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"Lighting Conditions and Retinal Development in Goldfish:
Absolute Visual Sensitivity"

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Lighting Conditions and Retinal Development in Goldfish: Absolute Visual Sensitivity

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Goldfish (*Carassius auratus*) were reared from hatching in constant light (340 lux), cyclic light (12 hr 320 lux, 12 hr dark) or constant dark. Absolute visual threshold was determined psychophysically in animals that still responded to visual stimuli after 1–3 years of exposure, by means of a classically conditioned respiration suppression technique wherein animals were presented with different intensities of large diffuse flashes of monochromatic light. Fish reared in constant light and fish reared in cyclic light responded reliably to stimuli above threshold, but fish reared in constant light were on average 0.58 log unit less sensitive at 532 nm, near the peak of the rod action spectrum. Two of the four fish reared in darkness did not respond to the stimuli, and thus could not be conditioned, and another fish reared in darkness responded only occasionally; threshold could not be measured in these three fish. The one fish reared in darkness that responded consistently enough to be conditioned was more than 5 log units less sensitive than normally reared fish on the first day of testing, and became progressively less sensitive over the next 2 days. Rearing under constant dark or constant light had no obvious effect on spectral sensitivity at absolute threshold. The effect of rearing in constant light on absolute threshold correlates with morphological changes in rod density,[1] but the effect of rearing in constant darkness does not. Invest Ophthalmol Vis Sci 29:37–43, 1988

In the preceding paper[1] we showed that exposure to constant light or constant dark from hatching to ≥12 months prevents the development of normal rod densities in goldfish retina. Cone densities were unaffected by rearing in either constant light or constant dark, as were the lengths of outer segments of both rods and cones. Thus, at least at the light microscopic level, exposure to constant visual conditions appears to influence only the rods, regardless of whether the conditions are constant light or constant dark.

In this paper we describe the effects of rearing in constant light (LL) or dark (DD) on the ability of the goldfish to detect dim lights. We find that LL and DD affect absolute sensitivity differently, despite their similar effects on rod density. Rearing in LL results in rather small deficits that are reasonably predictable from the 30–40% reduction in rod density observed in retinas exposed for more than 1 year to *either* LL or DD,[1] but rearing in DD produces much larger behavioral deficits that are not easy to relate to changes in rod density. The larger reduction in absolute sensitivity after rearing in DD could be related instead to the general disorganization and distortion of retinal tissue observed in these animals.

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Materials and Methods

Animals and Exposure Conditions

Procedures adhered to the ARVO Resolution on the Use of Animals in Research. Five goldfish (LL1, LL2, LL3, DD4 and DD5) were reared from embryos placed in continuous light (LL) or continuous dark (DD) prior to hatch. These embryos were obtained by breeding adult *Carassius auratus* purchased from Ozark Fisheries (Stoutland, MO), and were from the same spawns as fish used in Series 1 and Series 2 in the companion morphometric study.[1] Two additional fish (DD1, DD3) were placed into DD at 3 months of age. They had been purchased as embryos from Carolina Biological Supply (Burlington, NC) and were maintained in a combination of fluorescent room illumination and natural daylight before the experiment began.

Five fish purchased as juveniles from Ozark Fisheries were cyclic light controls (LD). They were approximately the same size (nose to base of tail, 4.8 ± 1.18 cm) as the experimental animals at the time of testing, and were maintained under daylight fluorescent lighting (12L:12D) throughout the experiment.

Details of light exposure were described in the previous paper.[1] Fish were kept three to five per tank in 10 gallon aquaria in three windowless rooms. The daylight fluorescent bulbs at ceiling height in LD and LL rooms provided 320 lux (86 $\mu W/cm^2$) and 340 lux (91 $\mu W/cm^2$) at the water's surface, respectively. DD fish were housed in a lightproof cabinet in a photographic darkroom. All animals were fed once a day. LD fish were always fed during the light part of the cycle; DD fish were fed with the aid of a dim red (Kodak Wratten filter 29, Rochester, NY) flashlight.

Conditioning was first attempted when the fish were large enough to fit into a modified restraining box of the type used by Powers and Easter.[2] Animals smaller than about 3 cm standard body length (sbl) could not be tested in this apparatus because their heads did not remain reliably positioned and because it was difficult to handle them without injury. In this set of experiments (the present paper and ref. 1) animals reached 3 cm sbl at 1–3 years (M. Powers, unpublished observations). We could not measure thresholds in fish younger than 1 year.

Measurement of Absolute Threshold

From previous work we know that detection threshold of 9–10 cm goldfish is reached at retinal fluxes of about 1 quantum per 2000–4000 rods, when the stimulus is a large, long duration flash near the peak of the rod absorption spectrum.[2] It has also been demonstrated that cones contribute to the psychophysical action spectrum in the fully dark-adapted goldfish, so that the spectral sensitivity of this animal is considerably broader than would be predicted from the rod action spectrum alone.[2] Because the spectral sensitivity of normally reared goldfish has been well specified previously, in a similar apparatus under nearly identical stimulus conditions, in the present study we measured threshold at two or three wavelengths and compared the results to the earlier values. Absolute threshold was first measured at 532 nm, near the peak of the rod absorption spectrum. Fish were subsequently tested at 636 nm and (for LL animals) at 452 nm.

To measure absolute threshold, fish were trained to suppress respiratory movements when they detected a suprathreshold light, and they were then tested for their responses to successively dimmer lights.[2] All stimuli were presented to well dark-adapted fish, with no background illumination present.

The apparatus and stimulus conditions have been described before.[2] Briefly, the fish was held in a restraining box suspended from the side of an aerated 10 gallon aquarium in a lightproof enclosure, with the right eye adjacent to a rear projection screen. Monochromatic stimuli were produced from a quartz-halogen source by placing narrow-band interference filters (Melles Griot, Irvine, CA, bandpass at half height 8–10 nm) in a collimated portion of the beam. Intensity was varied in approximately 0.3 log unit steps with neutral density filters (Melles Griot).

Training: Training was accomplished by means of a classical conditioning paradigm.[2] Fish were dark-adapted for at least 1 hr prior to each training session, regardless of experimental condition. They were then presented with 10 trials of a 5 sec, 532 nm diffuse spot, 140 deg in angular subtense, followed by a 5–15 V tail shock, 100 msec in duration. Animals showed no ill effects of this treatment, remaining healthy and eating well throughout the experiment when returned to their home aquaria. Onset of the shock (the unconditional stimulus) was contiguous with offset of the light (the conditional stimulus). The intertrial interval was variable, with an average of about 1.5 min. Unless otherwise noted, the intensity of the training stimulus was 3–4 log units above absolute threshold for 532 nm in normal fish.[2] Training sessions were repeated daily until the fish became conditioned (see next paragraph) or until the experimenter judged that the training was not effective.

Respiration rate was monitored with a glass bead thermistor placed near the fish's mouth.[2] During each intertrial interval six 5 sec samples of breathing rate were taken, to be compared to breathing rate during stimulation. A "response" was defined as ≥50% decrease in respiration rate from the average intertrial rate. When the fish responded to eight out of ten stimuli in two successive training sessions we considered it to be conditioned, and testing was begun.

Testing: Threshold was measured in trained fish from frequency-of-seeing curves derived from responses in a staircase psychophysical procedure.[2] The fish was dark-adapted for at least 1 hr before the first stimulus was presented; this stimulus was 2–3 log units above absolute threshold for normal fish, or an intensity to which the experimenter knew from previous sessions the fish would respond. If the fish responded, the intensity was decreased by 0.3 log unit on the next trial. This procedure continued until the fish did not respond to the visual stimulus. At that point the intensity was increased by 0.3 log unit until a response again occurred. Shock followed each visual stimulus on every trial during testing.

Test sessions for LD fish were terminated after 25 trials. Sessions for LL and DD fish contained a variable number of trials, depending upon how consistent the animal's responses had been (see below). All stimuli were the same duration as training stimuli. Data for a given animal were combined across sessions to yield frequency-of-seeing curves; absolute threshold was defined as the intensity for which the probability of response was 0.5.[2]

For LD animals, two to three sessions of 532 nm stimuli were followed by two to three sessions of 636 nm stimuli. The procedure was somewhat different for LL and DD animals, because we wanted to obtain data as rapidly as possible. For these fish, if the experimenter observed at least five reversals in intensity within a session (ie, oscillations of the stimulus intensity around threshold), he or she could decide to test another wavelength within the same session. For all animals, the sequence of wavelengths was 532, 636, 452 nm.

Threshold values at each wavelength are reported in units of quanta per sec incident per cm^2 of cornea, as computed from calibrations made during the experiment by placing a calibrated photodiode (United Detector Technology, Culver City, CA, PIN10 DFP) at the plane of the pupil.[2] Absolute sensitivity, plotted in Figures 1 and 2, is the reciprocal of threshold corneal irradiance determined in this way.

Optomotor Responses

The results to be described below show that dark-reared fish were difficult to train in the classical conditioning task. For this reason, we adopted a second test of visual function that required no training. After ten unsuccessful classical conditioning training sessions, one fish (DD5) was light-adapted for 1 hr and placed in a 15 cm diameter clear Plexiglas cylindrical aquarium centered in a field of vertical square-wave stripes. The striped fields were photographic enlargements of Ronchi gratings. They could be rotated at different speeds clockwise or counterclockwise with respect to the axis of the cylinder. This apparatus was illuminated with ordinary fluorescent room illumination (Sylvania F40/CWRS/SS; 620 lux or 150 $\mu W/cm^2$ at tank level) throughout the test, which took about 15 min. Stripes subtending 27 deg, 13 deg, 7 deg and 2 deg^{-1} were rotated at various speeds around the fish, while an observer recorded the animal's following behavior (swimming in the same direction as the stripes and/or reversing direction when the stripes reversed). Two different observers (MKP and CJB) scored the fish's behavior independently, using the same stimulus set. For comparison, LL2 and LL3 were also tested in this apparatus, as was an LD control animal.

Results

Control Animals (LD)

Goldfish reared in cyclic light became conditioned after three to six training sessions. Their mean absolute visual threshold, in units of corneal irradiance, was 4.66 log quanta sec^{-1} cm^{-2} (±0.07 sem) at 532 nm. At this intensity, only one rod in about 3000 absorbs a photon each second. This low quantum-to-rod ratio, together with the similarity of the value to previous measurements[2] makes it likely that the rod system was mediating visual responses in LD fish at their absolute threshold for seeing.

Day-to-day variability in threshold for individual LD fish at 532 nm ranged from 0 to 0.38 log unit (see Table 1). The number of training sessions needed to acquire the detection task and the amount of variability in threshold are comparable to values reported before for larger fish reared in LD[2] but the thresholds reported here are slightly higher. This difference reflects normal developmental changes in absolute sensitivity in this species, which correlate closely with changes in the planimetric density of the rods during growth, even in adulthood.[3]

The dark-adapted spectral sensitivity of fish reared in cyclic light was also normal. The data from LD animals are shown in the upper portion of Figure 1, superimposed on a smooth curve from the earlier study, where complete spectral sensitivity functions were obtained.[2] The curve from the previous study has been placed on the vertical axis so that it passes through mean log threshold for LD fish (in this study) at 532 nm. The spectral sensitivity of the dark-adapted goldfish reflects input from more than one receptor mechanism, and normally does not match the absorption spectrum of rod porphyropsin in this species.[2] Thresholds for the LD fish are consistent with this finding, in that the relative sensitivity to 636 nm is higher than would be predicted from the absorption spectrum of the porphyropsin in goldfish rods.[4] Absolute threshold was 0.92 log unit higher at 636 nm than at 532 nm for the normally-reared fish in this experiment, compared to an expected difference of 1.40 if rods were mediating photon catch in the long wavelengths.

Effect of Rearing in Constant Illumination (LL)

Table 1 gives the number of training sessions and the day-to-day range in threshold for the three fish

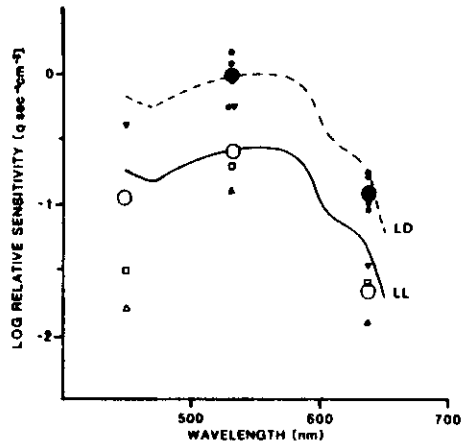

Fig. 1. Goldfish reared and maintained in continuous room illumination for 2–3 years show decreased sensitivity to large diffuse flashes of light; spectral sensitivity seems to be less affected than absolute sensitivity. Threshold of dark-adapted LL fish (open symbols) was lower than LD controls (filled symbols) at the three wavelengths tested. Large symbols show means; smaller symbols show data for individual animals. LL1 (open squares) was tested after 3 years of exposure. LL2 (open triangles) and LL3 (open inverted triangles) after 2 years (see Table 1 for details). The curve drawn through the points is the dark-adapted spectral sensitivity of adult goldfish from Powers and Easter.[2] Zero on the ordinate = 4.66 log photons sec^{-1} cm^{-2} incident at the cornea.

reared for 2–3 years in constant light. Although the Ns are small, no obvious differences were noted between animals tested after 25 months exposure to LL and the fish tested after 38 months. The number of sessions required to train all three fish was well within the range of the LD fish, and the day-to-day variability of two of the three LL fish was also within the range of normally-reared fish. We interpret this to mean that rearing in LL did not produce a generalized learning or performance deficit.

All three LL fish had higher absolute thresholds than LD fish for 532 nm stimuli (Table 1). The difference due to rearing condition was highly significant ($t = 4.919$, $df = 6$, $P < 0.005$). On average, LL fish were 0.58 log unit less sensitive than normally reared fish. This is equivalent to a 26% reduction in sensitivity.

The lower curve in Figure 1 shows the dark-adapted absolute sensitivity of light-reared animals at different regions of the spectrum. All points are plotted relative to the mean log threshold for LD fish at 532 nm, again illustrating that LL fish were less sensitive than LD fish at this wavelength. All animals were less sensitive at 636 nm, but the difference in sensitivity between 532 nm and 636 nm was slightly larger, on average, for LL fish than for LD fish (0.90, 1.03, and 1.23 log units, respectively, for LL1, LL2 and LL3, compared to an average of 0.92 log unit for LD fish). This difference in *spectral* sensitivity between LL and LD fish was not statistically significant. The data at 452 nm are somewhat more variable, but together with the long wavelength points they suggest little change in spectral sensitivity at absolute threshold in light-reared goldfish. If anything, the action spectrum is somewhat narrower in animals reared in LL, suggesting relatively less influence of cones on absolute spectral sensitivity due to rearing in LL.

Effect of Rearing in Constant Darkness (DD)

Animals reared in DD were dramatically less responsive to light than those reared for comparable times in LL (Table 2). Of the four animals tested after 12–25 months exposure, only one responded regularly enough during training sessions to be considered conditioned (see below). Two of the others did not respond at all, even to lights of different wavelength (636 nm) or high intensity (nearly ten orders of magnitude above absolute threshold for LD animals). We tried to condition one fish (DD1) twice, at 12 and 24 months of age, without success; this animal was returned to DD for 12 more months after the first series of training sessions at 12 months.

Table 1. Absolute sensitivity of light-reared fish at 532 nm

Fish	*Age at begin exposure (months)*	*Exposure time (months)*	*Number of training sessions**	*Threshold (log q sec^{-1} cm^{-2} at 532 nm)†*	*Day-to-day range in threshold‡ (log)*
LD (N = 5)	—	—	4.2 (3–6)	4.66 (4.47–4.89)	0.11 (0.00–0.38)
LL1	0	38	4	5.24	0.42
LL2	0	25	3	5.40	0.11
LL3	0	25	3	5.07	0.28

* Number of training sessions required to obtain two successive sessions wherein P (response) ≥0.8. Mean (and range) is given for LD fish. Sessions were ten trials each.

† Absolute threshold, determined as described in text, where P (detection) = 0.5. Mean (and range) is given for LD fish. LD values represent data pooled over two test sessions for four of the LD fish and data from one session for the fifth. LL values were obtained over two to three sessions.

‡ The range of threshold values obtained over the various days of testing. Mean (and range) is given for LD fish.

Table 2. Visual responses of dark-reared fish

Fish	*Age at begin exposure (months)*	*Exposure time (months)*	*Number of training sessions**	*Max percent responses/ session†*	*Successfully conditioned*
DD1	3	12	15	0	No
		24	5	0	No
DD3	3	12	13	0	No
DD4	0	25	4	100	Yes
DD5	0	25	10	20	No

* Number of training sessions required to obtain two successive sessions wherein P (response) ≥0.8 (DD4 only) or to judge that the fish was not trainable (DD1, DD3, DD5). Sessions were ten trials each.

† The percent of trials that elicited a response per session on the best day for each fish.

Figure 2 shows the absolute sensitivity of DD4, the only fish we could train, at two wavelengths over 3 successive days of testing. This fish became conditioned in the usual number of training sessions (Table 2), but during the first test session its absolute threshold at 532 nm was 5.7 log units higher than the average LD fish, and 5.1 log units higher than fish reared in LL. Absolute sensitivity declined even further during the 3-day testing period shown in Figure 2, and finally, on day 4 of testing, DD4 would no longer respond to stimuli that were the maximum intensities we could produce with our optical system: 9–10 log units above absolute threshold for normal animals.

Reference to Table 1 shows that thresholds for LD and LL fish varied by a maximum of 0.42 log unit over testing days. Yet for fish DD4, sensitivity over the 3 days of testing spanned 2 log units, with sensitivity on day 2 lower than on day 1 and a further decline in sensitivity on day 3. Clearly this fish's day-to-day variation in threshold was not due to random factors, as could be argued for LD and LL fish.

Because DD4 was successfully conditioned, it seems unlikely that the animals reared in DD did not respond because they could not learn or could not organize an appropriate response. Observations with DD1 and DD3 also implied this was not the case, because they did show some evidence of respiratory suppression on the initial trials of some training sessions. Nonetheless, we tested the last DD animal (DD5) in an optomotor drum, where visually-mediated following behavior is reflexive.[5] After 25 months exposure to DD and failure to become trained in the classical conditioning task, DD5 followed stripes of 13 deg visual angle under fluorescent room illumination. This fish did not follow stripes of 2 deg subtense, and 7 deg stripes produced intermittent following behavior. In contrast, LL2 and LL3 followed stripes of all sizes, as did a control LD fish. The smallest subtense tested was 2 deg.

Condition of the Retinas in LL and DD

The retinas of four fish from this experiment were examined following completion of testing. Histological procedures were described in the previous paper,[1] where the state of these retinas was summarized under the heading "Additional comments on retinal structure." Here we describe the tissue in more detail.

The retinas of LL2 and LL3 appeared normal. There was no obvious derangement of photoreceptors or of any other structure, and no evidence of folding or scalloping. Both these fish learned the detection task, but had thresholds that were elevated above normal. Poor fixation precluded photoreceptor counts, but we presume densities would approximate those reported before.[1]

The retinas of DD4 were badly disorganized, with scalloping throughout except for a small central segment around the optic disk. This fish learned the detection task but had extremely high thresholds. The retinas of DD5, a fish that did not learn the task, were disrupted and folded across the entire extent, but not as badly as DD4. However, there was no sparing of the area surrounding the optic disk in DD5's retinas. It was not possible to determine photoreceptor densities in the DD retinas because of their overall disorganization.

Discussion

Goldfish reared in constant light or constant dark have reduced sensitivity to light at 1–3 years of age. While the effect of rearing in DD may be worse than that of rearing in LL, the magnitude of the damage due to LL is considerably smaller than that reported for mammals reared under similar conditions[6] (however see ref 7) and could be related to capacities for regeneration and continued growth in goldfish not seen in mammalian species.

The reduction in sensitivity appears to be approximately equal across the spectrum in both LL and DD animals. Although only two or three wavelengths

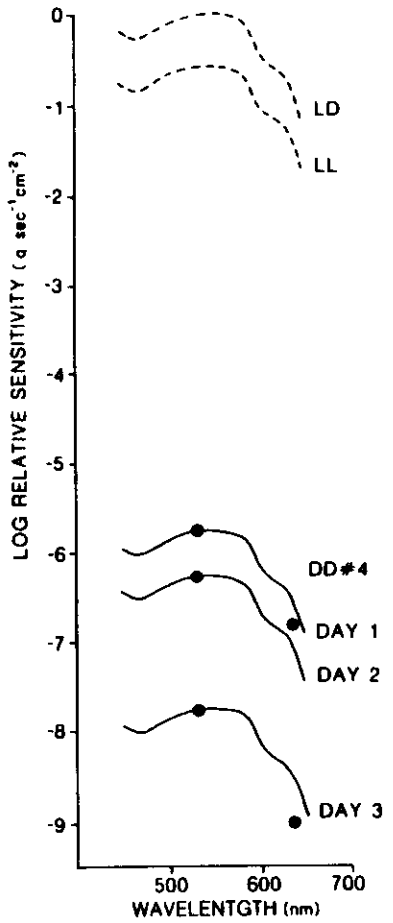

Fig. 2. Dark-adapted visual sensitivity of a goldfish reared and maintained in continuous darkness for 2 years. Ordinate same as Figure 1. The upper two curves show dark-adapted sensitivity of LD and LL fish for comparison. On the first day of testing, the fish's threshold was 5.7 log units higher than normal fish. It became progressively less sensitive on days 2 and 3 of testing, and on day 4 would no longer respond to stimuli 9–10 log units above threshold for normal fish. Day 1 and 3 curves have two points, Day 2 has one.

were used in this experiment, they were selected to take advantage of the fact that the goldfish is mesopic at absolute visual threshold.[2,8] The 532 nm stimulus was chosen to be near the peak of the rod-mediated part of the spectrum, and the 636 nm stimulus stimulates long-wavelength sensitive cones in normally reared goldfish.[2] Under this assumption, we conclude that the rod and long-wave cone *systems* were affected approximately equally by rearing in constant lighting conditions, even though only the rods were reduced in density.[1]

Goldfish reared in constant light had thresholds that were on average 26% higher than fish reared in cyclic light. In the companion study we found that fish treated identically to the LL group had reduced density of rods. The magnitude of the deficit in rod density was 37%, on average, for seven fish after about 1 year in LL.[1] The similarity between these numbers implies that the reduction in sensitivity is related to the reduction in rod density. This conclusion is consistent with the general notion that absolute visual threshold is regulated by the planimetric density of rod photoreceptors in goldfish.[3]

Attractive though this hypothesis is, alternate interpretations cannot be ruled out. It is possible, for example, that fish reared in LL suffer damages unrelated to vision that impair their ability to learn or to perform a visual task. This seems unlikely given that the number of trials required to become conditioned and the number of sessions required to obtain thresholds did not differ between LL and LD fish. A more likely explanation is that dark adaptation was incomplete in LL animals; that their ability to regenerate porphyropsin was impaired somehow by long-term exposure to light. Or, exposure to darkness following LL could have triggered massive shedding of ROS[9,10] which in turn could have interfered with the absorption of photons. Indeed, there is evidence that absolute threshold is related to ROS length in goldfish.[11] Whatever the actual mechanism, we find it remarkable that exposure to continuous light for up to 3 years has such small effects on the goldfish's ability to detect light.

Interpretation of the effect of constant darkness during rearing is more problematic. On the surface, it would appear that dark rearing produces more damage than rearing in LL, but we offer that conclusion tentatively because only one animal could be tested. One of the fish reared in DD that did not become conditioned followed the stripes in an optomotor drum, but its acuity (under photopic conditions) was at least a factor of three lower than LL and LD fish. This suggests an impairment unrelated to vision, or perhaps one that is specific to the rod system. The animal that became conditioned seemed to lose sensitivity progressively over test sessions; would this fish have shown sensitivity closer to LD fish if we could have tested it on the first day of exposure to light (instead of spending 4 days training it)? This result raises the possibility that retinas of goldfish reared in darkness are highly susceptible to damage by light, as is the case in the rat.[12]

The difference in absolute sensitivity between animals reared in LL and those reared in DD is not easily explained by changes in photoreceptor densities observed at the light microscopic level. In the companion study, we found no differences in the number of rod or cone nuclei between LL and DD fish, no differences in outer segment lengths, and no differences in the overall disorganization of the photoreceptor layer.[1] Yet when tested behaviorally, DD fish gave little evidence of vision while LL fish performed quite well. This anomaly could be related to the condition of the retinas of the particular fish used in this experiment: the dark-reared specimens were badly scalloped and folded, while the light-reared specimens were not. Another possibility is that the difference in absolute threshold between LL and DD fish is due to an effect at the ultrastructural level, perhaps related to the number or density of synaptic connections between neurons; this remains to be investigated.

Finally, we must ask whether younger fish, with shorter exposures to constant lighting conditions, would show similar deficits. We were unable to test fish younger than about 1 year in this experiment due to technical limitations; when those limitations are overcome, it will be important to determine whether shorter exposures consistently produce larger behavioral effects than can be accounted for by the retinal effects, especially in goldfish reared in constant darkness.

Key words: goldfish, absolute threshold, constant light, retinal development, constant dark

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