

mechanisms for coding e −**vector Ultraviolet polarization vision in fishes: possible**

Craig W. Hawryshyn

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Ultraviolet polarization vision in fishes: **possible mechanisms for coding e-vector**

Craig W. Hawryshyn

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Polarization vision in vertebrates has been marked with significant controversy over recent decades. In the last decade, however, models from two laboratories have indicated that the spatial arrangement of Polarization vision in vertebrates has been marked with significant controversy over recent decades. In
the last decade, however, models from two laboratories have indicated that the spatial arrangement of
photoreceptors p the last decade, however, models from two laboratories have indicated that the spatial arrangement of photoreceptors provides the basis for polarization sensitivity. Work in my laboratory, in collaboration with I. Novales photoreceptors provides the basis for polarization sensitivity. Work in my laboratory, in collaboration with
I. Novales Flamarique and F. I. Harosi, has shown that polarization sensitivity depends on a well-defined
square I. Novales Flamarique and F. I. Harosi, has shown that polarization sensitivity depends on a well-defined
square cone mosaic pattern and that the biophysical properties of the square cone mosaic probably
account for polari square cone mosaic pattern and that the biophysical properties of the square cone mosaic probably
account for polarization vision in the ultraviolet spectrum. The biophysical mechanism appears to be
based on the selective account for polarization vision in the ultraviolet spectrum. The biophysical mechanism appears to be based on the selective reflection of axial-polarized light by the partitioning membrane, formed along the contact zone be this short review, I discuss the historical development of this research problem.

Keywords: polarization vision; ultraviolet sensitivity; cone mosaic; ontogeny; neural coding; e-vector

1. INTRODUCTION

Animals often perceive the world in a manner quite dictive the world in a manner quite
different from the way humans see it. That animals may
see things that we may not presents a paradox with Animals often perceive the world in a manner quite
different from the way humans see it. That animals may
see things that we may not presents a paradox with
respect to how scientists so about investigating the different from the way humans see it. That animals may
see things that we may not presents a paradox with
respect to how scientists go about investigating the
sensory world of any animal These constraints were very see things that we may not presents a paradox with
respect to how scientists go about investigating the
sensory world of any animal. These constraints were very
much in evidence in the initial efforts concerning the respect to how scientists go about investigating the
sensory world of any animal. These constraints were very
much in evidence in the initial efforts concerning the
research on ultraviolet (IIV) photosensitivity in fishes research on ultraviolet (These constraints were very
much in evidence in the initial efforts concerning the
research on ultraviolet (UV) photosensitivity in fishes. It
is now common to see reports of UV sensitivity in a much in evidence in the initial efforts concerning the
research on ultraviolet (UV) photosensitivity in fishes. It
is now common to see reports of UV sensitivity in a
broad range of species research on ultraviolet (
is now common to see
broad range of species.
Our current research now common to see reports of UV sensitivity in a
coad range of species.
Our current research effort on UV vision has shifted
our cataloguing species of aquatic organisms exhibiting

broad range of species.
Our current research effort on UV vision has shifted
from cataloguing species of aquatic organisms exhibiting
IIV vision to examining the functional significance of IIV Our current research effort on UV vision has shifted E
from cataloguing species of aquatic organisms exhibiting cl
UV vision to examining the functional significance of UV
vision in the aquatic ecosystem While there are nu from cataloguing species of aquatic organisms exhibiting
UV vision to examining the functional significance of UV
vision in the aquatic ecosystem. While there are numerous
possibilities, the focus of my research is on the UV vision to examining the functional significance of UV
vision in the aquatic ecosystem. While there are numerous
possibilities, the focus of my research is on the role of UV
vision in the detection of polarized light. Ma vision in the aquatic ecosystem. While there are numerous
possibilities, the focus of my research is on the role of UV
vision in the detection of polarized light. Many inverte-
brates have UV polarization vision and this m possibilities, the focus of my research is on the role of UV vision in the detection of polarized light. Many invertebrates have UV polarization vision and this motivated us vision in the detection of polarized light. Many inverte-
brates have UV polarization vision and this motivated us
to test for polarization sensitivity in goldfish possessing
IIV sensitivity (Hawryshyn & McFarland 1987) brates have UV polarization vision and this motive to test for polarization sensitivity in goldfish po
UV sensitivity (Hawryshyn & McFarland 1987). **2. PHOTORECEPTOR MECHANISMS**

**2. PHOTORECEPTOR MECHANISMS
AND NEURONAL PROCESSING RELATED**
TO BOLABIZATION SENSITIVITY PHOTORECEPTOR MECHANISMS
NEURONAL PROCESSING RELATED
TO POLARIZATION SENSITIVITY

TO POLARIZATION SENSITIVITY

Our knowledge of the specific mechanisms mediating

Performances of polarization vision is more thoroughly TO POLARIZATION SENSITIVITY

Our knowledge of the specific mechanisms mediating

the process of polarization vision is more thoroughly

understood in invertebrates and is based on the organiza-Our knowledge of the specific mechanisms mediating
the process of polarization vision is more thoroughly
understood in invertebrates and is based on the organiza-
tion and orientation of visual nigment-bearing membrane the process of polarization vision is more thoroughly
understood in invertebrates and is based on the organiza-
tion and orientation of visual pigment-bearing membrane understood in invertebrates and is based on the organization and orientation of visual pigment-bearing membrane
in photoreceptors (Wehner *et al.* 1975). Visual pigment
molecules within a given rhadomeric microvillus are tion and orientation of visual pigment-bearing membrane
in photoreceptors (Wehner *et al.* 1975). Visual pigment
molecules, within a given rhadomeric microvillus, are
aligned in one axis permitting preferential absorption in photoreceptors (Wehner *et al.* 1975). Visual pigment molecules, within a given rhadomeric microvillus, are aligned in one axis permitting preferential absorption of plane-polarized light molecules, within a given rhadomeric microvillus, are aligned in one axis permitting preferential absorption of plane-polarized light. gned in one axis permitting preferential absorption of
ane-polarized light.
Waterman and his associates (Waterman & Aoki 1974;
aterman & Hashimoto, 1974), first, examined, the

plane-polarized light.
Waterman and his associates (Waterman & Aoki 1974;
Waterman & Hashimoto 1974) first examined the
receptor mechanisms underlying polarization sensitivity Waterman and his associates (Waterman & Aoki 1974;
Waterman & Hashimoto 1974) first examined the
receptor mechanisms underlying polarization sensitivity **Phil. Trans. R. Soc. Lond. B** (2000) **355**, 1187-1190 1187 **1187** C 2000 The Royal Society

in fishes. These studies revealed one class of polarization
sensitivity in all single units recorded from the ontic in fishes. These studies revealed one class of polarization
sensitivity in all single units recorded from the optic
tectum regardless of the test wavelengths of the polarized in fishes. These studies revealed one class of polarization
sensitivity in all single units recorded from the optic
tectum, regardless of the test wavelengths of the polarized
light stimuli Our studies on rainbow trout (P sensitivity in all single units recorded from the optic
tectum, regardless of the test wavelengths of the polarized
light stimuli. Our studies, on rainbow trout (Parkyn & tectum, regardless of the test wavelengths of the polarized
light stimuli. Our studies, on rainbow trout (Parkyn &
Hawryshyn 1993) and goldfish (Hawryshyn & McFarland
1987), have since been extended into the UV part of the light stimuli. Our studies, on rainbow trout (Parkyn & Hawryshyn 1993) and goldfish (Hawryshyn & McFarland 1987), have since been extended into the UV part of the spectrum and have used chromatic adaptation to isolate Hawryshyn 1993) and goldfish (Hawryshyn & McFarland
1987), have since been extended into the UV part of the
spectrum and have used chromatic adaptation to isolate
the spectral sensitivity of individual cone mechanisms 1987), have since been extended into the UV part of the spectrum and have used chromatic adaptation to isolate the spectral sensitivity of individual cone mechanisms. Polarization sensitivity can then be evaluated with a spectrum and have used chromatic adaptation to isolate
the spectral sensitivity of individual cone mechanisms.
Polarization sensitivity can then be evaluated with a
polarized light stimulus, which is coincident with the the spectral sensitivity of individual cone mechanisms.
Polarization sensitivity can then be evaluated with a
polarized light stimulus, which is coincident with the
spectral sensitivity peak of the isolated cone mechanism Polarization sensitivity can then be evaluated with a polarized light stimulus, which is coincident with the spectral sensitivity peak of the isolated cone mechanism. polarized light stimulus, which is coincident with the spectral sensitivity peak of the isolated cone mechanism.
Experiments that use white or spectral stimuli without chromatic adaptation offer questionable conclusions ab spectral sensitivity peak of the isolated cone mechanism.
Experiments that use white or spectral stimuli without
chromatic adaptation offer questionable conclusions about
the mechanisms of polarization sensitivity (Hawrysh Experiments that use white or spectral stimuli without
chromatic adaptation offer questionable conclusions about
the mechanisms of polarization sensitivity (Hawryshyn &
McEarland 1987) chromatic adaptation
the mechanisms of
McFarland 1987).
Our experiments e mechanisms of polarization sensitivity (Hawryshyn &
CFarland 1987).
Our experimental results have identified the presence
two differentially sensitive classes of polarization-

McFarland 1987).
Our experimental results have identified the presence
of two differentially sensitive classes of polarization-
sensitive cone mechanisms in cyprinid and salmonid Our experimental results have identified the presence
of two differentially sensitive classes of polarization-
sensitive cone mechanisms in cyprinid and salmonid
fishes I ike colour vision polarization vision depends on % of two differentially sensitive classes of polarization-
sensitive cone mechanisms in cyprinid and salmonid
fishes. Like colour vision, polarization vision depends on
the possession of at least two differentially sensiti sensitive cone mechanisms in cyprinid and salmonid
fishes. Like colour vision, polarization vision depends on
the possession of at least two differentially sensitive
receptor (cone) mechanisms (Bernard & Webper 1977) fishes. Like colour vision, polarization vision depends on
the possession of at least two differentially sensitive
receptor (cone) mechanisms (Bernard & Wehner 1977).
Most research on invertebrate polarization systems has the possession of at least two differentially sensitive
receptor (cone) mechanisms (Bernard & Wehner 1977).
Most research on invertebrate polarization systems has
shown that differential polarization sensitivity is mediate receptor (cone) mechanisms (Bernard & Wehner 1977).
Most research on invertebrate polarization systems has
shown that differential polarization sensitivity is mediated
by visual receptors possessing the same spectral sensi Most research on invertebrate polarization systems has
shown that differential polarization sensitivity is mediated
by visual receptors possessing the same spectral sensi-
tivity However our initial experiments on goldfish shown that differential polarization sensitivity is mediated
by visual receptors possessing the same spectral sensi-
tivity. However, our initial experiments, on goldfish and by visual receptors possessing the same spectral sensi-
tivity. However, our initial experiments, on goldfish and
rainbow trout, have revealed that differential polarization
sensitivity results from cone receptors that dif tivity. However, our initial experiments, on goldfish and
rainbow trout, have revealed that differential polarization
sensitivity results from cone receptors that differ in spec-
tral sensitivity a scenario that would seem rainbow trout, have revealed that differential polarization
sensitivity results from cone receptors that differ in spec-
tral sensitivity, a scenario that would seem to suggest a
confounding influence of colour Nonetheless sensitivity results from cone receptors that differ in spectral sensitivity, a scenario that would seem to suggest a confounding influence of colour. Nonetheless, both electrotral sensitivity, a scenario that would seem to suggest a
confounding influence of colour. Nonetheless, both electro-
physiological and behavioural experiments have demon-
strated that polarization vision depends on the confounding influence of colour. Nonetheless, both electro-
physiological and behavioural experiments have demon-
strated that polarization vision depends on the
acquisition of UV polarized light stimuli (Coughlin & physiological and behavioural experiments have demonstrated that polarization vision depends on the acquisition of UV polarized light stimuli (Coughlin & Hawryshyn 1995: Hawryshyn et al. 1990). So while in strated that polarization vision depends on the acquisition of UV polarized light stimuli (Coughlin & Hawryshyn 1995; Hawryshyn *et al.* 1990). So, while in acquisition of UV polarized light stimuli (Coughlin & Hawryshyn 1995; Hawryshyn *et al.* 1990). So, while in theory spectral confounds are possible, functional polarization vision appears to operate only in the UV part of Hawryshyn 1995; Hawryshyn *et al.* 1990). So, while in theory spectral confounds are possible, functional polarization vision appears to operate only in the UV part of the spectrum theory spectral
zation vision ap
the spectrum.

Figure 1. Schematic diagram showing the cone mosaics crainbow trout and sunfish and the axial transmission of plane-polarized light (a) R ainbow trout cone mosaic rainbow trout and sunfish and the axial transmission of plane-polarized light. (a) Rainbow trout cone mosaic nission of
mosaic
, horizontal
mosaic e-vector; \mathbf{E}_{v} , vertical e-vector.(b) Sunfish cone mosaic ized light. (*a*) Rainbow trout cone mosaic
7-, S-, M- and L-sensitive cones. \mathbf{E}_{h} , horizont, vertical e-vector.(*b*) Sunfish cone mosaic
sensitive twin cones and M-sensitive single co showing UV-, S-, M- and L-sensitive cones. \mathbf{E}_{h} , horizontal
e-vector; \mathbf{E}_{v} , vertical e-vector.(b) Sunfish cone mosaic
showing L-sensitive twin cones and M-sensitive single cones.
Double-beaded arrows, within t e -vector; E_v , vertical e-vector.(b) Sunfish cone mosaic
showing L-sensitive twin cones and M-sensitive single cones.
Double-headed arrows, within the square mosaic, indicate
the dominant plane of polarization. (Adante Double-headed arrows, within the square mosaic, indicate
the dominant plane of polarization. (Adapted from Novales Double-headed arrows, within the square mosaic, indicate
the dominant plane of polarization. (Adapted from Novales
Flamarique *et al.* (1998), which should be consulted for more
details on this illustration.) the dominant plane of polariz
Flamarique *et al.* (1998), whic
details on this illustration.)

In both salmonids and cyprinids, the UV-sensitive
ne mechanism exhibits maximum polarization In both salmonids and cyprinids, the UV-sensitive
cone mechanism exhibits maximum polarization
sensitivity to the vertically orientated e-vector while the In both salmonids and cyprinids, the UV-sensitive
cone mechanism exhibits maximum polarization
sensitivity to the vertically orientated e-vector while the
mid-wavelength-sensitive (M cones) and long-wavelengthcone mechanism exhibits maximum polarization
sensitivity to the vertically orientated e-vector while the
mid-wavelength-sensitive (M cones) and long-wavelength-
sensitive (L cones) cone mechanisms show maximum sensitivity to the vertically orientated e-vector while the
mid-wavelength-sensitive (M cones) and long-wavelength-
sensitive (L cones) cone mechanisms show maximum to
sensitivity to the horizontally orientated e-vector (H mid-wavelength-sensitive (M cones) and long-wavelength-
sensitive (L cones) cone mechanisms show maximum
sensitivity to the horizontally orientated e-vector (Hawryshyn
& McEarland 1987) Further electrophysiological studies sensitive (L cones) cone mechanisms show maximum
sensitivity to the horizontally orientated e-vector (Hawryshyn
& McFarland 1987). Further electrophysiological studies
on rainbow trout, by Coughlin & Hawryshyn (1995) sensitivity to the horizontally orientated e-vector (Hawryshyn & McFarland 1987). Further electrophysiological studies
on rainbow trout, by Coughlin & Hawryshyn (1995),
have shown that $\frac{1}{2}$ UV/L sensitive colour-oppon & McFarland 1987). Further electrophysiological studies
on rainbow trout, by Coughlin & Hawryshyn (1995),
have shown that UV/L-sensitive colour-opponent have shown that UV/L-sensitive colour-opponent
neurons project primarily to the torus semicircularis in
the central nervous system. There is good evidence that
these neurons are specifically tuned to UV polarized neurons project primarily to the torus semicircularis in
the central nervous system. There is good evidence that
these neurons are specifically tuned to UV polarized
stimuli as the capability of discriminating one plane of the central nervous system. There is good evidence that
these neurons are specifically tuned to UV polarized
stimuli as the capability of discriminating one plane of
polarization from another is restricted to the UV part o these neurons are specifically tuned to UV polarized
stimuli as the capability of discriminating one plane of
polarization from another is restricted to the UV part of stimuli as the capability of discriminating one plane of
polarization from another is restricted to the UV part of
the spectrum (α -band of UV cone mechanism and
8-band of the L cone mechanism) This differential polarpolarization from another is restricted to the UV part of
the spectrum (α-band of UV cone mechanism and
β-band of the L cone mechanism). This differential polar-
ization sensitivity between cone mechanisms appears to the spectrum (α -band of UV cone mechanism and β -band of the L cone mechanism). This differential polarization sensitivity between cone mechanisms appears to *Phil. Trans. R. Soc. Lond.* B (2000) *Phil. Trans. R. Soc. Lond.* B (2000)

provide the potential for e-vector coding and hence polarization discrimination within the UV part of the spectrum.

3. ONTOGENETIC CHANGES IN THE SPATIAL PATTERN OF CHANGES IN THE SPATTERN OF CONE MOSAICS
PATTERN OF CONE MOSAICS
ND POLAPIZATION SENSITIVITY **PATTERN OF CONE MOSAICS
AND POLARIZATION SENSITIVITY**

Rainbow trout exhibit an ontogenetic loss of UV **EXECUTE AND FOLARIZATION SENSITIVITY**

Rainbow trout exhibit an ontogenetic loss of UV

photosensitivity (Hawryshyn *et al.* 1989). Juvenile

rainbow trout weighing less than 30*g* displayed sensi-Rainbow trout exhibit an ontogenetic loss of UV
photosensitivity (Hawryshyn *et al.* 1989). Juvenile
rainbow trout weighing less than 30 g displayed sensi-
tivity to UV light with a neak sensitivity of 360 nm Trout rainbow trout weighing less than 30g displayed sensitivity to UV light with a peak sensitivity of 360 nm. Trout rainbow trout weighing less than 30g displayed sensi-
tivity to UV light with a peak sensitivity of 360 nm. Trout
larger than 30g exhibited a characteristic loss of UV
sensitivity both within individual trout and between f tivity to UV light with a peak sensitivity of 360 nm. Trout
larger than 30 g exhibited a characteristic loss of UV
sensitivity, both within individual trout and between fish
measurements. It was inferred from these results larger than 30g exhibited a characteristic loss of UV
sensitivity, both within individual trout and between fish
measurements. It was inferred from these results that
trout UV cones degenerated soon after transition to the sensitivity, both within individual trout and between fish
measurements. It was inferred from these results that
trout UV cones degenerated soon after transition to the
adult stage (a similar conclusion was made by Bowmake measurements. It was inferred from these results that
trout UV cones degenerated soon after transition to the
adult stage (a similar conclusion was made by Bowmaker
& Kunz (1987) for brown trout) This inference was trout UV cones degenerated soon after transition to the
adult stage (a similar conclusion was made by Bowmaker
& Kunz (1987) for brown trout). This inference was
further supported by the premature loss of UV sensitivity adult stage (a similar conclusion was made by Bowmaker & Kunz (1987) for brown trout). This inference was further supported by the premature loss of UV sensitivity in rainbow trout treated with thyroxine (Browman & & Kunz (1987) for brown trout). This inference was
further supported by the premature loss of UV sensitivity
in rainbow trout treated with thyroxine (Browman &
Hawryshyn 1994) a hormone known to play a key role in further supported by the premature loss of UV sensitivity
in rainbow trout treated with thyroxine (Browman &
Hawryshyn 1994), a hormone known to play a key role in
the development of all vertebrates. Although a square in rainbow trout treated with thyroxine (Browman & Hawryshyn 1994), a hormone known to play a key role in the development of all vertebrates. Although a square mosaic was found in the majority of the retinae examthe development of all vertebrates. Although a square
mosaic was found in the majority of the retinae exam-
ined, accessory corner cones (putative UV cones) were
not present in the cone mosaic of trout treated with thymosaic was found in the majority of the retinae examined, accessory corner cones (putative UV cones) were
not present in the cone mosaic of trout treated with thyr-
oxine (see figure 1a for spatial arrangement of cone ined, accessory corner cones (putative UV cones) were
not present in the cone mosaic of trout treated with thyr-
oxine (see figure la for spatial arrangement of cone
mosaic in invenile rainbow trout) not present in the cone mosaic of trout treated with thyroxine (see figure la for spatial arrangement of cone mosaic in juvenile rainbow trout). ine (see figure la for spatial arrangement of cone

osaic in juvenile rainbow trout).

In a recent study, Beaudet *et al.* (1997) found that sexu-

v mature salmonids possessed a cone mosaic with

mosaic in juvenile rainbow trout).

In a recent study, Beaudet *et al.* (1997) found that sexually mature salmonids possessed a cone mosaic with

accessory corner cones suggesting that there may be In a recent study, Beaudet *et al.* (1997) found that sexually mature salmonids possessed a cone mosaic with accessory corner cones, suggesting that there may be some potential for IV cone regeneration. The mechanism ally mature salmonids possessed a cone mosaic with
accessory corner cones, suggesting that there may be
some potential for UV cone regeneration. The mechanism
for the regeneration of HV cones is unknown HV-sensitive accessory corner cones, suggesting that there may be
some potential for UV cone regeneration. The mechanism
for the regeneration of UV cones is unknown. UV-sensitive
accessory corner cones may regenerate from pluripotent some potential for UV cone regeneration. The mechanism
for the regeneration of UV cones is unknown. UV-sensitive
accessory corner cones may regenerate from pluripotent
cells within the retina or it is possible that rod pre for the regeneration of UV cones is unknown. UV-sensitive
accessory corner cones may regenerate from pluripotent
cells within the retina or it is possible that rod precursor
cells differentiate into accessory corner cones. accessory corner cones may regenerate from pluripotent
cells within the retina or it is possible that rod precursor
cells differentiate into accessory corner cones. Thus, in the
life-history stage leading up to and during cells within the retina or it is possible that rod precursor
cells differentiate into accessory corner cones. Thus, in the
life-history stage leading up to and during sexual
maturity salmonids may conceivably possess the cells differentiate into accessory corner cones. Thus, in the life-history stage leading up to and during sexual maturity, salmonids may conceivably possess the life-history stage leading up to and during sexual
maturity, salmonids may conceivably possess the
capability of UV polarization vision. My laboratory is
currently conducting research to address some of the maturity, salmonids may conceivably possess the
capability of UV polarization vision. My laboratory is
currently conducting research to address some of the
unresolved issues concerning the optogenetic changes in capability of UV polarization vision. My laboratory is
currently conducting research to address some of the
unresolved issues concerning the ontogenetic changes in
IIV polarization in salmonids (Browman & Hawrysbyn currently conducting research to address some of the
unresolved issues concerning the ontogenetic changes in
UV polarization in salmonids (Browman & Hawryshyn
1994: Beaudet et al. 1997) unresolved issues concernii
UV polarization in salmoi
1994; Beaudet *et al.* 1997).

**4. BIOPHYSICAL MODEL OF CONE PHOTORECEPTOR CAL MODEL OF CONE PHOTORE
POLARIZATION SENSITIVITY**

on rainbow trout, by Coughlin & Hawryshyn (1995), orientation and the M- and L-sensitive cones prefer the have shown that UV/L-sensitive colour-opponent horizontal e-vector, single unit recordings have shown neurons projec **POLARIZATION SENSITIVITY**

Our observations that salmonids use different cone

rechanisms to accomplish the task of polarization vision **EXECUTE SENSITIVITY**
Our observations that salmonids use different cone
mechanisms to accomplish the task of polarization vision
has presented an interesting challenge for determining Our observations that salmonids use different cone
mechanisms to accomplish the task of polarization vision
has presented an interesting challenge for determining
the biophysical characteristics of photorecentors necessary mechanisms to accomplish the task of polarization vision
has presented an interesting challenge for determining
the biophysical characteristics of photoreceptors necessary has presented an interesting challenge for determining
the biophysical characteristics of photoreceptors necessary
to generate cone-selective sensitivity to the e-vector.
While Hawrysbyn & McFarland (1987) showed that $\rm I$ the biophysical characteristics of photoreceptors necessary
to generate cone-selective sensitivity to the e-vector.
While Hawryshyn & McFarland (1987) showed that UV-
sensitive cones have a preference for the vertical e-ve to generate cone-selective sensitivity to the e-vector.
While Hawryshyn & McFarland (1987) showed that UV-
sensitive cones have a preference for the vertical e-vector
orientation and the M- and L-sensitive cones prefer the While Hawryshyn & McFarland (1987) showed that UV-
sensitive cones have a preference for the vertical e-vector
orientation and the M- and L-sensitive cones prefer the
horizontal e-vector, single unit recordings have shown sensitive cones have a preference for the vertical e-vector
orientation and the M- and L-sensitive cones prefer the
horizontal e-vector, single unit recordings have shown
that e-vector coding occurs only in the UV part of that e-vector coding occurs only in the UV part of the horizontal e-vector, single unit recordings have shown
that e-vector coding occurs only in the UV part of the
spectrum and only when UV-sensitive cones are
expressed in the spectral sensitivity (Coughlin & Hawrythat e-vector coding occurs only in the UV part of the
spectrum and only when UV-sensitive cones are
expressed in the spectral sensitivity (Coughlin & Hawry-
shyn 1995). Therefore, despite, the observation that spectrum and only when UV-sensitive cones are
expressed in the spectral sensitivity (Coughlin & Hawry-
shyn 1995). Therefore, despite the observation that
different cone types have different polarization sensitivity expressed in the spectral sensitivity (Coughlin & Hawryshyn 1995). Therefore, despite the observation that different cone types have different polarization sensitivity, shyn 1995). Therefore, despite the observation that
different cone types have different polarization sensitivity,
neuronal coding of the e-vector appears to occur as a
result of differential polarization responses in IIV c different cone types have different polarization sensitivity,
neuronal coding of the e-vector appears to occur as a
result of differential polarization responses in UV cones
within the cone mosaic. So how can spectrally di neuronal coding of the e-vector appears to occur as a
result of differential polarization responses in UV cones
within the cone mosaic. So how can spectrally different

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cone types participate in polarization vision, yet e-vector cone types participate in polarization vision, yet e-vector coding occur only within the UV part of the spectrum?
The explanation for this paradox appears to be in the ne types participate in polarization vision, yet e-vector
ding occur only within the UV part of the spectrum?
The explanation for this paradox appears to be in the
atial pattern of cone, photoreceptors within the cone

coding occur only within the UV part of the spectrum?
The explanation for this paradox appears to be in the
spatial pattern of cone photoreceptors within the cone The explanation for this paradox appears to be in the spatial pattern of cone photoreceptors within the cones.
mosaic and the ultrastructural properties of double cones.
The polarization sensitivity observed in salmonids a spatial pattern of cone photoreceptors within the cone
mosaic and the ultrastructural properties of double cones.
The polarization sensitivity observed in salmonids and
cyprinids cannot be explained by other models of pola mosaic and the ultrastructural properties of double cones.
The polarization sensitivity observed in salmonids and
cyprinids cannot be explained by other models of polariza-
tion sensitivity such as the ellintical-waveguide The polarization sensitivity observed in salmonids and
cyprinids cannot be explained by other models of polariza-
tion sensitivity such as the elliptical-waveguide hypothesis
since studies have shown there is little eviden cyprinids cannot be explained by other models of polariza-
tion sensitivity such as the elliptical-waveguide hypothesis
since studies have shown there is little evidence for such
biophysical mechanisms (Novales Flamarique tion sensitivity such as the elliptical-waveguide hypothesis
since studies have shown there is little evidence for such
biophysical mechanisms (Novales Flamarique *et al.* 1995).
Rather a recent study by Novales Flamarique since studies have shown there is little evidence for such biophysical mechanisms (Novales Flamarique *et al.* (1995). Rather, a recent study by Novales Flamarique *et al.* (1998) has shown that double cones possess a par biophysical mechanisms (Novales Flamarique *et al.* 1995).
Rather, a recent study by Novales Flamarique *et al.* (1998)
has shown that double cones possess a partitioning
membrane that separates the two elements of the dou Rather, a recent study by Novales Flamarique *et al.* (1998) has shown that double cones possess a partitioning membrane that separates the two elements of the double cone Furthermore the partitioning membrane tilts at the has shown that double cones possess a partitioning
membrane that separates the two elements of the double
cone. Furthermore, the partitioning membrane tilts at the
distal end of the inner segments. The degree of tilt is membrane that separates the two elements of the double
cone. Furthermore, the partitioning membrane tilts at the
distal end of the inner segments. The degree of tilt is
 $ca \quad 10^{-95^{\circ}}$ and is orientated towards neighbouri cone. Furthermore, the partitioning membrane tilts at the they appear to lack the biophysical basis for it. There are distal end of the inner segments. The degree of tilt is species such as the common white sucker that pos distal end of the inner segments. The degree of tilt is *ca*. $10-25^{\circ}$ and is orientated towards neighbouring UV cones. The cone of rays incident on this tilted surface is estimated to be about 20° and thus we hypothes cones. The cone of rays incident on this tilted surface is estimated to be about 20° and thus we hypothesize that the receptor organization shows a random mosaic of cone
partitioning membrane reflects anisotropically polarized types and hence there is no geometric plan for t estimated to be about 20° and thus we hypothesize that the
partitioning membrane reflects anisotropically polarized
light onto neighbouring UV cones (i.e. transversely, at an
angle of incidence facilitating dichroic absorp partitioning membrane reflects anisotropically polarized
light onto neighbouring UV cones (i.e. transversely, at an
angle of incidence facilitating dichroic absorption of polar-
ized light). The tilted segment of the doubl light onto neighbouring UV cones (i.e. transversely, at an angle of incidence facilitating dichroic absorption of polarized light). The tilted segment of the double cone partitioning membrane is orientated so that axial re angle of incidence facilitating dichroic absorption of polarized light). The tilted segment of the double cone partitioning membrane is orientated so that axial reflection of polarized light is directed onto adjacent $\frac{1$ ized light). The tilted segment of the double cone partitioning membrane is orientated so that axial reflection of polarized light is directed onto adjacent UV cones (figure $1a$ left panel). Thus as the e-vector orientati tioning membrane is orientated so that axial reflection of
polarized light is directed onto adjacent UV cones
(figure la, left panel). Thus, as the e-vector orientation of
incident polarized light is rotated anisotropic re polarized light is directed onto adjacent UV cones tioning membrane of the double cones.
(figure la, left panel). Thus, as the e-vector orientation of incident polarized light is rotated, anisotropic reflection (figure la, left panel). Thus, as the e-vector orientation of
incident polarized light is rotated, anisotropic reflection
from the double cone partitioning membrane would result
and the LIV cones would be transversely illu incident polarized light is rotated, anisotropic reflection
from the double cone partitioning membrane would result
and the UV cones would be transversely illuminated with
a plane of polarization aligned parallel to the ax from the double cone partitioning membrane would result
and the UV cones would be transversely illuminated with
a plane of polarization aligned parallel to the axis of the
disk membranes. The tight spacing of cones in the and the UV cones would be transversely illuminated with
a plane of polarization aligned parallel to the axis of the
disk membranes. The tight spacing of cones in the trout a plane of polarization aligned parallel to the axis of the
disk membranes. The tight spacing of cones in the trout
retina would further facilitate this process. The right panel
of figure la shows a tangential view of the disk membranes. The tight spacing of cones in the trout
retina would further facilitate this process. The right panel
of figure la shows a tangential view of the cone mosaic and
in this perspective it should be clear that retina would further facilitate this process. The right panel
of figure la shows a tangential view of the cone mosaic and
in this perspective it should be clear that axial reflection
from tilted partitioning membrane surfa of figure la shows a tangential view of the cone mosaic and
in this perspective it should be clear that axial reflection
from tilted partitioning membrane surfaces is directed in
two directions since double cones are arran in this perspective it should be clear that axial reflection
from tilted partitioning membrane surfaces is directed in
two directions since double cones are arranged quadrilat-
erally in the square cone mosaic. The two dir from tilted partitioning membrane surfaces is directed in
two directions since double cones are arranged quadrilat-
erally in the square cone mosaic. The two directions of
reflection, are, arranged, orthogonally, to one, a two directions since double cones are arranged quadrilaterally in the square cone mosaic. The two directions of reflection are arranged orthogonally to one another. Hence, reflection in orthogonal directions would set up reflection are arranged orthogonally to one another.
Hence, reflection in orthogonal directions would set up
conditions for differential tuning of e-vector required for a
two-detector polarization system. That is within a Hence, reflection in orthogonal directions would set up
conditions for differential tuning of e-vector required for a
two-detector polarization system. That is, within a square
cone mosaic unit: (i) vertically orientated p two-detector polarization system. That is, within a square cone mosaic unit: (i) vertically orientated polarized light two-detector polarization system. That is, within a square
cone mosaic unit: (i) vertically orientated polarized light
would transversely strike the outer segments of two corner
IIV cones, obliquely positioned in the corne cone mosaic unit: (i) vertically orientated polarized light
would transversely strike the outer segments of two corner
UV cones, obliquely positioned in the corners of the cone
mosaic: and (ii) horizontally orientated pola would transversely strike the outer segments of two corner
UV cones, obliquely positioned in the corners of the cone
mosaic; and (ii) horizontally orientated polarized light
would strike the outer segments of the two other UV cones, obliquely positioned in the corners of the cone mosaic; and (ii) horizontally orientated polarized light would strike the outer segments of the two other corner mosaic; and (ii) horizontally orientated polarized light
would strike the outer segments of the two other corner
UV cones, obliquely positioned but in opposite corners of
the cone mosaic would strike the cone
UV cones, oblique
the cone mosaic.
Thus double con V cones, obliquely positioned but in opposite corners of
e cone mosaic.
Thus double cones could play an important role in the
unslation of polarization orientation information into

the cone mosaic.
Thus double cones could play an important role in the
translation of polarization orientation information into Thus double cones could play an important role in the
translation of polarization orientation information into
intensity modulation that UV cones monitor. While the
IIV cones receive the transverse reflection, the outer translation of polarization orientation information into
intensity modulation that UV cones monitor. While the
UV cones receive the transverse reflection, the outer
segments of the double cones receive the residual polariintensity modulation that UV cones monitor. While the UV cones receive the transverse reflection, the outer segments of the double cones receive the residual polari-
zation distal to the partition membrane reflection. Note UV cones receive the transverse reflection, the outer
segments of the double cones receive the residual polarization distal to the partition membrane reflection. Note
also that blue-sensitive cones, which are the central c segments of the double cones receive the residual polarization distal to the partition membrane reflection. Note also that blue-sensitive cones, which are the central cones
in the square mosaic unit, do not receive transve zation distal to the partition membrane reflection. Note
also that blue-sensitive cones, which are the central cones
in the square mosaic unit, do not receive transverse reflec-
tions from the double cone partitioning memb also that blue-sensitive cones, which are the central cones
in the square mosaic unit, do not receive transverse reflec-
tions from the double cone partitioning membranes and in the square mosaic unit, do not receive transverse reflections from the double cone partitioning membranes and hence do not exhibit polarization sensitivity. This pattern of intensity variation over the cone mosaic permi tions from the double cone partitioning membranes and
hence do not exhibit polarization sensitivity. This pattern
of intensity variation over the cone mosaic permits the
detection of polarization by comparing signals among hence do not exhibit polarization sensitivity. This pattern
of intensity variation over the cone mosaic permits the
detection of polarization by comparing signals among
different cones within the cone mosaic. Signal integr of intensity variation over the cone mosaic permits the detection of polarization by comparing signals among different cones within the cone mosaic. Signal integration, detection of polarization by comparing signals among
different cones within the cone mosaic. Signal integration,
by interneurons, within and across mosaic units would
operate to amplify polarization sensitivity and conceidifferent cones within the cone mosaic. Signal integration,
by interneurons, within and across mosaic units would
operate to amplify polarization sensitivity and concei-
vably provide a code for e-vector orientation by interneurons, within and across mosaic u
operate to amplify polarization sensitivity a
vably provide a code for e-vector orientation. *Phil. Trans. R. Soc. Lond.* B (2000)

Green sunfish, on the other hand, have been reported
to possess polarization sensitivity (Cameron & Pugh
1991): however, these data have not been replicated Green sunfish, on the other hand, have been reported
to possess polarization sensitivity (Cameron & Pugh
1991); however, these data have not been replicated
despite the various attempts to do so (Novales Flamarioue 1991); however, these data have not been replicated despite the various attempts to do so (Novales Flamarique 1991); however, these data have not been replicated
despite the various attempts to do so (Novales Flamarique
& Hawryshyn 1997). Figure 1*b* illustrates that the parti-
tioning membrane between members of twin cones in despite the various attempts to do so (Novales Flamarique
& Hawryshyn 1997). Figure 1b illustrates that the parti-
tioning membrane between members of twin cones, in
sunfish do not exhibit tilt and hence cannot generate th & Hawryshyn 1997). Figure 1b illustrates that the partitioning membrane between members of twin cones, in sunfish, do not exhibit tilt and hence cannot generate the transverse reflection onto neighbouring cones and thus tioning membrane between members of twin cones, in sunfish, do not exhibit tilt and hence cannot generate the transverse reflection onto neighbouring cones and thus sunfish, do not exhibit tilt and hence cannot generate the
transverse reflection onto neighbouring cones and thus
there is no reflection of polarized light. Furthermore,
attemnts to identify birefringent inclusions in the transverse reflection onto neighbouring cones and thus
there is no reflection of polarized light. Furthermore,
attempts to identify birefringent inclusions in the inner
segment of these cones have been unsuccessful (Novale there is no reflection of polarized light. Furthermore,
attempts to identify birefringent inclusions in the inner
segment of these cones have been unsuccessful (Novales
Flamarique et al. 1995) Therefore it is not surprisi attempts to identify birefringent inclusions in the inner
segment of these cones have been unsuccessful (Novales
Flamarique *et al.* 1995). Therefore it is not surprising that
sunfish do not exhibit polarization sensitivit segment of these cones have been unsuccessful (Novales
Flamarique *et al.* 1995). Therefore it is not surprising that
sunfish do not exhibit polarization sensitivity because
they appear to lack the biophysical basis for it Flamarique *et al.* 1995). Therefore it is not surprising that sunfish do not exhibit polarization sensitivity because they appear to lack the biophysical basis for it. There are species such as the common white sucker th they appear to lack the biophysical basis for it. There are they appear to lack the biophysical basis for it. There are
species such as the common white sucker that possess UV
photosensitivity yet lack polarization sensitivity. Histo-
logical examination of common white sucker, pho species such as the common white sucker that possess UV
photosensitivity yet lack polarization sensitivity. Histo-
logical examination of common white sucker photo-
receptor organization shows a random mosaic of cone photosensitivity yet lack polarization sensitivity. Histo-
logical examination of common white sucker photo-
receptor organization shows a random mosaic of cone-
types and hence there is no geometric plan for the conelogical examination of common white sucker photo-
receptor organization shows a random mosaic of cone-
types and hence there is no geometric plan for the cone-
specific reflection patterns observed in cynrinids and receptor organization shows a random mosaic of cone
types and hence there is no geometric plan for the cone-
specific reflection patterns observed in cyprinids and
salmonids (Novales Flamarique & Hawryshyn 1998) types and hence there is no geometric plan for the cone-
specific reflection patterns observed in cyprinids and
salmonids (Novales Flamarique & Hawryshyn 1998).
Thus the critical factors determining polarization are the specific reflection patterns observed in cyprinids and salmonids (Novales Flamarique & Hawryshyn 1998). Thus the critical factors determining polarization are the salmonids (Novales Flamarique & Hawryshyn 1998).
Thus the critical factors determining polarization are the
geometric pattern of the cone mosaic and the tilted parti-
tioning membrane of the double cones Thus the critical factors determining polynometric pattern of the cone mosaic and
tioning membrane of the double cones.

5. CONCLUSION

5. CONCLUSION
My analysis of polarization vision in salmonid fishes
dicates that a neural network for e-vector coding could **indicates that a neural network for e-vector coding could**
indicates that a neural network for e-vector coding could
occur at the level of the horizontal cells in the retina. Our My analysis of polarization vision in salmonid fishes
indicates that a neural network for e-vector coding could
occur at the level of the horizontal cells in the retina. Our
future efforts should be concentrated on examini indicates that a neural network for e-vector coding could
occur at the level of the horizontal cells in the retina. Our occur at the level of the horizontal cells in the retina. Our
future efforts should be concentrated on examining the
polarization tuning of horizontal cells at multiple levels
within the outer plexiform layer. This will pr future efforts should be concentrated on examining the polarization tuning of horizontal cells at multiple levels
within the outer plexiform layer. This will provide valu-
able insights into the interneuronal interaction s polarization tuning of horizontal cells at multiple levels
within the outer plexiform layer. This will provide valu-
able insights into the interneuronal interaction shaping
the e-vector coding observed in central nervous able insights into the interneuronal interaction shaping neurons.

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