The Journal of Experimental Biology 206, 1643-1648

doi:10.1242/jeb.00337

Rearing in different photic and spectral environments changes the optomotor response to chromatic stimuli in the cichlid fish *Aequidens pulcher*

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Accepted 26 February 2003

Summary

Developmental plasticity of spectral processing in vertebrates was investigated in fish by using an innate behavior, the optomotor response. Rearing blue acara (*Aequidens pulcher*; Cichlidae) under white lights of different intensities as well as deprivation of long wavelengths induced significant changes in the animals' responses to chromatic stimuli. Deprivation of short wavelengths had no effect. With this and previous studies on animals reared under similar conditions, we have demonstrated that developmental plasticity in spectral processing is present at a wide range of neural levels, spanning from photoreceptors to behavior. We hypothesize that earlier studies did not reveal such effects because of the rearing and testing conditions used.

Key words: color vision, spectral processing, developmental plasticity, vertebrate, cichlid fish, *Aequidens pulcher*.

Introduction

In a series of previous studies, we have reported that rearing blue acara (*Aequidens pulcher*; Cichlidae) under spectral deprivation and different light intensities induces considerable changes in the outer retina. Rearing in light of short wavelength induced (1) a selective loss of short-wavelength-sensitive cones and elongation of the outer segments of middle- and long-wavelength-sensitive double cones (Kröger et al., 1999; Wagner and Kröger, 2000), (2) changes in the synaptic complexes between cones and horizontal cells (Kröger and Wagner, 1996) and (3) changes in the spectral responses of horizontal cells (Kröger et al., 2001). Light of long wavelength had no direct effect. Preliminary results suggest, however, that short-wavelength-sensitive cones were eliminated when animals reared in long-wavelength light were transferred to white light (Wagner and Kröger, 2000). Rearing in white lights of different intensities led to differences in (1) the connectivities of cone-specific horizontal cells (Braun et al., 1997), (2) cone outer segment lengths (Kröger et al., 1999) and (3) horizontal cell spectral responses (Kröger et al., 2001). Clearly, developmental plasticity is present in the early stages of chromatic processing in *A. pulcher*.

In contrast to findings concerning early stages of chromatic processing, previous studies on higher neural levels (from optic nerve fibers to behavior) reported no or small effects of spectral and/or visual deprivation in a variety of vertebrate species (primates, Boothe et al., 1975; Brenner et al., 1985, 1990; Di et al., 1987; ground squirrels, McCourt and Jacobs, 1983; tree shrews, Petry and Kelly, 1991; ducks, Peterson, 1961; pigeons, Brenner et al., 1983; and goldfish, Mecke, 1983). These findings had suggested that the developmental program of spectral processing and color vision is genetically determined. We now report that rearing *A. pulcher* in different visual environments not only induces neural plasticity in the retina but also changes behavioral responses to chromatic stimuli.

Materials and methods

Animals

Aequidens pulcher (Gill, 1858) were reared from early larval stages (2–4 weeks after fertilization) for 17–19 months under five different lighting conditions. Three equi-irradiant (approximately 10^{16} quanta s^{-1} m^{-2}), spectrally narrow-banded lights were produced with halogen lamps in combination with neutral-density and interference filters (Ealing). The central wavelengths and bandwidths of the lights, respectively, were: 'red' 590 nm, 9.4 nm; 'green' 513 nm, 7.1 nm; and 'blue' 452 nm, 17.1 nm. The spectral locations of the rearing lights were chosen to achieve maximally differential stimulation of the three spectral cone types of *A. pulcher* (Wagner and Kröger, 2000). Two further groups were reared under dim (approximately 0.5 lux) and bright (approximately 700 lux) white light (DW and BW groups, respectively). For comparison, the green light was about as bright (0.5 lux) as the dim white light. The DW group was therefore used as the control group for effects of spectral

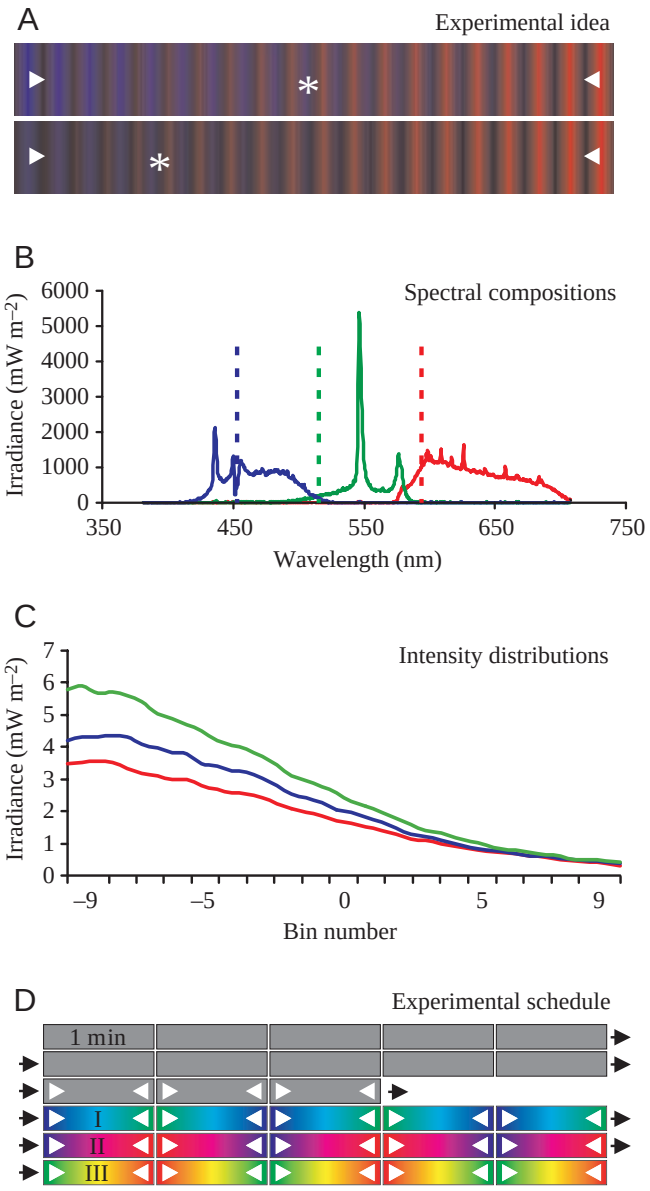

Fig. 1. Schematic illustration of the experimental procedures. (A) Two vertical, sinusoidal gratings were projected on the front wall of a long, narrow tank. The projected gratings had opposing gradients of intensity and directions of motion (arrowheads). Upper panel: when both gratings drove the optomotor response with equal strength, the fish swam to the centre of the tank, where it experienced balanced motion stimuli from both sides. Lower panel: when one color was less efficient in driving the response (illustrated for the blue grating by making it darker), the fish moved away from the centre of the tank. The position of the fish indicated the point of perceived equi-luminance (asterisks) between the presented gratings. (B) Spectral compositions of the projected gratings measured at the output lens of the projector and the spectral locations of the rearing lights (broken vertical lines). (C) Intensity gradients at peak values of the projected sinusoidal gratings measured in the experimental tank at the white film used as a projection screen. The fishes were mainly active in bins –5 to +5 (see Fig. 2), where the intensity gradients were almost linear. (D) Diagram of the experimental schedule in blocks of 1 min. White arrowheads indicate that moving gratings were presented; black arrows show the flow of time. The order of the presented color combinations (I, II, III) was rotated after each fish (I II III, II III I, III I II, I II III, etc.) to avoid possible bias by chromatic adaptation.

deprivation. The aquaria of both white light groups were illuminated with the same type of fluorescent lamp (Osram Dulux EL, 7W). All groups were held under 12 h:12 h light:dark cycles. More details on the rearing conditions can be found in Kröger and Wagner (1996) and Kröger et al. (1999, 2001). We studied innate behavior in order to avoid training periods that, prior to testing, would expose the animals to spectral environments different from the rearing lights.

Optomotor response

In the optomotor response, animals follow a moving visual pattern if there are no other stronger cues for orientation. To elicit the behavior, we presented pairs of patterns moving in opposite directions, similar to the apparent motion stimuli used by Neuhauss et al. (1999).

The dimensions of the experimental tank were 2.0 m×0.25 m×0.25 m (length × width × height). The front wall was covered with white adhesive film on which the stimulation patterns were projected. The other walls were black, and the bottom was of dark-red color that absorbed almost all visible light but diffusely reflected far-red and near-infrared wavelengths. We used a data projector (Mitsubishi L VP-X-100E) to project moving (0.17 m s^{-1}) pairs of sinusoidal vertical gratings (38 cycles m^{-1}) on the front wall of the experimental tank. The two gratings had opposing gradients of brightness and directions of motion, with each grating moving towards its darker portion (Fig. 1A). The spectra and the gradients of brightness of the projected lights are shown in Fig. 1B,C. The animals followed the grating they perceived as brighter down its intensity gradient until they reached the point of equi-luminance between the two gratings. At this location, the animals experienced a balanced, converging motion stimulus from both sides. This is similar to the visual flow field during backward motion. In response, the animals swam forward against the wall of the tank. They remained at the front wall of the experimental tank within a narrow lateral region including the point of equi-luminance, thereby indicating which relative strengths the presented gratings had to drive the optomotor response.

To ensure complete light adaptation, the experiments were started at the earliest 2 h after lights-on in the rearing aquaria and were terminated at the latest 2 h before lights-off. After a fish had been transferred to the experimental tank, it was allowed to acclimate under stationary white illumination for 10 min. For the next 3 min, two identical, sinusoidal black-and-white gratings were projected. The point of equi-luminance was at the centre of the tank, such that all fish had about the same starting position for chromatic testing. Thereafter, a pair of colored gratings (I, II or III in Fig. 1D) was projected. After 1 min, the two colors switched places. When five such runs had been completed, a new pair of colors

Table 1. *Analysis of variance*

	Color pair					
	Blue/green		Blue/red		Green/red	
	Origin of variance (%)	Level of significance	Origin of variance (%)	Level of significance	Origin of variance (%)	Level of significance
Groups	2.2	NS	4.6	$P<0.05$	5.7	$P<0.01$
Fishes	15.1	$P<0.001$	28.7	$P<0.001$	14.5	$P<0.001$
Measurements	82.7	–	66.7	–	79.8	–

Variances in the results from each pair of stimulation colors were analysed with two-level nested analysis of variance (ANOVA; Sokal and Rohlf, 1995). Most of the variance resulted from differences between individual measurements from each fish. Furthermore, there were highly significant differences between individual fishes in each rearing group under all stimulation conditions. Significant differences between rearing groups were present in the data obtained during stimulation with blue/red and green/red color pairs. NS, not significant at the 5% level.

Table 2. *Summary of results*

	Rearing group (number of animals)				
Color pair	BW (12)	DW (12)	Red (12)	Green (7)	Blue (12)
Blue/green	–1.65±0.51	–2.45±0.40	–2.84±0.44	–1.41±0.28	–2.94±0.39
Blue/red	–1.76±0.46	–3.23±0.51	–2.69±0.77	–1.11±0.62	–1.14±0.36
t-tests	$P<0.05$	–	NS	$P<0.01$	$P<0.01$
Green/red	+0.30±0.31	0.80±0.42	–0.12±0.36	+1.23±0.76	+1.48±0.44
t-tests	$P<0.05$	–	NS	$P<0.01$	$P<0.001$

Values are averaged bin numbers (positions in experimental tank) ± S.E.M. Bin number 0 was at the centre of the tank. A negative (or positive) value means that the first color in the respective color pair (leftmost column) was less (or more) efficient in driving the optomotor response than the second color. The dim-white light (DW) group served as the reference in all *t*-tests. No tests were performed on the data obtained with the blue/green color pair, since the ANOVA (Table 1) did not detect any significant differences in that set of data.

The animals in the red group chose positions in the experimental tank that were not significantly different from the positions preferred by the fishes in the DW group. In all other groups, including the BW (bright-white light) group, the positions of the animals differed significantly from the positions of the fishes in the DW group.

NS, not significant at the 5% level.

was tested in the same way. The order of color pairs was changed after each fish: I II III, II III I, III I II, I II III, and so on.

The experimental schedule is illustrated in Fig. 1D. Each fish was exposed to light of spectral composition different from the rearing light for only about 30 min, including the time the fish was given to familiarize itself with the experimental tank.

For recordings, the experimental tank was illuminated from above with infra-red light-emitting diodes (peak emission at 875 nm). The animals were video-taped with an infra-red-sensitive CCD camera (BC-2, AVT Horn). After each change in the direction of grating motion or combination of colors, we waited for 20 s to allow the fish to find the new point of equi-luminance. Then, five images were grabbed at intervals of 10 s. For analysis, the tank was divided into 19 bins of 10 cm in width (15 cm for bins –9 and +9, which were rarely visited by the animals). Bin number 0 was at the centre of the tank. The binned positions of the fish were digitally determined from the grabbed images (25 measurements), switched between left and right in parallel to the switches in color positions, and averaged for each combination of colors before further analysis.

Results

We collected data on the optomotor responses of 12 fish in each group, except for the green group in which only seven animals were available. Most fishes readily followed the moving patterns and stayed within a narrow area at the point of equi-luminance. However, a few fish did not react to the moving patterns and stayed at one end of the aquarium. These animals were tested again at a later time when they were more ‘cooperative’. Occasionally, a fish did not react to a change in pattern orientation. These runs were not eliminated from the analysis because of lack of objective criteria (see Discussion).

Statistically significant (by analysis of variance) effects of the rearing conditions were detectable by stimulation with blue/red and green/red color pairs (Table 1). Rearing blue acara in long-wavelength light (red group) did not change the points of equi-luminance. Rearing in middle-wavelength (green group) and short-wavelength (blue group) light resulted in a significant shift of the point of equi-luminance towards long wavelengths (Table 2; Fig. 2). This indicates that the animals were less sensitive to long-wavelength light than the animals in the DW reference group (or more sensitive to middle- and

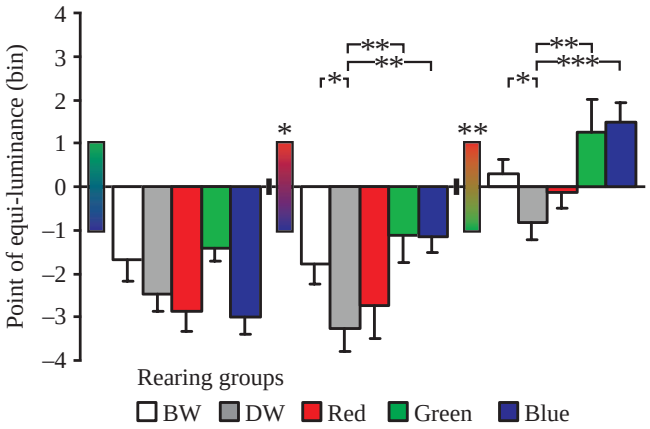

Fig. 2. Group means of fish positions in the experimental tank during chromatic stimulations. The colored bars crossing the abscissa (centre of the tank) indicate the color pairs and their orientations used for stimulation. Error bars represent S.E.M. Statistical analyses were performed using analysis of variance (ANOVA) to test for differences between groups for each color pair (Table 1) and Student's *t*-test to test whether group means were different from the mean in the dim-white control group (Table 2). Only statistically significant differences are indicated. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. BW, bright-white rearing light; DW, dim-white rearing light.

short-wavelength light, or a combination of both effects). In the BW group, short and middle wavelengths were more efficient relative to long wavelengths in driving the optomotor response than in the DW group (Table 2; Fig. 2).

Sources of variance

'Failures' of fish to react to a change of color positions occurred in approximately 10% of all runs. When the fish was in bin N during one orientation of colors, the same position was assigned to bin –N after the change in color positions. Even small numbers of failures therefore led to large amounts of variance among measurements and fishes (Table 1). Furthermore, group means were somewhat biased towards 0 (centre of aquarium). We did not eliminate any 'bad' runs from the analysis because it was impossible to detect them by criteria that were objective and equally applicable to all data sets. When the fish remained stationary close to the centre of the aquarium, it was unclear whether the animal had ceased to react or whether it was at its point of equi-luminance. Furthermore, when a fish remained at the same position in the aquarium during a cycle of changes in color positions, we could not determine whether N or –N was the real point of equi-luminance.

Discussion

Effects of spectral deprivation

The effects induced by spectral deprivation that we had previously observed in the outer retina of *A. pulcher* suggested the presence of compensatory mechanisms in the retina that aim to maintain a balanced signal transfer from all spectral cone types to second-order neurons. The amount of deprivation of long wavelengths seemed to be the critical parameter since only rearing in short-wavelength light induced profound effects, while rearing in middle- and long-wavelength light was of little or no consequence (one possible exception mentioned below; Wagner and Kröger, 2000; Kröger et al., 2001).

In agreement with the observations in the outer retina, rearing in red light had no effect on the optomotor response (Fig. 2; Table 2). In the other rearing groups, however, the results differed somewhat from what was expected from the findings in the outer retina. When long wavelengths were tested against middle and short wavelengths, the fish in the green and blue groups had virtually identical points of equi-luminance, which differed significantly from the DW group. In studies on the outer retina, the green group had been similar to the DW group (synaptic complexes of cones, Kröger and Wagner, 1996; survival of short-wavelength-sensitive cones, Kröger et al., 1999; Wagner and Kröger, 2000). With the reservation that fewer fish could be tested in the green group ($N=7$) than in the other groups ($N=12$), our current findings suggest that the mechanisms controlling spectral sensitivity in the blue acara are more complex than a simple short *vs* long wavelength compensation. Furthermore, it is likely that regulatory mechanisms are present on several levels of chromatic processing, since the effects observed in the outer retina cannot fully explain the effects on the behavioral level.

The existence of several levels of compensatory mechanisms is also suggested by a preliminary observation of an effect of rearing in red light. In fish reared in red light, a substantial proportion of short-wavelength-sensitive (SWS) cones was eliminated after the animals had been transferred to white light. We suggest that this might serve to counter-compensate in the outer retina for a compensation on a higher level induced by the initial rearing under red light (Wagner and Kröger, 2000).

Comparison with other species

In light of the strong effects of spectral deprivation on retinal morphology and visual behavior in the blue acara, it seems surprising that similar effects have not been found in other vertebrates. A likely reason is that most research groups used long-wavelength light during rearing (Peterson, 1961; McCourt and Jacobs, 1983; Brenner et al., 1985, 1990), which turned out to be ineffective in the blue acara too. Closest to our study is the work on goldfish (*Carassius auratus*) by Mecke (1983). In that and our studies, fish were reared for long times (>1 year) under narrow-banded lights of short and long wavelengths. In contrast to our approach, Mecke initially used a training paradigm that exposed the monochromatically reared fish to various spectral lights for about a week prior to testing. When these experiments did not reveal any significant differences in color discrimination ability between control and monochromatically reared animals, the author surmised that the goldfish might have recovered from the effects of spectral deprivation during the

training period. Some animals reared in red light were therefore trained only under red light before testing. Even under those carefully controlled conditions, no significant effect of spectral deprivation was detected (Mecke, 1983). This is in agreement with our results, since changes in the optomotor response of the blue acara were only present in the blue and green groups and not in the red group.

Pigeons reared in red and blue lights were also tested only after they had been exposed to broad-spectrum light for some time (Brenner et al., 1983). The apparent differences between our findings and the results of earlier studies may be resolved when more is known about the time-scale of recovery from the effects of spectral deprivation.

Interestingly, developmental plasticity in color vision has recently been demonstrated in a mantis shrimp (*Haptosquilla trispinosa*, Stomapoda); Cronin et al., 2001]. Developmental fine-tuning of spectral sensitivity and processing may be present in many visual systems.

Effects of the intensity of white light

It may seem surprising that the intensity of white light during rearing induced changes in the optomotor response to stimuli of different colors (Table 2; Fig. 2). The functional explanation for this phenomenon might be found in photoreceptor noise. Rieke and Baylor (2000) have shown that the dark noise of long-wavelength-sensitive (LWS) cones of the salamander is dominated by thermally induced isomerisations of the photopigment, while the dark noise of SWS cones has other origins. Even in complete darkness, thermally induced isomerisations keep the LWS cones in a partially light-adapted state, such that their responses to dim flashes are much lower than those of SWS cones (Rieke and Baylor, 2000). Such pre-adaptation of LWS cones by dark noise only plays a role in dim light, since in bright light all cones will be in the light-adapted state. In our DW group, pre-adaptation of the LWS cones may have reduced their signals relative to SWS cone signals. In response, compensatory mechanisms during rearing may have increased the gain in channels processing LWS cone signals and/or reduced the gain in channels processing SWS signals, making the animals from the DW group during testing relatively more sensitive to long-wavelength light than fish from the BW group (Table 2; Fig. 2).

Previously, we have observed effects of the intensity of white light at the level of cone-specific horizontal cells (CHCs). Rearing in bright white light led to a significant reduction of synaptic contacts between SWS cones and CHCs of the H2-Cb type, which biphasically encode chromaticity (Braun et al., 1997). Furthermore, the spectral responses of H2-Cb cells differed significantly between the DW and BW groups (Kröger et al., 2001). In fishes, the strength of feedforward signalling by cones is influenced by sign-inverting feedback from CHCs to the cones' output synapses (Stell et al., 1994; Kamermans and Spekreijse, 1995; Kamermans et al., 2001). Such feedback from CHCs to cones may have a role in bringing about the effects of light intensity.

Input channels to the optomotor response

Under mesopic conditions, input from both cones and rods may contribute to the optomotor response. Since the gratings were projected over a large area and were viewed from behind the white film that served as a projection screen, light intensities during chromatic stimulations (Fig. 1C) may have been in the mesopic range. It is nevertheless unlikely that rods made any contribution to the optomotor responses investigated in this study. In the blue acara, the retinomotor movements of cones, rods and melanosomes in the retinal pigment epithelium cells (Burnside and Nagle, 1983) are strongly influenced by a circadian oscillator. In the light-adapted state, only cones are in the focal plane of the eye. The myoids of rods are elongated and their outer segments are screened from incoming light by the melanosomes of the retinal pigment epithelium. Once entrained to a daily light:dark cycle, rods and cones remain in their light-adapted positions throughout the entire light phase, even during prolonged darkness (Douglas et al., 1992). During morphological studies (Kröger and Wagner, 1996; Braun et al., 1997; Kröger et al., 1999), we observed that cones contracted fully in animals reared in long-wavelength light. A slight reduction of the contraction of single cones present in young animals (6 months old; Kröger and Wagner, 1995) was not found in adults (R. H. H. Kröger, B. Knoblauch and H.-J. Wagner, unpublished observations).

Schaerer and Neumeyer (1996) have reported that the optomotor response of the goldfish receives positive input only from LWS cones and that there seems to be only weak negative input from SWS cones. By contrast, the optomotor response of *A. pulcher* seems to be driven by several spectral cone types. Involvement of rods is unlikely (see above) and the absorbances of the cone pigments were insensitive to the rearing conditions (Kröger et al., 1999). If a single spectral cone type drives the response, all animals should have had identical relative sensitivities to the pairs of colors used in this study. Our results therefore suggest that several spectral types of cone are involved and that their relative contributions, which may be positive and negative, to the optomotor response are influenced by the spectral environment during development.

This should be kept in mind during comparisons of visual capabilities of different stocks of animals. Different results from different groups of conspecifics may not only be due to genetic differences and different procedures if several research groups are involved but may also be caused by different lighting conditions during development of the animals.

Dorsal light reaction

If illuminated from the side, fish orient their dorso-ventral body axis parallel to a vector resulting from the addition of the gravity vector (vertical) and the light vector (horizontal) (von Holst, 1935). The brighter the light, the more strongly the animals tilt towards the light source. This dorsal light reaction has previously been used to determine spectral sensitivities in other fish species (Silver, 1974; Powers, 1978). *A. pulcher*, however, showed only negligible tilt when illuminated with light levels that induced an almost 90° tilt in the goldfish we

used for comparison. The dorsal light reaction in *A. pulcher* was thus too weak to be used for measurements of spectral sensitivities.

Conclusions

The optomotor response of *A. pulcher* to chromatic stimuli is dependent on the spectral and photic conditions during rearing. This and previous findings indicate that in this species developmental plasticity is not only present in the retina but is also evident at the behavioral level. The circuitry of spectral processing and color vision in vertebrates may therefore not be as strictly genetically determined as has been suggested by the results of earlier studies.

We thank Almut Kelber for critically reading the manuscript and gratefully acknowledge financial support by the Deutsche Forschungsgemeinschaft, Wa 348/17-2.

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