

acara (Aequidens pulcher) morphological organization of the outer retina of the blue Effects of long−**term spectral deprivation on the**

H.J. Wagner and R.H.H. Kröger

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Effects of long-term spectral deprivation on the
 Effects of long-term spectral deprivation on the Effects of long-term spectral deprivation on the
 morphological organization of the outer retina

of the blue seers (Aequidens pulsher) **of the blue acara (***Aequidens pulcher***)**

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Anatomisches Institut, Universität Tübingen, Osterbergstraße 3, D-72074 Tübingen, Germany
To investigate the developmental plasticity of colour vision, we reared fish with a trichromatic cone
system (Aequidens bulcher) und To investigate the developmental plasticity of colour vision, we reared fish with a trichromatic cone
system *(Aequidens pulcher)* under three near-monochromatic lights, differentially stimulating each spectral
cone type f system (*Aequidens pulcher*) under three near-monochromatic lights, differentially stimulating each spectral cone type from the larval stage to the age of at least one year. Control conditions comprised white lights system (*Aequidens pulcher*) under three near-monochromatic lights, differentially stimulating each spectral
cone type from the larval stage to the age of at least one year. Control conditions comprised white lights
of two cone type from the larval stage to the age of at least one year. Control conditions comprised white lights
of two intensities. The treatments did not affect the visual pigments, but led to significant changes in cone
outer of two intensities. The treatments did not affect the visual pigments, but led to significant changes in cone
outer segment lengths. Furthermore, in the blue-reared group the density of single cones within the retina
was r outer segment lengths. Furthermore, in the blue-reared group the density of single cones within the retina
was reduced by two-thirds after 18 months of exposure, while no changes were observed in the other
groups. The conn was reduced by two-thirds after 18 months of exposure, while no changes were observed in the other
groups. The connectivity of cone horizontal cells with the single cones was influenced by the intensity and
spectral compos groups. The connectivity of cone horizontal cells with the single cones was influenced by the intensity and spectral composition of the rearing lights: H1 cells were more sensitive to the spectral component, whereas H2 cel spectral composition of the rearing lights: H1 cells were more sensitive to the spectral component, whereas H2 cells responded to intensity cues. In the blue-light group the dynamics of horizontal cell synaptic spinule for whereas H2 cells responded to intensity cues. In the blue-light group the dynamics of horizontal cell
synaptic spinule formation and degradation were severely compromised. These observations show that
long-term spectral de and horizontal cells. While the reactions of photoreceptors may be interpreted mostly in terms of compenlong-term spectral deprivation leads to significant morphological changes at the level of photoreceptors
and horizontal cells. While the reactions of photoreceptors may be interpreted mostly in terms of compen-
sation, the and horizontal cells. While the react
sation, the functional consequences
determined electrophysiologically.

Keywords: spectral deprivation; cone visual pigments; cone outer segments; spectral cone types; ne visual pigments; cone ot
horizontal cells; spinules

1. INTRODUCTION

The visual system offers many examples for experience-The visual system offers many examples for experience-
dependent processes in the development of neural
circuitry. The classical and maybe best-studied cases The visual system offers many examples for experience-
dependent processes in the development of neural
circuitry. The classical, and maybe best-studied cases
concern the primary visual cortex of mammals with its dependent processes in the development of neural circuitry. The classical, and maybe best-studied cases concern the primary visual cortex of mammals with its ocular dominance and orientation columns (see Senomiel circuitry. The classical, and maybe best-studied cases
concern the primary visual cortex of mammals with its
ocular dominance and orientation columns (see Sengpiel
 et el (1999) for a review). The neural basis of colour concern the primary visual cortex of mammals with its
ocular dominance and orientation columns (see Sengpiel
et al. (1999) for a review). The neural basis of colour
vision by contrast, has turned out to be highly resista ocular dominance and orientation columns (see Sengpiel *et al.* (1999) for a review). The neural basis of colour vision, by contrast, has turned out to be highly resistant to artificial manipulation of the chromatic envir *et al.* (1999) for a review). The neural basis of colour vision, by contrast, has turned out to be highly resistant to artificial manipulation of the chromatic environment, at least as far as can be deduced from behaviour vision, by contrast, has turned out to be highly resistant to artificial manipulation of the chromatic environment, at least as far as can be deduced from behavioural experito artificial manipulation of the chromatic environment,
at least as far as can be deduced from behavioural experi-
ments and the development of retinal ganglion cells
(summarized in Kröger *et al.* 1999). The suggestion at least as far as can be deduced from behavioural experiments and the development of retinal ganglion cells (summarized in Kröger *et al.* 1999). The suggestion that colour vision is more 'hard-wired' than other component ments and the development of retinal ganglion cells
(summarized in Kröger *et al.* 1999). The suggestion that
colour vision is more 'hard-wired' than other components
of visual processing has however not been rigorously (summarized in Kröger *et al.* 1999). The suggestion that colour vision is more 'hard-wired' than other components of visual processing has, however, not been rigorously tested on a cell biological level. of visual processing has, however, not been rigorously visual processing has, however, not been rigorously
ted on a cell biological level.
The adaptive state of the teleost retina is indicated by
perphological changes at the light and electron micro-

tested on a cell biological level.
The adaptive state of the teleost retina is indicated by
morphological changes at the light and electron micro-
scopic level. They comprise retinomator movements of The adaptive state of the teleost retina is indicated by
morphological changes at the light and electron micro-
scopic level. They comprise retinomotor movements of
photoreceptor, and retinal pigment enithelium cells morphological changes at the light and electron microscopic level. They comprise retinomotor movements of photoreceptor and retinal pigment epithelium cells, changes in the synaptic complexes of rods and cones scopic level. They comprise retinomotor movements of
photoreceptor and retinal pigment epithelium cells,
changes in the synaptic complexes of rods and cones,
including the size of synaptic ribbons and the formation photoreceptor and retinal pigment epithelium cells, changes in the synaptic complexes of rods and cones, including the size of synaptic ribbons and the formation changes in the synaptic complexes of rods and cones,
including the size of synaptic ribbons and the formation
or retraction of spinules, as well as the electrical coupling
of cone horizontal cells (see Diamaga et al. (199 including the size of synaptic ribbons and the formation
or retraction of spinules, as well as the electrical coupling
of cone horizontal cells (see Djamgoz *et al.* (1995) for a
review) Such adaptation-dependent reorganiz or retraction of spinules, as well as the electrical coupling
of cone horizontal cells (see Djamgoz *et al.* (1995) for a
review). Such adaptation-dependent reorganizations are
likely to be manifestations of changes in sen of cone horizontal cells (see Djamgoz *et al.* (1995) for a review). Such adaptation-dependent reorganizations are likely to be manifestations of changes in sensitivity. Furthermore, some of these processes, especially the review). Such adaptation-dependent reorganizations are likely to be manifestations of changes in sensitivity.
Furthermore, some of these processes, especially the Furthermore, some of these processes, especially the *Author for correspondence (hjwagner@anatu.uni-tuebingen.de).

dynamics of horizontal cell spinules, have been implicated in the processing of spectral information, since they are associated with changes in chromatic feedback activity (Weiler & Wagner 1984). We therefore started our investiassociated with changes in chromatic feedback activity
(Weiler & Wagner 1984). We therefore started our investigation of the developmental plasticity of colour vision by
quantifying such morphological parameters (Weiler & Wagner 1984). We therefore started
gation of the developmental plasticity of colo
quantifying such morphological parameters.
In order to induce long-term plastic It is discribed to induce long-term plasticity of colour vision by
antifying such morphological parameters.
In order to induce long-term plastic changes, we
posed fishes from the larval stage to the age of at least

quantifying such morphological parameters.
In order to induce long-term plastic changes, we
exposed fishes from the larval stage to the age of at least
one year to near-monochromatic lights at wavelengths In order to induce long-term plastic changes, we
exposed fishes from the larval stage to the age of at least
one year to near-monochromatic lights at wavelengths
chosen to maximally stimulate each spectral cone type exposed fishes from the larval stage to the age of at least
one year to near-monochromatic lights at wavelengths
chosen to maximally stimulate each spectral cone type,
and simultaneously deprived them of the other two spec one year to near-monochromatic lights at wavelengths
chosen to maximally stimulate each spectral cone type,
and simultaneously deprived them of the other two specchosen to maximally stimulate each spectral cone type,
and simultaneously deprived them of the other two spec-
tral channels. We used a cichlid species (the blue acara,
Aequidens hulcher), which has a trichromatic cone s and simultaneously deprived them of the other two spectral channels. We used a cichlid species (the blue acara, *Aequidens pulcher*), which has a trichromatic cone system and a bigbly ordered mosaic spatial arrangement of tral channels. We used a cichlid species (the blue acara, *Aequidens pulcher*), which has a trichromatic cone system and a highly ordered mosaic spatial arrangement of cones and horizontal cells in order to simplify the as *Aequidens pulcher*), which has a trichromatic cone system and a highly ordered mosaic spatial arrangement of cones and horizontal cells, in order to simplify the assessment of and a highly ordered mosaic spatial arrangement of cones
and horizontal cells, in order to simplify the assessment of
functional morphology of the outer retina. In this paper,
we summarize the morphological effects of this and horizontal cells, in order to simplify the assessment of
functional morphology of the outer retina. In this paper,
we summarize the morphological effects of this treatment
and report some new results on the time-course functional morphology of the outer retina. In this paper,
we summarize the morphological effects of this treatment
and report some new results on the time-course of
induced effects we summarize th
and report som
induced effects.

2. MATERIAL AND METHODS

Groups of fish were reared in $12 h : 12 h$ light/dark cycles of Groups of fish were reared in 12 h:12 h light/dark cycles of

equi-irradiant (*ca*. 10¹² quanta s⁻¹cm⁻²) lights of three different

equi-irradiant (*ca*. 10¹² quanta s⁻¹cm⁻²) lights of three different Groups of fish were reared in 12 h:12 h light/dark cycles of
equi-irradiant (*ca*. 10¹² quantas⁻¹cm⁻²) lights of three different
wavelengths: 590 nm (red), for preferential stimulation of the
lang view consitiue (1) wavelengths: 590 nm (red), for preferential stimulation of the long-wave-sensitive (L) larger member of the unequal double wavelengths: 590 nm (red), for preferential stimulation of the
long-wave-sensitive (L) larger member of the unequal double
cones (DCs); 513 nm (green) for preferential stimulation of the
middle wave consitive (M) emaller long-wave-sensitive (L) larger member of the unequal double
cones (DCs); 513 nm (green) for preferential stimulation of the
middle-wave-sensitive (M) smaller member of the unequal
DCs, and 450 nm (blue) for the preferenti middle-wave-sensitive (M) smaller member of the unequal DCs; and 450 nm (blue) for the preferential stimulation of the

short-wave-sensitive (S) single cones $(SCs;$ figure 1*b*). The stimulating lights were created with interference filters (halfshort-wave-sensitive (S) single cones (SCs; figure 1b). The stimulating lights were created with interference filters (half-
maximum bandwidths: 5-10 nm); their position within the
absorption spectra of the three cone time absorption spectra of the three cone types is shown in figure 1*b*.
absorption spectra of the three cone types is shown in figure 1*b*.
Two control groups were brought up under white light of 33 lux
(bright white group) an absorption spectra of the three cone types is shown in figure 1*b*.
Two control groups were brought up under white light of 33 lux ('bright-white group') and 0.2 lux ('dim-white group'), the latter appearing slightly dimme ('bright-white group') and 0.2lux ('dim-white group'), the latter to the human observer. Further details of the rearing conditions appearing slightly dimmer than the green monochromatic light
to the human observer. Further details of the rearing conditions
are described in Kröger *et al.* (1999). The various rearing
regimes started after hatching: mos to the human observer. Further details of the rearing conditions
are described in Kröger *et al.* (1999). The various rearing
regimes started after hatching; most fish were studied 12 months
later Additional intervals were regimes started after hatching; most fish were studied 12 months
later. Additional intervals were used to investigate the survival of S cones (see figure $1c$).

The absorption spectra of photoreceptor outer segments were of S cones (see figure *lc*).
The absorption spectra of photoreceptor outer segments were
determined with a computer-controlled dual-beam Liebman-
tune microspectrophotometer (cross section of measuring beam: The absorption spectra of photoreceptor outer segments were
determined with a computer-controlled dual-beam Liebman-
type microspectrophotometer (cross-section of measuring beam:
 $2 \text{ um: see Kröger at al. (1999) for details}$) type microspectrophotometer (cross-section of measuring beam: 2 µm; see Kröger *et al.* (1999) for details). be microspectrophotometer (cross-section of measuring beam:

im; see Kröger *et al.* (1999) for details).

For the study of spinule numbers and cone type frequencies,

lated ratings ware fixed in a naraform clutaraldebyde

2 μ m; see Kröger *et al.* (1999) for details).

For the study of spinule numbers and cone type frequencies,

isolated retinae were fixed in a paraform-glutaraldehyde (PA/
 GA) mixture, comicated and prepared for light isolated retinae were fixed in a paraform-glutaraldehyde (PA/GA) mixture, osmicated and prepared for light and electron microscopy according to routine protocols. Relative cone densi-GA) mixture, osmicated and prepared for light and electron GA) mixture, osmicated and prepared for light and electron
microscopy according to routine protocols. Relative cone densi-
ties were determined in tangential 1 µm sections through the
layer of cano, inner secreants stained microscopy according to routine protocols. Relative cone densi-
ties were determined in tangential 1 μ m sections through the
layer of cone inner segments stained with methylene blue.
Confocel lesse seen microscopy of 0. layer of cone inner segments stained with methylene blue.
Confocal laser scan microscopy of 0.1 mm radial sections of PA/ layer of cone inner segments stained with methylene blue.
Confocal laser scan microscopy of 0.1 mm radial sections of PA/
GA-fixed material incubated in 0.5% Lucifer Yellow (LY, Sigma,
Deisenbefon, Cormany) was used to det Confocal laser scan microscopy of 0.1 mm radial sections of PA/
GA-fixed material incubated in 0.5% Lucifer Yellow (LY, Sigma,
Deisenhofen, Germany) was used to determine the lengths of
sone outer secrecity of used to appr GA-fixed material incubated in 0.5% Luciter Yellow (LY, Sigma,
Deisenhofen, Germany) was used to determine the lengths of
cone outer segments as well as the connectivities of horizontal
sells and sone podicles. Colvi l Deisenhofen, Germany) was used to determine the lengths of
cone outer segments as well as the connectivities of horizontal
cells and cone pedicles. Golgi-like label of single cells was
obtained with LV applied to fresh rat cone outer segments as well as the connectivities of horizontal
cells and cone pedicles. Golgi-like label of single cells was
obtained with LY applied to fresh retinas (Braun *et al.* 1997).
Stacks of 0.5 um optical sectio cells and cone pedicles. Golgi-like label of single cells was
obtained with LY applied to fresh retinas (Braun *et al.* 1997).
Stacks of 0.5 µm optical sections were reconstructed in three
dimensions using the software of Stacks of $0.5 \mu m$ optical sections were reconstructed in three dimensions, using the software of the ZEISS LSM 410 system to Stacks of 0.5 μ m optical sections were reconstructed in three
dimensions, using the software of the ZEISS LSM 410 system to
measure entire individual outer segments, and to establish the
connectivity of cano enocifie b dimensions, using the software of the ZEISS LSM 410
measure entire individual outer segments, and to esta
connectivity of cone-specific horizontal cells (CHCs). **3. RESULTS AND DISCUSSION**

(a) *Photoreceptors*

(i) *Visual pigments*

(a) **Photoreceptors**
 $Visual\ pair$
A tangential section of the photoreceptor layer just
tral to the external limiting membrane shows the (i) *Visual pigments*
A tangential section of the photoreceptor layer just
distal to the external limiting membrane shows the
square-mosaic-type arrangement of cones consisting of a A tangential section of the photoreceptor layer just
distal to the external limiting membrane shows the
square-mosaic-type arrangement of cones, consisting of a
majority of unequal DCs with a larger L and a smaller M partner surrounding a central single cone (S, figure la). majority of unequal DCs with a larger L and a smaller M
partner surrounding a central single cone (S, figure 1a).
Some cases of equal, 'twin' cones with L characteristics
were also observed I DCs had neak absorbances (1) partner surrounding a central single cone (S, figure 1*a*).
Some cases of equal, 'twin' cones with L characteristics
were also observed. L DCs had peak absorbances (λ_{max})
at 570 nm M DC partners had a λ at 530 nm Some cases of equal, 'twin' cones with L characteristics
were also observed. L DCs had peak absorbances (λ_{max})
at 570 nm, M DC partners had a λ_{max} at 530 nm, and S
SCs were maximally sensitive at 453 nm (Kröger were also observed. L DCs had peak absorbances (λ_{max}) at 570 nm, M DC partners had a λ_{max} at 530 nm, and S
SCs were maximally sensitive at 453 nm (Kröger *et al.* 1999). Monochromatic rearing did not change the SCs were maximally sensitive at 453 nm (Kröger *et al.* 1999). Monochromatic rearing did not change these peak absorbances more than within the range of standard deviation. The observed variability was probably due to 1999). Monochromatic rearing did not change these peak
absorbances more than within the range of standard
deviation. The observed variability was probably due to
polymorphism or varying amounts of porphyropsin absorbances more than within the range of standard
deviation. The observed variability was probably due to
polymorphism, or varying amounts of porphyropsin
(Kröger et al. 1999). We may therefore conclude that deviation. The observed variability was probably due to polymorphism, or varying amounts of porphyropsin (Kröger *et al.* 1999). We may therefore conclude that monochromatic rearing does not affect cone absorbances (Kröger *et al.* 1999). We may therefore conclude that monochromatic rearing does not affect cone absorbances. (Kröger *et al.* 1999). We may therefore conclude that monochromatic rearing does not affect cone absorbances.
This is in contrast to findings in other teleosts where external cues and seasonal migrations lead to shifts i monochromatic rearing does not affect cone absorbances.
This is in contrast to findings in other teleosts where
external cues and seasonal migrations lead to shifts in the
relative amounts of rhodonsin and porphyronsin all This is in contrast to findings in other teleosts where
external cues and seasonal migrations lead to shifts in the
relative amounts of rhodopsin and porphyropsin, allowing
plasticity in the spectral sensitivity (Bowmaker external cues and seasonal migrations lead to shifts in the relative amounts of rhodopsin and porphyropsin, allowing plasticity in the spectral sensitivity (Bowmaker 1990). What drives these changes is presently unknown.

(ii) *Cone outer segment lengths*

In each of three specimens from each rearing group, 15 (ii) Cone outer segment lengths

In each of three specimens from each rearing group, 15

DC outer segments were assessed irrespective of their

spectral identity Their lengths were expressed relative to In each of three specimens from each rearing group, 15
DC outer segments were assessed irrespective of their
spectral identity. Their lengths were expressed relative to
the lengths of the inner segment. No statistically si spectral identity. Their lengths were expressed relative to
the lengths of the inner segment. No statistically significant

differences were found between the dim-white group, the
green and the red rearing group. However, in the blue differences were found between the dim-white group, the green, and the red rearing group. However, in the blue
rearing group, the relative DC outer segment lengths differences were found between the dim-white group, the green, and the red rearing group. However, in the blue rearing group, the relative DC outer segment lengths were increased by ca 44% with respect to this baseline green, and the red rearing group. However, in the blue
rearing group, the relative DC outer segment lengths
were increased by ca . 44% with respect to this baseline $(p < 0.001)$, whereas in the bright-white group, outer were increased by *ca*. 44% with respect to this baseline ($p < 0.001$), whereas in the bright-white group, outer segments were shorter by 27% ($p < 0.001$); Kröger *et al*. 1999). Both of these effects may be interpr segments were shorter by 27% ($p < 0.00$ l; Kröger *et al.* 1999). Both of these effects may be interpreted in terms of compensatory mechanisms, which result in keeping the rate of photon catch constant. In the bright-white 1999). Both of these effects may be interpreted in terms of compensatory mechanisms, which result in keeping the rate of photon catch constant. In the bright-white group, they constitute a process *hhototasis*, which aims compensatory mechanisms, which result in keeping the rate of photon catch constant. In the bright-white group, they constitute a process, *photostasis*, which aims at equal-
izing luminosity signals (Penn & Williams 1986) rate of photon catch constant. In the bright-white group,
they constitute a process, *photostasis*, which aims at equal-
izing luminosity signals (Penn & Williams 1986). Similar
effects, have been reported previously in go they constitute a process, *photostasis*, which aims at equalizing luminosity signals (Penn & Williams 1986). Similar effects have been reported previously in goldfish rods (Raymond *et al.* 1988). This is the first time t izing luminosity signals (Penn & Williams 1986). Similar effects have been reported previously in goldfish rods (Raymond *et al.* 1988). This is the first time that cones have been shown to react in this way. The elongatio effects have been reported previously in goldfish rods (Raymond *et al.* 1988). This is the first time that cones have been shown to react in this way. The elongation of L/M DC outer segments in blue light suggests the (Raymond *et al.* 1988). This is the first time that cones
have been shown to react in this way. The elongation of
 L/M DC outer segments in blue light suggests the
presence of similar mechanisms which aim at balancing have been shown to react in this way. The elongation of L/M DC outer segments in blue light suggests the presence of similar mechanisms, which aim at balancing the relative sensitivities to different spectral ranges L/M DC outer segments in blue light suggests
presence of similar mechanisms, which aim at balai
the relative sensitivities to different spectral ranges. the relative sensitivities to different spectral ranges.
(iii) *Loss of single cones*

distal to the external limiting membrane shows the from animals reared under blue light of slightly longer square-mosaic-type arrangement of cones, consisting of a wavelengths $(\lambda_{\text{max}} = 485 \text{ nm})$, where the number of S m Figure *lc* shows the time-course of S SC densities in the (iii) Loss of single cones

Figure 1c shows the time-course of S SC densities in the

central retina between four and 18 months after exposure

to the different lighting conditions. We had previously Figure $1c$ shows the time-course of S SC densities in the central retina between four and 18 months after exposure to the different lighting conditions. We had previously observed that in the one-vear-old blue-light grou to the different lighting conditions. We had previously observed that in the one-year-old blue-light group, there to the different lighting conditions. We had previously observed that in the one-year-old blue-light group, there was a centro-peripheral gradient of S SCs, with a full complement in the periphery next to the growth zone observed that in the one-year-old blue-light group, there
was a centro-peripheral gradient of S SCs, with a full
complement in the periphery next to the growth zone,
and loss of un to 30% in the retinal fundus dorsal of th was a centro-peripheral gradient of S SCs, with a full
complement in the periphery next to the growth zone,
and loss of up to 30% in the retinal fundus dorsal of the
ontic nerve head (Kröger *et al* 1999) S SC populati complement in the periphery next to the growth zone, and loss of up to 30% in the retinal fundus dorsal of the optic nerve head (Kröger *et al.* 1999). S SC populations in and loss of up to 30% in the retinal fundus dorsal of the optic nerve head (Kröger *et al.* 1999). S SC populations in the white- and green-light groups were unaffected, whereas a certain degree of fluctuation was appa optic nerve head (Kröger *et al.* 1999). S SC populations in
the white- and green-light groups were unaffected,
whereas a certain degree of fluctuation was apparent in
the red-light group (figure lc) Following the fate of the white- and green-light groups were unaffected,
whereas a certain degree of fluctuation was apparent in
the red-light group (figure lc). Following the fate of the S
SCs for another six months shows a stable situation fo whereas a certain degree of fluctuation was apparent in the red-light group (figure $1c$). Following the fate of the S
SCs for another six months shows a stable situation for the red-light group (figure lc). Following the fate of the S
SCs for another six months shows a stable situation for
these latter groups, and also demonstrates that in the
blue-light group, the decrease of SC density con SCs for another six months shows a stable situation for
these latter groups, and also demonstrates that in the
blue-light group, the decrease of SC density continues
steadily to a point where only about one-third of contro these latter groups, and also demonstrates that in the blue-light group, the decrease of SC density continues steadily to a point where only about one-third of control numbers is preserved With this trend opgoing it may be blue-light group, the decrease of SC density continues
steadily to a point where only about one-third of control
numbers is preserved. With this trend ongoing it may be
expected that two years of exposure to monochromatic steadily to a point where only about one-third of control
numbers is preserved. With this trend ongoing it may be
expected that two years of exposure to monochromatic
blue light will completely deplete the population of S numbers is preserved. With this trend ongoing it may be expected that two years of exposure to monochromatic blue light will completely deplete the population of S SCs in the central retina. This is in contrast to results obtained blue light will completely deplete the population of S SCs
in the central retina. This is in contrast to results obtained
from animals reared under blue light of slightly longer
wavelengths $(1) = 485 \text{ nm}$ where the numbe in the central retina. This is in contrast to results obtained
from animals reared under blue light of slightly longer
wavelengths (λ_{max} = 485 nm), where the number of S
cones seemed to stabilize after about one yea from animals reared under blue light of slightly longer
wavelengths $(\lambda_{\text{max}} = 485 \text{ nm})$, where the number of S
cones seemed to stabilize after about one year (Kröger *et*
 al 1999) The specific effectiveness of the short wavelengths $(\lambda_{\text{max}} = 485 \text{ nm})$, where the number of S cones seemed to stabilize after about one year (Kröger *et al.* 1999). The specific effectiveness of the short-wave component is further highlighted by the results o cones seemed to stabilize after about one year (Kröger *et al.* 1999). The specific effectiveness of the short-wave component is further highlighted by the results of two preliminary experiments, where fish were transferre al. 1999). The specific effectiveness of the short-wave component is further highlighted by the results of two preliminary experiments, where fish were transferred to white light from monochromatic rearing conditions after component is further highlighted by the results of two preliminary experiments, where fish were transferred to
white light from monochromatic rearing conditions after
ten months. In the red-light group only two months of
exposure to white light, which in contrast to the rearin white light from monochromatic rearing conditions after
ten months. In the red-light group only two months of
exposure to white light, which in contrast to the rearing
light has a short-wavelength component led to the disa ten months. In the red-light group only two months of
exposure to white light, which in contrast to the rearing
light has a short-wavelength component, led to the disap-
pearance of ca 40% of the S SCs. Stimulating fish exposure to white light, which in contrast to the rearing
light has a short-wavelength component, led to the disap-
pearance of *ca*. 40% of the S SCs. Stimulating fish of the
blue-light group with white light resulted in pearance of $ca. 40\%$ of the S SCs. Stimulating fish of the pearance of *ca*. 40% of the S SCs. Stimulating fish of the blue-light group with white light resulted in a reappearance of S SCs almost to control levels. This suggests that new S SCs were inserted into the cone mosaic in blue-light group with white light resulted in a reappearance of S SCs almost to control levels. This suggests that new S SCs were inserted into the cone mosaic in an orderly fashion. However, a larger and more focused ance of S SCs almost to control levels. This suggests that
new S SCs were inserted into the cone mosaic in an
orderly fashion. However, a larger and more focused
study is necessary to produce statistically useful sets of new S SCs were inserted into the cone mosaic in an orderly fashion. However, a larger and more focused study is necessary to produce statistically useful sets of data and to determine the mechanisms of cone regeneraorderly fashion. However, a larger and more focused
study is necessary to produce statistically useful sets of
data and to determine the mechanisms of cone regenera-
tion and cell guidance study is necessary to product and to determine the stinular controller and cell guidance.
The effects on cone of

ta and to determine the mechanisms of cone regenera-
in and cell guidance.
The effects on cone outer segment lengths and S SC
undance suggest that the relative spectral sensitivity of tion and cell guidance.
The effects on cone outer segment lengths and S SC
abundance suggest that the relative spectral sensitivity of
the retinalistic sumder regulatory control. Since these The effects on cone outer segment lengths and S SC
abundance suggest that the relative spectral sensitivity of
the retina is under regulatory control. Since these
processes occur over a long time span, the underlying abundance suggest that the relative spectral sensitivity of the retina is under regulatory control. Since these processes occur over a long time span, the underlying the retina is under regulatory control. Since these
processes occur over a long time span, the underlying
mechanisms are probably different from those leading to
colour constancy observed at the level of CHC responses processes occur over a long time span, the underlying
mechanisms are probably different from those leading to
colour constancy observed at the level of CHC responses
(Kamermans et al. 1998), which results from adjustments mechanisms are probably different from those leading to colour constancy observed at the level of CHC responses (Kamermans *et al.* 1998), which results from adjustments

THE ROYAL

PHILOSOPHICAL
TRANSACTIONS \overline{O}

BIOLOGICAL
SCIENCES

Figure 1. (a) Tangential section (1 µm) through the region of cone ellipsoids just distal of the external limiting membrane (right
margin of micrograph). In the blue acara, most double cones consist of a long (L) and a me Figure 1. (a) Tangential section (1 μ m) through the region of cone ellipsoids just distal of the external limiting membrane (right margin of micrograph). In the blue acara, most double cones consist of a long (L) and a margin of micrograph). In the blue acara, most double cones consist of a long (L) and a medium (M) wave partner arranged in
a square mosaic enclosing a central short-wave(S)-sensitive single cone. (Magnification \times 1800 a square mosaic enclosing a central short-wave(S)-sensitive single cone. (Magnification \times 1800.) (*b*) Position of the stimulating
lights (450 nm, 513 nm and 590 nm) relative to the microspectrophotometric data of norm lights (450nm, 513nm and 590nm) relative to the microspectrophotometric data of normalized absorbances (%) for the visu
pigments of the three spectral cone types of the blue acara (Kröger *et al.* 1999). (*c*) Survival of various spectral environments. Relative S SC densities were determined in each retina of two fishes per rearing group and
time-point (three fishes at 18 months). In blue light (diamonds), elimination of S SCs starts at fou to be ongoing at 18 months. Large fluctuations in the frequencies of SCs between time-points and specimens from the red group time-point (three fishes at 18 months). In blue light (diamonds), elimination of S SCs starts at four months or earlier and seems
to be ongoing at 18 months. Large fluctuations in the frequencies of SCs between time-points to be ongoing at 18 months. Large fluctuations in the frequencies of SCs between time-points and specimens from the red group
(triangles) may be due to transient effects with individual differences in time-course because o in the short- and middle-wavelength domains. In the white (circles) and green (squares) lights, there is no notable loss of S cones
over time. The error bars (transfer experiments) show ranges of results.

over time. The error bars (transfer experiments) show ranges of r
of synaptic feedback and feedforward interactions
between cones and CHCs. However, CHCs may also play of synaptic feedback and feedforward interactions
between cones and CHCs. However, CHCs may also play
a central role in the developmental balancing of the input of synaptic feedback and feedforward interactions
between cones and CHCs. However, CHCs may also play
a central role in the developmental balancing of the input
from the various spectral cone types in our experiments between cones and CHCs. However, CHCs may also play
a central role in the developmental balancing of the input
from the various spectral cone types in our experiments,
since they are in a strategic position to compare the a central role in the developmental balancing of the input
from the various spectral cone types in our experiments,
since they are in a strategic position to compare the rela-
tive strengths of stimulation. Their long-term from the various spectral cone types in our experiments,
since they are in a strategic position to compare the rela-
tive strengths of stimulation. Their long-term message
could be relayed to the photoreceptors by means of since they are in a strategic position to compare the relative strengths of stimulation. Their long-term message could be relayed to the photoreceptors by means of neuro-trophins, which have been localized in HC_8 (Gao. tive strengths of stimulation. Their long-term message

could be relayed to the photoreceptors by means of neuro-

trophins, which have been localized in HCs (Gao &

Hollyfield 1992) and lead to apontotic removal of SCs a could be relayed to the photoreceptors by means of neuro-
trophins, which have been localized in HCs (Gao &
Hollyfield 1992), and lead to apoptotic removal of SCs, a
phenomenon observed in preliminary examination of our trophins, which have been localized in HCs (Gao & material.

(b) *Horizontal cells*

(i) *Types and connectivities*

Three types of HCs are present in the blue acara (i) Types and connectivities
Three types of HCs are present in the blue acara
retina, one of which contacts only rods, whereas the other
two are CHCs. The HI CHC has the typical brush-like Three types of HCs are present in the blue acara
retina, one of which contacts only rods, whereas the other
two are CHCs. The H1 CHC has the typical brush-like
morphology with short dendrites directed towards the two are CHCs. The H1 CHC has the typical brush-like morphology with short dendrites directed towards the

ults.
cone pedicles and a single axon descending into the inner
nuclear layer. H1 CHCs contact all spectral cone types: cone pedicles and a single axon descending into the inner
nuclear layer. H1 CHCs contact all spectral cone types;
the density of contacts decreases with increasing distance cone pedicles and a single axon descending into the inner
nuclear layer. H1 CHCs contact all spectral cone types;
the density of contacts decreases with increasing distance
from the perikaryon, which is localized exactly b nuclear layer. H1 CHCs contact all spectral cone types;
the density of contacts decreases with increasing distance
from the perikaryon, which is localized exactly beneath a the density of contacts decreases with increasing distance
from the perikaryon, which is localized exactly beneath a
central SC (Braun *et al.* 1997). H2 CHCs situated vitread
to the former cells have larger dendritic fiel from the perikaryon, which is localized exactly beneath a central SC (Braun *et al.* 1997). H2 CHCs situated vitread to the former cells have larger dendritic fields. Similar to the H2 cells in cyprinids (Stell *et al.* 1 central SC (Braun *et al.* 1997). H2 CHCs situated vitread
to the former cells have larger dendritic fields. Similar to
the H2 cells in cyprinids (Stell *et al.* 1994), the H2 CHCs
of *A hulcher* show a marked preference f to the former cells have larger dendritic fields. Similar to
the H2 cells in cyprinids (Stell *et al.* 1994), the H2 CHCs
of *A. pulcher* show a marked preference for M and S cones.
By using the position within the mosaic the H2 cells in cyprinids (Stell *et al.* 1994), the H2 CHCs of *A. pulcher* show a marked preference for M and S cones.
By using the position within the mosaic as a clue for iden-
tifying the cone types, we found an aver of *A. pulcher* show a marked preference for M and S cones.
By using the position within the mosaic as a clue for identifying the cone types, we found an average of 7.05 SCs, 9.72 smaller DC partners and 1.42 larger DC partners tifying the cone types, we found an average of 7.05 SCs, 9.72 smaller DC partners and 1.42 larger DC partners invaginated by an H2 CHC $(n = 10; \text{ Braun } et \text{ al. } 1997)$. These cells may therefore be expected to vield binhasic 9.72 smaller DC partners and 1.42 larger DC partners
invaginated by an H2 CHC ($n = 10$; Braun *et al.* 1997).
These cells may therefore be expected to yield biphasic,
chromaticity, responses, whereas, H1 CHCs, would invaginated by an H2 CHC $(n = 10; \text{ Braun } et al. 1997)$.
These cells may therefore be expected to yield biphasic,
chromaticity responses, whereas H1 CHCs would These cells may therefore be expected to yield biphasic, chromaticity responses, whereas H1 CHCs would generate monophasic luminosity signals. romaticity responses, whereas H1 CHCs would
nerate_monophasic_luminosity_signals.
Rearing fish in different light regimes affected the
mber of contacts of CHCs with the S SCs. Blue light

generate monophasic luminosity signals.

Rearing fish in different light regimes affected the

number of contacts of CHCs with the S SCs. Blue light

increased the number of S cones contacted by H1 cells number of contacts of CHCs with the S SCs. Blue light
increased the number of S cones contacted by H1 cells

BIOLOGICAL
SCIENCES

THE ROYAL

PHILOSOPHICAL
TRANSACTIONS

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(from 1.52 to 1.92), whereas in the bright-white light
group, the number of S cones contacted by H2 cells was
significantly reduced (from 705 to 2.81 $h < 0.01$ (from 1.52 to 1.92), whereas in the bright-white light
group, the number of S cones contacted by H2 cells was
significantly reduced (from 7.05 to 2.81, $p < 0.01$,
ANOVA: Braun 1997: Braun *et al* 1997) Therefore the significantly reduced (from 7.05 to 2.81, $p < 0.01$, ANOVA; Braun 1997; Braun *et al.* 1997). Therefore, the significantly reduced (from 7.05 to 2.81, $p < 0.01$, ANOVA; Braun 1997; Braun *et al.* 1997). Therefore, the connectivity of CHCs is determined by both the intensity and the spectral composition of the rearing lights Inte ANOVA; Braun 1997; Braun *et al.* 1997). Therefore, the connectivity of CHCs is determined by both the intensity and the spectral composition of the rearing lights. Inter-
estingly the luminosity-type HI cells are more sen connectivity of CHCs is determined by both the intensity
and the spectral composition of the rearing lights. Inter-
estingly, the luminosity-type H1 cells are more sensitive to
the spectral component, whereas the chromatic and the spectral composition of the rearing lights. Inter-
estingly, the luminosity-type HI cells are more sensitive to
the spectral component, whereas the chromaticity-type estingly, the luminosity-type H1 cells are more sensitive to
the spectral component, whereas the chromaticity-type
H2 cells respond to intensity cues. Our finding about the
involvement of the S cones in this process does h the spectral component, whereas the chromaticity-type H2 cells respond to intensity cues. Our finding about the involvement of the S cones in this process does, however, not rule out changes in the contacts between CHCs an H2 cells respond to intensity cues. Our finding about the involvement of the S cones in this process does, however, not rule out changes in the contacts between CHCs and the L/M DCs. These could affect the size of the syna involvement of the S cones in this process does, however, not rule out changes in the contacts between CHCs and the L/M DCs. These could affect the size of the synaptic not rule out changes in the contacts between CHCs and
the L/M DCs. These could affect the size of the synaptic
contacts, and would be accessible only at the electron
microsconic level the L/M DCs. The
contacts, and woul
microscopic level.

(ii) *Spinules*

BIOLOGICAL
SCIENCES

THE ROYAL

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Spinules are ¢nger-like extensions from the dendrites of (ii) $Spinules$
Spinules are finger-like extensions from the dendrites of
CHCs that invaginate the cone cytoplasm opposite the
synantic ribbons. Their presence during the day and Spinules are finger-like extensions from the dendrites of CHCs that invaginate the cone cytoplasm opposite the synaptic ribbons. Their presence during the day and absence during the night has been correlated with the CHCs that invaginate the cone cytoplasm opposite the
synaptic ribbons. Their presence during the day and
absence during the night has been correlated with the
adaptation-dependent dynamic of the biphasic response synaptic ribbons. Their presence during the day and
absence during the night has been correlated with the
adaptation-dependent dynamic of the biphasic response
of the H2 CHCs, and therefore implicated with chromatic absence during the night has been correlated with the adaptation-dependent dynamic of the biphasic response
of the H2 CHCs, and therefore implicated with chromatic
feedback processes within the M cone pedicles (Weiler &
Wagner 1984) Altering the balance between the spectral of the H2 CHCs, and therefore implicated with chromatic
feedback processes within the M cone pedicles (Weiler &
Wagner 1984). Altering the balance between the spectral
cone, channels, was, therefore, expected, to, affect, feedback processes within the M cone pedicles (Weiler & Wagner 1984). Altering the balance between the spectral
cone channels was therefore expected to affect the
number and/or dynamics of spinules Wagner 1984). Altering the balance between the spectral cone channels was therefore expected to affect the number and/or dynamics of spinules.

In the light-adapted state, the green-light group was no number and/or dynamics of spinules.
In the light-adapted state, the green-light group was no
different from the baseline values of the white-light
group: by contrast, spinules of the red-light group were In the light-adapted state, the green-light group was no
different from the baseline values of the white-light
group; by contrast, spinules of the red-light group were
more numerous and those in the blue-light group signif different from the baseline values of the white-light
group; by contrast, spinules of the red-light group were
more numerous and those in the blue-light group signifi-
cantly less numerous (Kröger & Wagner 1996) The situagroup; by contrast, spinules of the red-light group were
more numerous and those in the blue-light group signifi-
cantly less numerous (Kröger & Wagner 1996). The situa-
tion in SCs was similar to that, and statistically m more numerous and those in the blue-light group signifisignificant than, in DCs. Dark-adaptive reduction of tion in SCs was similar to that, and statistically more
significant than, in DCs. Dark-adaptive reduction of
spinule numbers was equal to controls in the red and blue
rearing groups, whereas, in the blue-light group, there rearing groups, in DCs. Dark-adaptive reduction of
spinule numbers was equal to controls in the red and blue
rearing groups, whereas, in the blue-light group, there
were as many spinules as during daytime indicating a spinule numbers was equal to controls in the red and blue
rearing groups, whereas, in the blue-light group, there
were as many spinules as during daytime, indicating a
complete absence of spinule dynamics. Spectral depriva rearing groups, whereas, in the blue-light group, there
were as many spinules as during daytime, indicating a
complete absence of spinule dynamics. Spectral deprivation in the medium- and long-wavelength domains thus complete absence of spinule dynamics. Spectral deprivation in the medium- and long-wavelength domains thus
has a severe impact on the formation and degradation of
spinules indicating changes in the control mechanisms. It tion in the medium- and long-wavelength domains thus
has a severe impact on the formation and degradation of
spinules, indicating changes in the control mechanisms. It
remains to be seen in electrophysiological recordings has a severe impact on the formation and degradation of
spinules, indicating changes in the control mechanisms. It
remains to be seen in electrophysiological recordings
whether this is accompanied by imbalances in the chro spinules, indicating changes in the control mechanisms. It remains to be seen in electrophysiological recordings
whether this is accompanied by imbalances in the chro-
matic feedback activity as reflected by the binhasic remains to be seen in electrophysiological recordings
whether this is accompanied by imbalances in the chro-
matic feedback activity as reflected by the biphasic
response pattern of the H2 HCHs. As long as these data whether this is accompanied by imbalances in the chromatic feedback activity as reflected by the biphasic
response pattern of the H2 HCHs. As long as these data
are not available it is difficult to interpret the functional matic feedback activity as reflected by the biphasic
response pattern of the H2 HCHs. As long as these data
are not available, it is difficult to interpret the functional significance of the changes in connectivity and synaptology between cones and CHCs.

4. CONCLUSIONS

Our observations demonstrate that the spectral composition, as well as the intensity of environmental lighting, Our observations demonstrate that the spectral composition, as well as the intensity of environmental lighting, strongly influences the morphology of cones and CHCs.
Such an approach mimics to a certain degree natural sition, as well as the intensity of environmental lighting,
strongly influences the morphology of cones and CHCs.
Such an approach mimics to a certain degree natural
conditions where some fish species may grow up and live strongly influences the morphology of cones and CHCs.
Such an approach mimics to a certain degree natural
conditions, where some fish species may grow up and live
in long-wave-dominated water bodies ('black waters') Such an approach mimics to a certain degree natural conditions, where some fish species may grow up and live
in long-wave-dominated water bodies ('black waters'), conditions, where some fish species may grow up and live
in long-wave-dominated water bodies ('black waters'),
and others in the long-wave-deprived mesopelagic habi-
tats of the oceans. Among the experimental conditions in long-wave-dominated water bodies ('black waters'),
and others in the long-wave-deprived mesopelagic habi-
tats of the oceans. Among the experimental conditions
blue light had the most profound effects. This may be due and others in the long-wave-deprived mesopelagic habitats of the oceans. Among the experimental conditions
blue light had the most profound effects. This may be due
to the fact that in the stimulation paradigm, the S tats of the oceans. Among the experimental conditions
blue light had the most profound effects. This may be due
to the fact that, in the stimulation paradigm, the S

pathway was most clearly separated from the L and M
channels but could also indicate a special role of this pathway was most clearly separated from the L and M
channels, but could also indicate a special role of this
particular pathway. The reactions of cone photoreceptors pathway was most clearly separated from the L and M
channels, but could also indicate a special role of this
particular pathway. The reactions of cone photoreceptors
are easily interpreted in terms of compensatory mechanchannels, but could also indicate a special role of this particular pathway. The reactions of come photoreceptors are easily interpreted in terms of compensatory mechanparticular pathway. The reactions of cone photoreceptors
are easily interpreted in terms of compensatory mechan-
isms. In the case of cone–HC connectivity and synap-
tology however ultrastructural studies of the synaptic are easily interpreted in terms of compensatory mechanisms. In the case of cone–HC connectivity and synaptology, however, ultrastructural studies of the synaptic complexes and electrophysiological recordings of lightisms. In the case of cone–HC connectivity and synaptology, however, ultrastructural studies of the synaptic complexes and electrophysiological recordings of light-evoked responses are necessary for a functional undertology, however, ultrastructural studies of the synaptic complexes and electrophysiological recordings of light-
evoked responses are necessary for a functional understanding of the induced changes.

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and K. Tiedemann are gratefully acknowledged.

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298, 1–9.