

# Goldfish Retina: Sign of the Rod Input in Opponent Color Ganglion Cells

**Abstract.** After light adaptation, all "on-center" ganglion cells in the dark became "red on-center," and all "off-center" cells turned into "red off-center" cells. On a chance basis, this similitude of effect between the rods and the red cones in opponent color cells was not expected. These findings indicate that in the goldfish there is some similarity between the connections of the rods and of the long-wavelength cones.

With respect to their receptor input, ganglion cells found in the retina are of three types: one type receiving a pure cone input, a second type receiving a pure rod input, and a third type receiving a mixed rod and cone input. In duplex retinas, the second type is generally absent and the third type is the most common. If the cones contain pigments having different spectral absorption characteristics, ganglion cells usually show an opponent color behavior (1).

In certain ganglion cells a color opponent mechanism is found to be present, both in the center and in the periphery of the receptive field of the ganglion cells. Such cells are common in the goldfish retina (2). An interesting question arises regarding the type of connection that the rod input has on such cells. For example, in a ganglion cell showing in the center of its receptive field a red-green opponent mechanism, where the red light produces an ON response and the green light an OFF response, there exist two distinct possibilities: the rod input can, in the center of the field, produce either an ON response as do the red cones or an OFF response as do the green cones. Of course, the same possi-

bilities exist in the surround. Neglecting the blue cones, one could predict for such a cell equal probability for the rod input to be excitatory like the red cones, or inhibitory like the green cones.

To provide an answer to this question, a series of experiments was undertaken on the isolated retina (3) of the Comet goldfish (*Carassius auratus*). Single-unit activity from ganglion cells was recorded extracellularly with tungsten microelectrodes. In order to maximize the probability of a complete characterization, both in the dark-adapted state and after light adaptation, I chose only cells having a spike amplitude greater than 100  $\mu\text{V}$  for study. Since regeneration of the rod pigment is very limited in an isolated retina, I had to study the dark-adapted characteristics first and then proceed to the light-adapted retina. This limited the study to one cell per retina.

Recordings from 20 cells (12 on-center, 8 off-center), which lasted more than 1 hour each, provide the following picture. All cells have a center-surround organization in the dark-adapted state, with the center either ON or OFF to all wavelengths and the surround with an antagonistic effect to the center. The evidence for a rod input in the dark-adapted state is from (i) the low threshold required to elicit a response (less than  $10^6$  quanta  $\text{cm}^{-2}$   $\text{sec}^{-1}$ ), (ii) the required light adaptation period before the opponent color responses can be observed at an intensity 3 log units above the rod threshold, and (iii) the spectral sensitivity measurements, as shown in Fig. 1. The shift of the experimental points toward the red is probably due to a red cone contamination because of the high cone/rod ratio (7/32) in *Carassius* (4). In terms of the center response only, all cells that are ON in the dark-adapted state became ON to red and OFF to green after light adaptation. Similarly, all OFF cells became OFF to red and ON to green. In the light-adapted state, these cells are all of the type described by Daw (2), having a color opponent or-

ganization both in the center and in the surround and a neutral point around 560 nm, indicating a red-green opponent cell. Figure 2 shows the complete response of these cells when one adds the rod input.

Because of the spectral absorption characteristics of the rod and cone pigments in the goldfish [455, 530, and 625 nm for the cones (5) and 522 nm for the rods (6)], this behavior is spectacular to observe experimentally. With the wavelength set at 520 nm and the spot of light covering the center of the receptive field, one can observe the response changing from ON to OFF, or from OFF to ON, as one changes from a dark-adapted condition to a light-adapted one. The phenomenon is so clear that a misclassification is impossible.

This association of the rods with the red cones is not limited to the goldfish. The finding is in agreement with Purkinje-shift studies done at the single-unit level, but in most cases recordings involved noncolor opponent cells. This is true in the fish (7), the frog (8), the cat (9), and the monkey (10), where the rod input has the same sign as the long-wavelength cone input. However, care must be taken when two cone pigments are known to exist on the long-wavelength side of the rod pigment. Only data indicating a shift to the longest-wavelength peak should be considered as supporting evidence. For retinas that have opponent color cells the data are rare. It is interesting to note that the ground squirrel retina, which has no red cone, has no rod either (11). Three opponent color cells have been found in the lateral geniculate of the cat (12). Two of them show rods with the same type of input as the blue cones; the third cell shows the rod input with the same sign as the long-wavelength cone input. In the monkey geniculate (13), 6 out of 25 cells were found to have a rod input. Four of them were type I cells, which are characterized by having a different spectral sensitivity in the center and in the surround. In one cell, the rod input had the same sign as the green cone input; the type of cone input in the three others was not mentioned. The last two cells that had a rod input were of type III, receiving inputs for possibly all three cones, and the rod input had the same sign as the cone input.

The finding that, in double opponent cells in the goldfish, the sign of the rod input is similar to that of the red

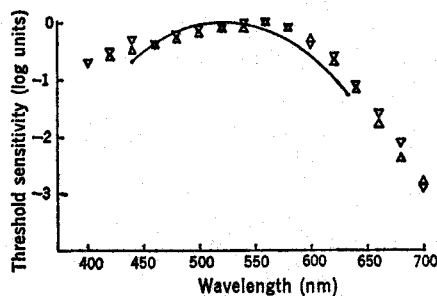


Fig. 1. Average spectral sensitivity of a few dark-adapted cells. Triangles pointing up represent on-center cells, and triangles pointing down, off-center cells. The solid line was generated from a nomogram for a pigment with its maximum at 522 nm. The shift of the experimental curve toward the long wavelengths could be attributed to a contamination from the red cone input.

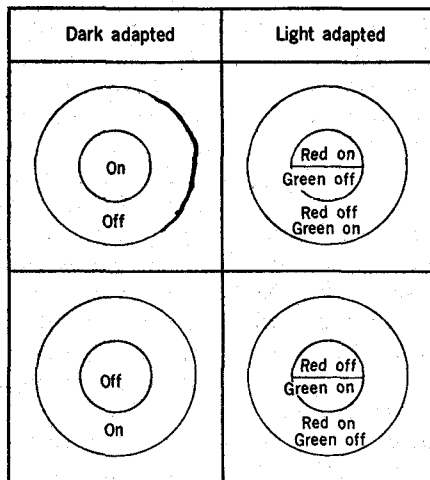


Fig. 2. Receptive field organization in the two states of light adaptation of the opponent color cells, which codes simultaneous color contrast. Note that the rod response is always similar to the red cone response.

cone input can be considered an extension of the Purkinje-shift rule to opponent color cells. However, the few cells that have been found to be exceptions to the rule have to be considered as evidence against a universal generalization that the rod input always has the same sign as the long-wavelength cone input.

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#### References and Notes

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