do not have a bipolar cell exclusively dedicated to rods. Rather, these animals use bipolar cells of both ON (Fig. 1A, yellow) and OFF types (Fig. 1A, brown) that receive mixed rod–cone input to transmit information (Scholes, 1975; Stell, 1967). When examined closer, however, these dissimilarities are not substantial: rod pathways in both animal classes are actually conveyed to the inner retina by ON and OFF pathways with distinct gains, as discussed below.

Anatomical connections between rods and OFF bipolar cells were described in a number of mammals (mouse: Tsukamoto, Morigiwa, Ueda, & Sterling, 2001; rat: Hack, Peichl, & Brandstatter, 1999; squirrel: Li & DeVries, 2007; West, 1978; cat: Fyk-Kolodziej, Qin, & Pourcho, 2003; rabbit: Li, Keung, & Massey, 2004). These mixed-input OFF bipolar cells are indicated for the mouse in Fig. 1B (brown neurons). In addition, mixed-input seems to be present in the ON pathway of the mammalian retina as well, since an ON "cone" bipolar cell of the mouse was shown to contact rods directly (Tsukamoto et al., 2007). This cell is represented in yellow in Fig. 1B.

Some of the mammalian OFF bipolar cells that contact rods are analogous to the primate DB2 OFF bipolar cell (Euler & Wässle, 1995; Fyk-Kolodziej et al., 2003), depicted in gray in Fig. 1C. This suggests that mixed-input bipolar cells might also exist in the primate retina. Although such rod–bipolar cell contacts have not been described in primates, it is possible that the bipolar cell connectivity in the primate retina—as well as in a number of other mammalian species—is simply not completely solved yet (i.e. see discussion in Protti, Flores-Herr, Li, Massey, & Wässle, 2005). Alternatively, there might be indeed no mixed-input bipolar cells in the primate retina. In this case, one has to realize that as far as rod-driven pathways are concerned, the mouse, rat,