Ultraviolet Vision in Vertebrates

GERALD H. JACOBS

Department of Psychology, University of California, Santa Barbara, California 93106

SYNOPSIS. Recent years have seen an upsurge of interest in the study of ultraviolet vision in vertebrates. The presence of retinal photopigments that allow for ultraviolet vision appear to be relatively common among birds and fishes, and there is evidence that such pigments are to be found in some species from each of the following classes: amphibians, reptiles, and mammals. Following a review of the distribution and nature of ultraviolet vision in vertebrates the issue of the utility of this capacity is discussed.

Solar illumination bathes the surface of the earth with a broad spectral irradiance. For the most part those biological mechanisms that have evolved to yield vision utilize energies in the narrow spectral band between 400 and 700 nm. Adaptations have emerged in some species to allow an expansion of this range. The best known are the abilities of a wide range of invertebrate species to translate ultraviolet (UV) radiation into visual behavior, and the classic example of this is the manner in which bees utilize ultraviolet coloration patterns of flowers as a guide to nectar locations (Menzel and Backhaus, 1991). In recent years it has become apparent that, counter to the traditionally held view, some vertebrates are also able to exploit ultraviolet light as a potentially useful source of visual information. This paper provides a review and analysis of these events.

PHOTOPIGMENT DETECTION OF UV LIGHT

The active process that results in vision is initiated by the absorption of photon energies by photopigment molecules. The absorption spectra of photopigments are broadly tuned to wavelength. Since the sensitivity bandwidths of photopigments vary systematically as a function of the location of peak absorption in a fashion that can be accurately captured by a routine transformation of the spectral absorption values, it is conventional to specify photopigments solely by reference to their peak values. In addition to the main sensitivity peak of photopigments, each shows a secondary region of heightened sensitivity. These secondary regions (called the cis-peak or beta band) are substantially lower in sensitivity than the main peak and broadly centered at a wavelength about two-thirds of the main peak value. Since photopigments are blind to wavelength differences, absorption of energy at any of the wavelengths to which the pigment is sensitive leads to qualitatively indiscriminable signals.

A consequence of this feature of photopigment absorption spectra is illustrated in Figure 1. Shown are the spectra for two photopigments, one absorbing maximally in the visible part of the spectrum (at 510 nm), and a second with an absorption peak in the UV (at 360 nm). Note that by virtue of beta-band absorption in the former pigment, an ultraviolet light will activate both of these pigments (though to differing extents). The point is that sensitivity to UV stimulation could be produced by the presence of either of these pigments (as it could, of course, by both).

In addition to the direct absorption of UV light in the fashion just illustrated, there are at least two other ways in which retinal photopigments might detect the presence of UV light. One is the possibility that the absorption of visible light initiates a bleaching sequence that manufactures photosensitive products whose absorption spectra are centered in the UV. Another is that stimulation by UV light could cause some ocular structure (e.g., the lens) to fluoresce, and the light re-emitted at a visible wavelength could then...
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FIG. 1. Absorption spectra for two photopigments. One of these pigments has peak sensitivity in the visible spectrum (at 510 nm); the other has a sensitivity peak in the UV (360 nm).

stimulate a photopigment sensitive in that part of the spectrum.

These several ways to achieve sensitivity to UV light may be difficult to separate in experiments involving the behavior of intact organisms; to answer, in particular, the question of whether the retina contains a photopigment with maximal sensitivity to UV light. One way to do this is to determine if sensitivity to UV light persists in the presence of an appropriate long-wavelength adapting light. The idea is that the adapting light will greatly desensitize any photopigments having maximum sensitivity in the visible wavelengths, thus rendering explanations based on beta-band sensitivity or fluorescence unlikely. On the other hand, the presence of a steady long-wavelength light might be expected to enhance the sensitivity to a UV test light if UV sensitivity were being produced solely as a result of the production of a photosensitive bleaching product.

MECHANISMS LIMITING THE VISUAL DETECTION OF UV LIGHT

Nucleic acids and proteins begin to absorb light strongly at wavelengths shorter than about 310 nm, thus the UV wavelengths available for the purposes of vision are classified as UVA, i.e., those falling between about 320 and 400 nm (Diffey, 1991). This window can be further narrowed, or indeed obscured completely, by the presence in the eye of one or more screening pigments (Muntz, 1972; Bowmaker, 1991). These pigments act as effective high-pass filters. One of these is the yellow pigment found in the lenses of many species. In cases such as that of the primate eye (Fig. 2, dashed line), the density of this pigment is sufficiently high that it effectively obviates most UV light from reaching the photopigments. An additional yellow pigment unique to the primate is the macular pigment which covers and thus screens the central portion of the retina. In some species of fish the cornea is pigmented and this too can limit the effectiveness of short-wavelength light. More specialized short-wavelength filters are the colored oil droplets characteristic of the retinas of some species of fishes, birds, reptiles and amphibians. These oil droplets are located in the ellipsoid region of the inner segments of cone photoreceptors; unlike lens and corneal pigmentation, these droplets effectively limit passage of short wavelengths to the photopigment of the receptor containing the oil droplet.

Several reasons are offered as to why it may be useful to screen the retina from UV radiation. The yellow filters have been argued to serve a role in minimizing the effects of chromatic aberration inherent in
ocular lenses, and in reducing the amount of scattered light reaching the retina. Both of these effects will be greatest for short-wavelength lights and, thus, the presence of short-wavelength filtering mechanisms can be seen as an adaptation to maximize visual resolution and contrast detection. UV light can also effect deleterious changes in several ocular tissues (van Norren, 1991): UVA has been implicated in the formation of lens cataracts, and there is evidence that senile macular degeneration in humans may be the unwanted legacy of a lifetime's exposure to short-wavelength limits.

**Vertebrates with Ultraviolet Vision**

Evidence that some vertebrate species can perceive UV light dates back to at least the 1920s, but most of the work is recent. The upsurge of interest in this issue is due, at least in part, to the availability of better methods for assessing UV sensitivity. Three approaches have been used: direct measurements of photopigments by microspectrophotometry (MSP), analysis of retinal potentials in ways that allow the detection of the contribution of UV sensitive receptors, and analysis of visual discriminations made in behavioral experiments. Species drawn from five classes of animal have been suggested to have specific UV sensitivity.

**Birds**

In 1980 Goldsmith trained three species of hummingbird (Archilochus alexandri, Lampornis clemenciae and Eugenes fulgens) to make visual discriminations based on the spectral content of a light used to indicate the presence of a baited feeder. He found hummingbirds could distinguish food sources marked by a 370 nm light—a light source, he noted, that could not be discerned by a human observer. The mechanism that allows such a discrimination is a UV sensitive pigment peaking at about 370 nm. Chen et al. (1984) and Chen and Goldsmith (1986) were able to detect this pigment by noting its contribution to retinal gross potentials recorded from each of fifteen species of passerine bird. The fact that the prominence of this signal varied from species-to-species suggests that the cones containing the UV pigment probably vary in relative representation in the different species.

Pigeons (Columba livia) are a popular laboratory animal whose vision has been much studied. As measured in behavioral discrimination experiments, pigeons show a heightened sensitivity in the UV (Kreithen and Eisner, 1978; Emmerton and Remy, 1983). The sensitivity to UV lights was
strikingly different (by as much as 1.5 log units) in these two behavioral studies. Emmerton and Remy (1983) suggest this difference might reflect the fact that the stimulus fields were projected onto different retinal locations in the two studies and that the cones containing UV pigment are much more densely represented in one than in the other. If this is correct, then that segment of the pigeon retina containing high representation of UV cones subserves the upper portion of the stimulus field, a region that might be important for the detection of skylight polarization patterns. Unfortunately, there are both positive (Delius et al., 1976) and negative (Coemans and Vos Hzn, 1989) claims about the pigeon’s ability to discriminate the orientation of polarized light. Linkages between UV sensitive cones and detection of the orientation of polarized light are considered below.

There is often a tendency to assume that the presence of UV pigments automatically implies a color capacity in that part of the spectrum. That need not be so for the presence of receptors containing UV sensitive photopigments might contribute to the detection of light, and thus be reflected in sensitivity measurements, but their outputs could be wired into the nervous system in a manner that would not allow color vision. It is even less forgivable to simply count the number of pigment types in a retina and then assume that this value automatically signifies the dimensionality of the animal’s color vision. Statements about color vision require direct behavioral substantiation. Such substantiation has been obtained in the case of the pigeon. Emmerton and Delius (1980) showed that these birds can make color discriminations in the UV, are in fact quite sensitive to small color differences in the vicinity of 360 nm (Fig. 3).

Although only a very small sample from among all bird species have been examined, the presence of specific UV sensitivity is sufficiently common to suggest that many others will also eventually be found to have the ability to translate UV light into vision. At the same time, it seems that it is not a universal capacity of this class. Some owls certainly (e.g., the tawny owl, Strix aluco—Bowmaker and Martin, 1978), and other nocturnal species (most likely) do not have UV photopigments. The chicken, a diurnal species, is also claimed to lack a UV pigment (Chen et al., 1984). These species could, of course, still achieve some sensitivity to UV light by virtue of the presence of photopigments with maximum absorption in the visible spectrum.

**Fishes**

Measurements of the penetration of UV light into water suggests that fishes living in relatively shallow waters might be able to make effective use of this source of information (Loew and McFarland, 1990). For
instance, about 40% of the available UV light is said to penetrate to a depth of 40 cm in average fresh water (Downing et al., 1986). A reasonably active research effort initiated less than ten years ago makes it clear that some species have capitalized on this opportunity. This was first appreciated from MSP experiments separately conducted on two species of cyprinids—the roach (*Rutilus rutilus*) and the Japanese dace (*Tribolodon hakonensis*) (Avery et al., 1983; Harosi and Hashimoto, 1983). In each case, the retinas of these fish contain UV sensitive cones (with peak at about 360 nm) in addition to cones whose pigments were broadly spread across the visible spectrum.

These discoveries of specific UV sensitive mechanisms in cyprinid fishes stimulated others to undertake similar tasks. Much as the pigeon has stood among birds, the goldfish (*Carassius auratus*) has been a favored species for the laboratory scientist. In several early experiments (e.g., Beauchamp et al., 1979) a heightened sensitivity to short wavelengths was observed in the goldfish. Various explanations were offered to account for what was thought an aberrancy. With the discovery of UV sensitive photopigments in cyprinid fishes, the reason for these earlier results became clear. Hawryshyn and Beauchamp (1985) conducted a thorough examination of the issue by using classically conditioned changes in heart rate to derive spectral sensitivity functions in the goldfish. The spectral sensitivity function obtained from one such fish appears in Figure 4. There is a prominent peak in the UV, located just short of 400 nm. Note that the spectral shape of the UV mechanism is considerably narrower than would be expected based on the shape of the absorption curve of a photopigment. This could arise for two reasons: (a) opponent neural interactions between the UV mechanism and other spectral mechanisms, and (b) the effects of spectral filtering by the lens or other ocular media. Although it is reasonably transparent, the lens of the goldfish does progressively attenuate short wavelength light (Hawryshyn et al., 1985). The effect of this filtering will be to truncate spectral sensitivity in the short wavelengths and to displace the sensitivity peaks to the long wavelengths relative to the pigment peak. By comparison to the location of the UV peak shown in the behavioral measurements of Figure 4, the goldfish UV pigment has maximum absorption at about 355–360 nm (Bowmaker et al., 1991).

Neumeyer (1985) provides two pieces of evidence that the UV mechanism in the goldfish can subserve color vision. One is that goldfish show relatively acute wavelength discrimination in the vicinity of 400 nm. The second is that in a color mixing task goldfish behave dichromatically over the UV/blue part of the spectrum. These experiments tie visual capacity to photopigment measurements in a direct and compelling fashion.

On the grounds that the spectral transmission of the ocular media might serve as a predictor to the likely prospects for UV vision, Douglas and McGuigan (1989) measured the transmissivity of lenses and corneas in fifty species of freshwater teleosts. They suggest that the ocular media of teleosts can be partitioned in a three-way classification, the basic difference being the spectral locations where the media begin to absorb light strongly. There is considerable uniformity of categorization of media within a given group of fish. Relatively clear lenses were found almost routinely among cyprinids, siluriforms, cyprinodontiforms and altheriniforms. The least transmissive lenses were found among many species of perciforms. As there is little apparent utility in pairing a UV pigment with low UV transmission of the ocular media, these measurements provide some predictions as to which fishes are likely to have UV sensitivity.

Several other species of fish have been examined and found to have UV sensitivity. A recent compilation of these results is provided by Douglas and Hawryshyn (1990).

It has been known for some time that anatomical patterning of receptors in the retinal mosaic differ in young and adult brown trout, *Salmo trutta* (Lyll, 1957). This fact is relevant to UV vision. Bowmaker and Kunz (1987) discovered through MSP measurements that, although cones containing UV pigment could be readily
recorded in young trout, they were no longer detectable in two-year-old fish (although they are apparently not absent entirely—Kunz, 1987). Hawryshyn et al. (1989) used behavioral measurements to establish that a similar loss occurs in the rainbow trout (*Salmo gairdneri*). This intriguing change is coincident with the growth of the fish, and it can be effected very rapidly (over a period of about one month). It is unclear why this loss of UV sensitivity occurs or, indeed, what its functional consequences might be. With regard to the latter, it has been suggested that this loss could reflect either a change in feeding behavior or a change in polarization sensitivity in these fish (see below).

Although the loss of UV sensitivity in trout appears not to depend on it (Hawryshyn *et al.*, 1989), such loss could result from a decrease in the transmission properties of the ocular media. Just such a change has been documented as occurring in the lenses of brown trout and goldfish (Douglas, 1989). In the brown trout, for instance, the 50% transmission points in the lens absorption curves progress out from about 310 to 390 nm over the first three years of life. Even without the loss of UV sensitive cones this loss would greatly restrict sensitivity to UV lights. This change recalls the gradual yellowing of the human lens that occurs over the lifespan. Whether the mechanisms causing increase in lens density are similar or not in these different species is not known.

**Reptiles / Amphibia**

These two large classes of animal are brought together here for the simple reason that although there is the suspicion that UV sensitivity may be present in a number of species, there is as yet very little experimental result to report.

The strongest (in fact the only) case to be made for UV vision in a reptile is that for the turtle (*Pseudemys scripta elegans*). Arnold and Neumeyer (1987) painstakingly measured spectral sensitivity, wavelength discrimination, and color mixing in turtles. They discovered that this species (a) has a sensitivity peak in the UV at about 380 nm, (b) shows relatively acute wavelength discrimination in the vicinity of 400 nm, and (c) gives dichromatic color matches in the vicinity of 400 nm. All of these facts argue for the presence in the turtle retina of a UV sensitive mechanism, very likely an independent photopigment. Although there have been numerous electrophysiological studies of turtle photoreceptors, no UV photopigment has yet been detected.
The evidence is even thinner with respect to amphibia, although here too there is suspicion about UV sensitivity. That suspicion is fueled by reports of heightened sensitivity in the ultraviolet for some amphibians as, for instance, the frog (Govardovskii and Zueva, 1974). Again, there is no direct evidence from photopigment measurements on frogs to substantiate the idea. There is a recent electrophysiological experiment indicating that there are cones in the tiger salamander (Ambystoma tigrinum) containing a UV-sensitive pigment (Perry and McNaughton, 1991). Beyond that, little presently exists. For amphibia, as for reptilia, the field is still wide open.

**Mammals**

Given the nature of photopigment absorption spectra, it is obvious that any species with sufficiently clear ocular media and a photopigment whose peak is in the visible portion of the spectrum can potentially sense UV light. It has long been established that lensless (aphakic) humans show greatly enhanced sensitivity to UV lights (Stark and Tan, 1982). Measurements of spectral sensitivity functions in such individuals show secondary peaks in the UV which are only 0.6-0.7 log unit lower than that of the principal peak in the visible spectrum (Stark, 1987). This sensitivity is due to absorption of light by the beta bands of the normal photopigments.

Aside from these atypical cases it has been routine to assume that mammals lack UV sensitivity, as Goldsmith (1990) recently did in the section of a review that he entitled, "Why Primates and Mammals Do Not Have Ultraviolet Receptors." The answer offered to the question was that ultraviolet receptors are incompatible with lenses that absorb strongly in the short wavelengths. Whereas it is certainly true that diurnal primates (Fig. 2) (along with some other mammals, principally sciurids) have strongly absorbing lenses, it is equally untrue that this is universal throughout the class. This fact has been known for some time. In their spectrophotometric measurements of the lenses of several species, Cooper and Robson (1969) included measurements of the lens of the guinea pig (Cavia porcellus). The lens of this animal shows very modest decreases in transmissivity through the longer wavelengths of UVA, and Cooper and Robson note that this pattern was similar to what they also measured in the lenses of horse, cow, pig, dog, cat and ferret. A measurement of absorption in the lens of the rat (Rattus norvegicus) illustrates this pattern (Fig. 2, continuous line); in this case absorption drops below 50% only for wavelengths shorter than about 340 nm. It seems wrong to suppose that all mammals are automatically denied UV receptors on the basis of lens transmissivity.

There is evidence to suggest that at least some mammals have achieved specific sensitivity to the UV lights. We recently examined several species of rodent with respect to the sensitivity of their eyes to UV stimulation (Jacobs et al., 1991). As judged by a gross electrical potential, the eyes of rats, house mice (Mus musculus), gerbils (Meriones unguiculatus) and gophers (Thomomys bottae) all show high sensitivity to the UV. Additional experiments ruled out the possibility that this UV sensitivity comes merely from beta-band absorption or can be traced to UV-sensitive photoproducts or fluorescence effects; rather, it appears to come from the operation of a retinal mechanism, probably a class of cone, having peak sensitivity at about 360 nm. These rodents can use this information to support visual discriminations. The spectral sensitivity functions of Figure 5 show that, under some conditions of examination, gerbils are actually more sensitive to UV than to visible light.

These experiments demolish the myth that all mammals are automatically incapable of using the information provided by UV light in the conduct of their affairs. Few mammals have been examined in a way that would reveal the presence of specific UV-sensitive mechanisms, and thus it is uncertain which species might share the capacities of these several rodents. A guess is that this capacity is not common among mammals. In birds and fishes it is not unusual to find three, four or more types of cone photopigment in the retina, often relatively evenly spaced across the spectrum. Excepting the primates, which have interesting variations of their own (Jacobs, 1991), there
appear usually to be only two cone pigment types in mammalian retinas (Jacobs, 1981). The usual pairing is of a cone pigment maximally sensitive in the range of 420–440 nm with another having its absorption peak beyond about 500 nm. Unusual among the four rodent species known to have a UV-sensitive pigment is that, although each has a version of the longer pigment, none has a second pigment with peak in the 420–440 nm range. Rather, each has a UV-sensitive pigment. This is quite unlike the situation in many birds and fishes where the UV pigment often is present in addition to a typical short-wavelength sensitive (SWS) cone.

These facts might suggest that in mammals the UV-sensitive cone is an alternative version of the SWS pigment. If this is so, no mammal that has the SWS pigment will have the UV pigment. To date the relationship between the molecular structure of SWS and UV pigments is unexplored, although the current active interest in sequencing cone pigment genes should shortly fill that gap. There is one bit of potentially relevant evidence. Szel and Rohlich (1990) used two monoclonal antibodies to label rat photoreceptors. In other mammals one of these labels SWS cones. A small population of rat cones were in fact labelled by this antibody, and Szel and Rohlich assumed that these must be typical SWS cones. However, the rat has no SWS cones (Neitz and Jacobs, 1986); instead, what were apparently being labelled were the UV-sensitive cones. At the level of specificity offered by these antibodies, the SWS cones of other mammals must be similar to rat UV cones.

### Utility of Ultraviolet Vision

It has been noted that the elegance and versatility of eyes provide the temptation to seek an adaptive explanation for every aspect of their design (Walls, 1942; Goldsmith, 1990). Such is the case for UV sensitive mechanisms of the types discussed here. Many of the studies noted above have speculated about the usefulness of the capacity. It is convenient to summarize the ideas as encompassing three possibilities. These ought not be thought of as exclusive or, indeed, as mutually incompatible.

A simple reason for acquiring a specific UV capacity is that it can allow an expansion of the spectral window through which animals may acquire visual information. For instance, with a UV photopigment the brown trout has an effective spectral range from about 320–750 nm. Many visual behaviors would seem to be automatically advantaged by the added amount of information provided by this large spectral range.
Several authors have made specific suggestions as to the way in which UV sensitivity might be used for making crucial visual discriminations—in food gathering, for instance, or in detection of other animals. One general idea is that either the absorption of UV light by a food source (e.g., drifting plankton in the case of some fishes) or, alternatively, scatter of UV light might serve to highlight the target against its background and thus aid in its detection. Burkhardt (1982) has pointed out that the petals of bird-pollinated flowers and various berries often have substantial UV reflectance which would provide attractive targets to species with specific UV sensitivity. The color patterns of fish (Harosi, 1985) as well as bird plumages (Burkhardt, 1989) often are highly reflective of the UV, and this could enhance the visibility of body coloration patterns to the UV-sensitive viewer.

Of course, one would like to know if these UV-defined patterns can actually be detected, but here there is relatively little to go on. In laboratory experiments Emmerton (1983) has shown that pigeons are capable of accurately performing elementary pattern discriminations when test stimuli are illuminated solely by UV light.

Another possibility about UV vision is that it may aid in the detection of polarized light. Although there are a number of early studies suggesting that various vertebrates can detect polarized light, the first indication that the UV receptor might have a role in this process comes from a behavioral experiment conducted by Hawryshyn and McFarland (1987). They used a chromatic adaptation paradigm to functionally isolate and then measure the sensitivity to e-vector orientation of each of the four spectral mechanisms in the goldfish, including the one maximally sensitive to UV light. The surprising result was that both of the long wavelength cone classes and the UV cone were very sensitive to e-vector orientation (the total variation in sensitivity as a function of orientation was on the order of 0.6–0.7 log unit). Interestingly, the preferred e-vector orientation for the UV cone was orthogonal to that of the other two cones. The latter fact suggests that these two groups of cone might form the input stage to a neural mechanism appropriate for discriminating the plane of polarization in the absence of any other consistent visual cues (e.g., brightness or color differences).

Hawryshyn and colleagues (Hawryshyn and Bolger, 1990; Hawryshyn et al., 1990) have gone on to show that trout can discriminate e-vector orientation as indexed by changes in their spatial orientation and that this behavior can be maintained even in partially polarized light. The utility of this capacity is far from obvious. The fact that polarization sensitivity is lost in older animals is perhaps correlated with the ontogenetic loss of UV sensitive cones (above). These authors suggest that the polarization ability may be important for supporting the impressive navigational skills shown by some salmonid fishes. An additional possible role for polarization sensitivity has been offered by Cameron and Pugh (1991) who demonstrated that green sunfish (Lepomis cyanellus) are quite sensitive to polarization contrast, and this sensitivity could provide the basis for a mechanism supporting object detection. Clearly, this is an additional role that UV sensitive cones might subserve in some species.

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