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Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*

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Summary. Spectral sensitivity functions of a passeriform bird, the Red-billed Leiothrix *Leiothrix lutea* (Timalidae) were determined in a behavioural test under different background illuminations.

1. With photopic illumination the spectral sensitivity of *Leiothrix lutea* covered the measured range from 320 nm to 680 nm. Four peaks of spectral sensitivity were found: a UV (370 nm), a blue (460 nm), a green (530 nm) and a red (620 nm) sensitivity peak. The spectral sensitivity was highest in the UV and decreased (over the blue and the green peak) towards the red sensitivity peak. The 4 peaks of spectral sensitivity point to 4 underlying cone mechanisms under photopic illumination and thus to a probably tetrachromatic colour vision of *Leiothrix lutea.*

2. With mesopic illumination the bird's spectral sensitivity covered the measured range from 320 nm to 680 nm. Neural interactions between cone and rod sensitivities are likely to determine this function. The increased overall sensitivity and a dominant sensitivity peak at 500 nm point to a typical rhodopsin as the likely rod photopigment.

3. Different aspects of the biological significance of the high UV sensitivity are discussed.

Key words: Spectral sensitivity – UV – Passeriform bird – Photopic – Mesopic

Introduction

Diurnal birds are highly visually guided animals with a visual system often regarded to be best adapted towards photopic conditions among all vertebrates. Compared to man, the range of spectral sensitivity may extend well into the ultraviolet (UV), as was shown first in 1972 by Huth and Burkhardt for the hummingbird *Colibri serrirostris*, and by Wright (1972) for the pigeon *Columba livia*.

More recently, electrophysiological studies (e.g. Chen et al. 1984; Chen and Goldsmith 1986) provided evidence that a variety of bird species possess a neural channel maximally sensitive at 370 nm in the UV. Visual pigments with maximum sensitivity in the UV, though recently found in teleost fishes (e.g. Bowmaker and Kunz 1987), have yet not been identified in birds. Compared to the number of receptorphysiologically investigated bird species, there is less information of UV-sensitivity in bird species from behavioural tests. Receptorphysiological data present evidence of the necessary prerequisites to perceive a certain stimulus, but only a behavioural analysis provides evidence for sensitivity of the animal to the given stimulus. Sensitivity to the UV has been reported for some hummingbirds (Goldsmith 1980) and some other bird species (Parrish et al. 1981). A behaviourally measured spectral sensitivity function including the UV exists only for the pigeon (e.g. Kreithen and Eisner 1978) and for a booby (*Sula nebouxii,* Reed 1987). Spectral sensitivity functions including the UV for passeriform birds, the bird order richest in species, could be of special importance for suggestions about the importance and implications of a UV-sensitivity in birds, yet none exist.

This paper presents behaviourally established spectral sensitivity functions, including the UV, for the Red-billed Leiothrix (*Leiothrix lutea,* Timalidae, Passeriformes) under photopic (preliminary results in Burkhardt and Maier 1989) and reduced illumination. The previously reported spectral sensitivity function was supplemented with additional measurements in the shortwave range. The presented study offers basic information for a series of further experiments to investigate *Leiothrix lutea's* colour vision, including the UV, in more detail.

Materials and methods

Subjects and their housing. Two young males (bird S1 and S2; probably caught wild) were bought from a pet shop. After their first moult they were tested under photopic, after their second moult under reduced (= mesopic) illumination.

The individuals' box-cages (700 × 700 × 700 mm) allowed social contact to the birds' partners (males, not tested) in neighbouring cages. The bottom and the walls of the cages were made of white

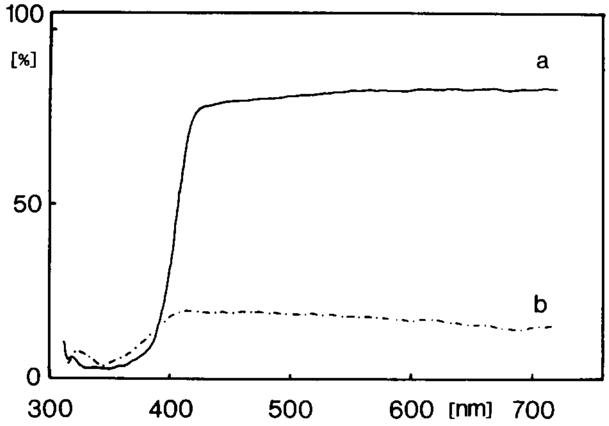

Fig. 1. Spectral reflexion characteristics of the white plastic of the cages (**a**), and of the grey plastic of the test chamber (**b**). Abscissa: wavelength (nm). Ordinate: reflexion (%, relative to the white standard: Zeiss MS 20)

plastic (reflexion characteristics see Fig. 1a), the top and the front of wire lattice. In the centre of the rearwall was an opening for the test apparatus. The animals were kept under a 12 h dark/12 h light cycle.

Test apparatus. The test apparatus (Fig. 2) consisted of a halogen light source (Osram Xenophot HLX, 12 V/100 W) and a quartz condensor (Spindler & Hoyer, Ø = 25 mm, f = 20 mm) which projected the light on the common end of an Y-quartz fibre optics (LOT GmbH). Interference filters and various neutral density filters located into the light path controlled stimulus quality and quantity. The two ends of the Y-fibre optics ended in two tubes, the inside of which was covered with aluminium foil. A manually operated shutter was positioned just behind both ends of the fibre optics. The reflexions within the tubes aided to illuminate diffusing screens homogeneously (UV-transmitting perspex, Ø = 25 mm) at the opposite end of the tubes. The screens were placed in the back of a chamber made of grey plastic (reflexion characteristics see Fig. 1b; 270 × 210 × 150 mm) with the front part made of wire lattice (270 × 210 × 120 mm). In the front wall of this chamber was an opening (70 × 80 mm) with a perch (= start position). Sitting on this perch, the birds could view the two screens and then jump into the test chamber. Beneath each of the two screens was a feeding apparatus (provided by the institute's workshop) with a feeding perch. Wire lattice (210 × 150 mm) between the two panels prevented the birds from jumping directly from one feeding perch to the other and thus forced the birds to make unambiguous choices. Under reduced illumination the plastic chamber was replaced by a wire lattice chamber of the same size, as the birds seemed unwilling to jump into the totally dark plastic chamber.

Illumination

a. Testfield illumination. Interference filters (LOT GmbH, FS10–25; Ø = 25 mm; HBW = 10 nm; with special respect for the UV filters it was checked that there were no longwave or infra-red windows) defined the wavelength at the screens, neutral density filters (LOT GmbH, FN46–25, Ø = 25 mm; equal transmission from 250–2500 nm) allowed stepwise intensity changes by the factor of 3. Wavelengths of maximum transmission of the interference filters were 320, 350, 370, 380, 410, 430, 440, 460, 470, 500, 530, 560, 590, 620, 650 and 680 nm. The 100% irradiance at the screens was measured with an optical powermeter (Photodyne Inc., model 66XLA) directly at the screens before and after each test series. Stimulus intensity was then calculated from these values and the photometrically calibrated factors of the neutral density filters.

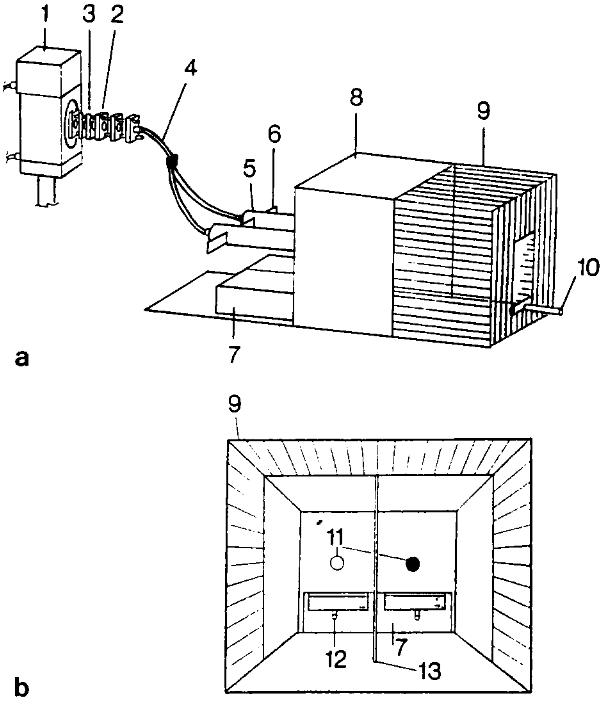

Fig. 2a and b. Test apparatus **a** Lateral view; **b** View into the test chamber (front wire lattice removed). 1 = halogen light source with quartz condensor; 2 = neutral density filter; 3 = interference filter; 4 = Y quartz fibre optics; 5 = aluminium covered tubes; 6 = shutter system; 7 = feeding apparatus; 8 = grey plastic chamber; 9 = wire lattice chamber; 10 = start position (perch); 11 = diffusing screens; 12 = feeding perches; 13 = wire lattice

b. Photopic illumination. Six daylight luminescent tubes (Osram 5000 Daylight de Luxe) provided an irradiance of 0.1 W/m^2 (illumination = 150 Lux) at the start position.

c. Reduced illumination. Two luminescent tubes (Osram Tageslicht 18 W/25) directed against the far wall of the laboratory provided a remaining irradiance of 0.5×10^{-3} W/m^2 (illumination < 1 Lux).

Training and test procedure

The initial training procedure for the birds (to get acquainted with the automatic feeders and the test chamber) lasted for two months. Then the birds were trained to jump to the start position and observe the two identically illuminated screens. Chosen randomly (random generator turbo pascal5) one of the two screens could be darkened with a manually operated shutter. To make a correct choice the bird had to jump to the feeding perch under the dark screen where it was rewarded with a food pellet (chicken pellets). Jumping to the feeding perch under the illuminated screen was counted as an incorrect choice that was neither rewarded nor punished. After each trial both screens were illuminated again, and the bird had to return to the start position before another choice situation was presented. It needed about 4 weeks of training for each individual until the birds checked the task. From then on they showed a very constant choice behaviour.

After another week of training under test conditions the actual test started. One h after laboratory morning the test chamber was introduced into the cage and the first choice situation was presented. After 10 trials the intensity of the illuminated screens was changed. During one test series a maximum of 40 choices was presented (the actual number of choices depended on the bird's willingness to respond). A maximum number of 8 to 10 test series were obtained during one day. One test series lasted about 20 min, intervalls between test series were about 40 min during which the birds had access to water but not to food. After each test series the test chamber was removed. About 1 h after the last test series per day the laboratory night cycle started. Under photopic illumination one wavelength, under reduced illumination two wavelengths were tested per day. The birds' behaviour was recorded by the experimenter through the front wire lattice.

Results

Spectral sensitivity under photopic illumination

At each test wavelength at least 6 intensity-response functions were obtained i.e. the choice frequency (% correct) was plotted against irradiance (quanta/cm^2 s). After determining the amount of quanta/cm^2 s at a threshold criterium of 75% choice frequency in all intensity-response functions, the mean threshold criterium, and the standard error of the mean for each tested wavelength could be calculated.

To obtain a common intensity-response function (see von Helversen 1972) mean intensity-response functions for each wavelength were plotted. Three typical of these functions are shown in Fig. 3. All the plotted intensity-response functions show the same characteristics: At high irradiances the birds' choice frequency was 100%. Within a log unit of reducing the irradiance the choice frequency changed from above 90% to below 60%. Displacing the intensity-response functions parallel to the X-axis so that all 75% values intersect at the same point shows great similarities of the intensity-response functions (correlation coefficient for the points in the linear part of this function: 0.84; significance 5%; $n = 32$) as shown in Fig. 4.

Plotting the mean threshold criteria against the corresponding wavelengths reveals the spectral threshold function. The inverse of this function is the spectral sensitivity function (see Fig. 5).

Photopic spectral sensitivity of *L. lutea* extended the measured spectral range from 320 nm to 680 nm. Both individuals' spectral sensitivity functions revealed 4 distinct peaks of sensitivity with maxima lying in the UV at 370 nm, in the blue at 460 nm, in the green at 530 nm, and in the red part of the spectrum at 620 nm. Spectral sensitivity was highest in the UV and declined over the blue and green to the red peak. There were only minor differences in some of the absolute sensitivity values between the results for two birds (based on 4001 choices for bird S1, 5080 for bird S2).

Spectral sensitivity under reduced illumination

All birds in the laboratory showed normal behaviour under reduced illumination. After a one-week accustoming period, bird S2 was tested.

Figure 6 compares the photopic spectral sensitivity function of bird S2 with the corresponding sensitivity function under reduced illumination. The latter function extended again the measured spectral range from 320 nm to 680 nm but showed a distinct peak in the green part of the spectrum with the maximum lying at 500 nm. This is in contrast to the photopic function were low sensitivity was observed at this wavelength.

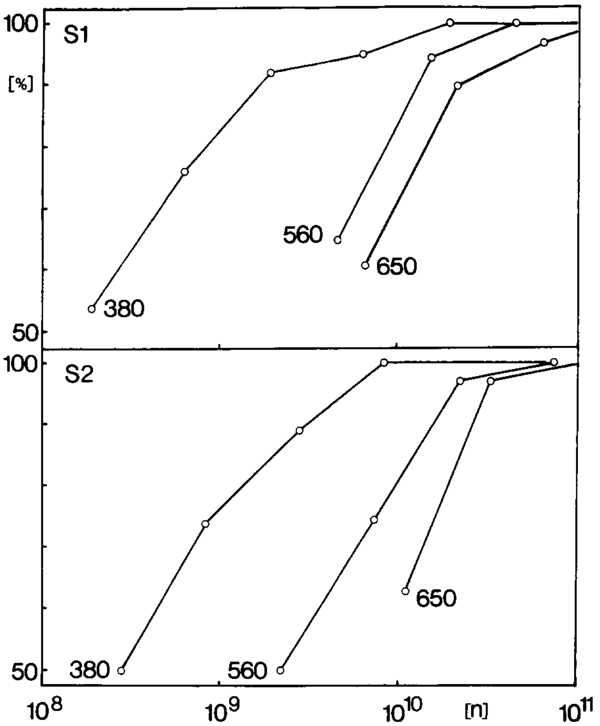

Fig. 3. Examples of typical intensity response functions of bird S1 and bird S2. Abscissa: irradiance (quanta/cm^2 s) at the illuminated screen. Ordinate: choice frequency (percentage of correct choices) (%). Numbers indicate maximum transmission wavelength of the interference filters used for each function

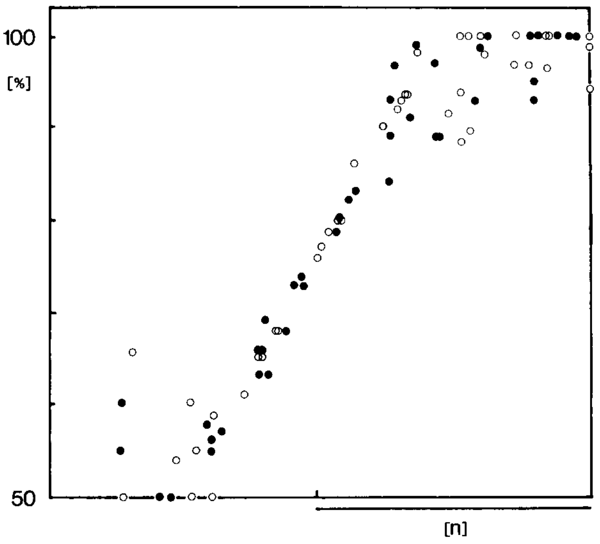

Fig. 4. Common intensity response function of *Leiothrix lutea*. All intensity response functions were displaced parallel to the abscissa, so that all 75% points lie above each other (bird S1 ●, bird S2 ○). Abscissa: intensity (quanta/cm^2 s); the line shows an intensity change by the factor of 10. Ordinate: choice frequency (%)

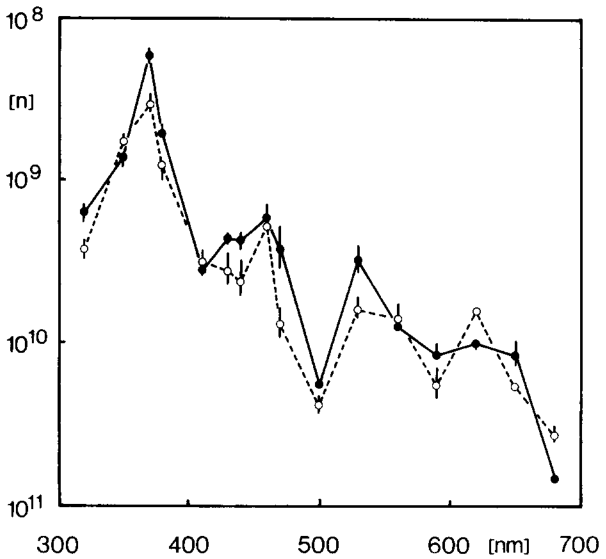

Fig. 5. Spectral sensitivity functions under photopic illumination for bird S1 (●) and bird S2 (○). Abscissa: wavelength (nm). Ordinate: mean amount of quanta/cm^2 s at the threshold criterium (with the standard error of the mean = sem; note the cases where the sem does not extend the diameter of the symbol for the mean)

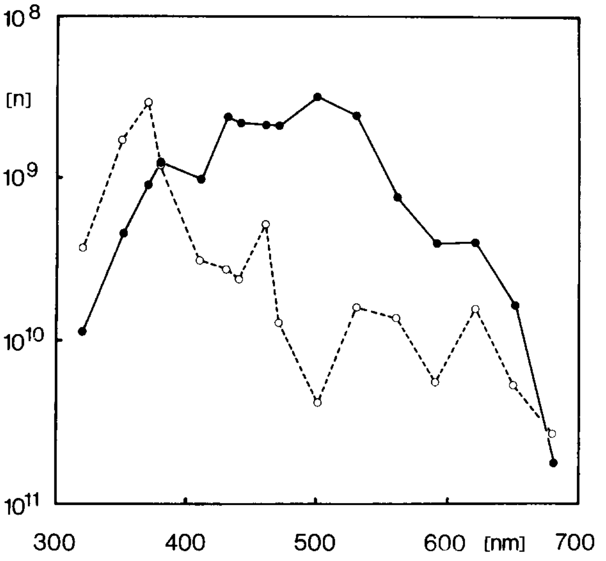

Fig. 6. Spectral sensitivity function of bird S2 under reduced illumination (●), compared to the spectral sensitivity function under photopic illumination (○). Abscissa: wavelength (nm). Ordinate: amount of quanta/cm^2 s at the threshold criterium

Under reduced illumination a small sensitivity peak in the UV with the maximum lying at 380 nm was found. Between 430 nm and 470 nm and between 590 nm and 620 nm the sensitivity function was flat. Below 380 nm and beyond 620 nm sensitivity declined rapidly. Between 320 nm and 380 nm the sensitivity was higher under photopic conditions than under reduced illumination. For the rest of the spectrum the overall sensitivity under reduced illumination was higher than under photopic illumination. A total of 1836 choices was evaluated.

Discussion

Leiothrix lutea is a highly social bird (Thielcke and Thielcke 1969) about the size of a house sparrow and is native to South East Asia. Its coloured plumage, food resource (insects, berries etc.), curiosity for new surroundings, and relatively easy handling make it an ideal subject for behavioural studies.

The method of rewarding the birds after choosing the dark screen was first used in similar experiments with honeybees by von Helversen (1972). It has the advantage that the rewarded stimulus stays constant during all the test (in contrast to conditions when the animal is trained towards the illuminated screen). Furthermore Neumeyer et al. (1991) showed that goldfish seem to discriminate on the basis of a colour cue when trained on the dark test field, but seem to discriminate on the basis of a brightness cue when trained on the illuminated test field. As one aim of my experiments was to build a basis for further investigations of *L. lutea's* colour vision (e.g. wavelength discrimination) I choose training the birds towards the dark test field.

Photopic spectral sensitivity

With it's wide range of spectral sensitivity *L. lutea* can use the total range of daylight radiation physiologically useable for visual processes (Kirschfeld 1982; Bowmaker 1980). These birds thus have access to a multitude of spectral information of their environment.

The results of this study confirm in general the data by Burkhardt and Maier (1989). Yet the supplement measurements in the shortwave range reveal that the actual maxima of the UV and the blue sensitivity peak are lying nearer at 370 nm and 460 nm than at 380 nm and 470 nm as proposed before. Furthermore the red sensitivity peak in the spectral sensitivity function of bird S2 is much more apparent.

The 4 spectral sensitivity peaks point to 4 underlying cone types: a UV, a blue, a green and a red receptor type. Selective chromatic adaptation tests confirm the fact that *L. lutea*'s photopic sensitivity is mediated by these 4 receptor types (Maier 1990). A set of 4 cone types seems to represent a common trait typical for diurnal bird species, e.g. for the pigeon (Govardovskij and Zueva 1977), for the duck (Jane and Bowmaker 1988), for the daw (Wessels 1974), and for a variety of other birds including some passeriform species (e.g. Chen and Goldsmith 1986). The mentioned species possess a longwave (= red), a middlewave (= green), and a shortwave (= blue) receptor type. Concerning the fourth receptor type, some bird species possess a very shortwave (= violet) cone type with maximum sensitivity lying at about 415 nm (e.g. the duck or the daw) or a UV cone type with maximum sensitivity lying at about 370 nm (e.g. Chen et al. 1984). A very shortwave (= violet) cone mechanism combined with ocular media transparent in the UV (as, at least to some degree, in the duck, Jane and Bowmaker 1988) provides a relatively limited UV-sensitivity compared to a UV sensitivity depending on a genuine UV cone mechanism. The reasons why some diurnal bird species possess a violet and others a UV cone mechanism are yet unknown. It could be an adaptation to certain (unknown) environmental conditions. There are also theoretical considerations that species with larger eyes could lack a UV cone type because here e.g. Raleigh-scattering could cause disturbing effects (Neumeyer 1988).

The maximum wavelengths of the UV, blue and green sensitivity peaks of *L. lutea* fit well to respective receptor-physiological data of other bird species. The maximum wavelength of the red sensitivity peak is shifted by about 30–50 nm towards longer wavelengths as compared to those data. Whether this represents species-specific differences or points towards the influence of neural interactions between different cone types was studied in more detail and will be discussed elsewhere.

Spectral sensitivity under reduced illumination

Under natural conditions, *L. lutea,* like many other birds, feeds not only during the day, but also at twilight. It was important, therefore, to determine its spectral sensitivity under reduced illumination. To get enough choices to calculate a spectral sensitivity function in a relatively short period of time under constant adaptation conditions, the bird was tested during the light phase of the 12 h dark/12 h light cycle with illumination intensity reduced. The birds' normal behaviour showed they were not disturbed under these conditions.

The higher overall sensitivity and the sensitivity peak at about 500 nm (Fig. 6) point towards a participation of rod sensitivity. A rhodopsin with an absorption maximum at about 500 nm is the likely rod photopigment for most birds (Goldsmith 1990). Therefore, the sensitivity function under reduced illumination was normalized with the maximum at 500 nm = 100%, and compared with a rhodopsin absorption function extending into the UV (Bridges 1967; Fig. 7).

Compared to the rhodopsin absorption function, the relative spectral sensitivity function shows one dominant and several minor peaks. This relative spectral sensitivity function lies between a pure photopic and a pure scotopic sensitivity function, and therefore fits the definition of a mesopic sensitivity function (Ripps and Weale 1976; Le Grand 1972).

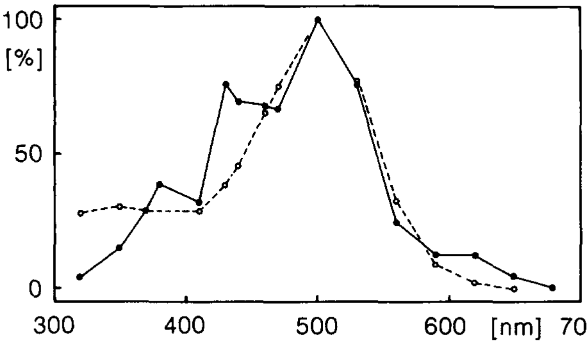

Fig. 7. Relative spectral sensitivity function of bird S2 under reduced illumination (●), compared to an absorption function of rhodopsin (○; Bridges 1967). Abscissa: wavelength (nm). Ordinate: relative spectral sensitivity/relative absorption (%; normalized at 500 nm)

Complicated neural interactions between cone and rod sensitivities define the human mesopic sensitivity function (Le Grand 1972). The same seems to hold for the mesopic function of *L. lutea.* The sensitivities of the UV, the blue and the red cone types probably interfere with the rod sensitivity function. Complicated neural interactions and/or different retinal areas used for the discrimination task could explain the fact that on one hand, the UV peak is lower, and on the other hand, the blue and red peaks are higher in the mesopic than in the photopic function.

General discussion

The high photopic spectral sensitivity of *L. lutea* in the UV could be an effect of adaptation due to the relative lack of UV radiation in the surrounding laboratory light and to the lack of UV reflexion from the cage walls. However, honeybees, adapted to natural daylight, have the highest spectral sensitivity in the UV (von Helversen 1972). Also, Kreithen and Eisner (1978) report on a considerably higher sensitivity of pigeons in the UV than at longer wavelengths. In pigeons, this phenomenon is due to a very high UV sensitivity in the lateral retinal field (Remy and Emmerton 1989). If the high UV sensitivity of *L. lutea,* as found in my study, is not caused by adaptation effects, then the question about its biological significance arises.

In natural daylight there is relatively weak UV radiation compared to that of the visible spectrum. Hence, there should be a more sensitive UV channel as compared to the other sensitivity channels in order to get a more or less equal response over all of the spectrum. The question how such a high UV sensitivity is achieved is yet open. It is unlikely that it is achieved by a very high percentage of UV cones in the retina. Birds' retinal cones are characterized by the presence of oil droplets (different classes of coloured, colourless and transparent oil droplets) in the inner segments. Since the coloured oil droplets act as shortwave cut-off filters, the transparent ones (transparent at wavelengths longer than 320 nm, Goldsmith et al. 1984) are the most likely candidates for oil droplets of UV-sensitive cones (or the violet sensitive cones). Extremely high percentages of transparent oil droplets were not found in most investigated bird species (e.g. Govardovskij and Zueva 1977; Jane and Bowmaker 1988; Chen et al. 1984; Goldsmith et al. 1984). Thus there is no hint of a very high portion of UV cones in the set of cone receptors.

The high sensitivity of the UV channel could point to the importance of UV patterns in the visually guided behaviour of *L. lutea.* Relevant UV patterns (reflecting as well as absorbing) may be expected in the context of intra- or interspecific communication (e.g. colours of the feathers), in coloured patterns of food resources or in the context of orientation (i.e. polarization sensitivity).

Some recent results show that many feathers indistinguishable to man by hue differ in their UV reflectance. Thus they should be very different to a UV sensitive bird (Burkhardt 1989). Preliminary results indicate that there are some UV patterns in the plumage of *L. lutea,* too (Maier 1989). Whether sexual dimorphism in the UV, as found in many butterflies (Silberglied 1979), might be present in birds, is not yet studied.

There are only very few reports on UV patterns of birds' food resources (Burkhardt 1982). Little is known about the UV reflectance of berries which are dispersed by birds. Concerning the mimicry of many butterflies, this mimicry seems to hold in the UV (Lutz 1933; for a review see Silberglied 1979). Goldsmith (1980) showed that a wild population of hummingbirds could be trained to use UV light cues to discriminate artificial feeders. The natural food resources of hummingbirds (flowers) might possess some common UV (absorbance or reflectance) characteristics significant to the feeding (and pollinating) birds. Eisner et al. (1969) noted the lack of special UV nectar guides in bird-pollinated flowers, which is in contrast to the conditions in many insect-pollinated flowers. Moreover, those flowers might have characteristic overall features in colouration due to the UV.

Specific UV receptors mediate some insects' polarization sensitivity (Rossel 1987; Schwind 1985). Polarization sensitivity was also demonstrated for several bird species (Able 1989; Helbig 1990; Waldvogel 1990), although it is still unknown, whether this polarization sensitivity is linked to a UV receptor type. Hawryshyn and McFarland (1987) present results for goldfish which suggest that vertebrates can use more than one receptor type for polarized light detection (in their study the UV-, the green- and red-sensitive cone receptor mechanism showed polarization sensitivity, whereas the blue-sensitive cone receptor mechanism was polarizationally insensitive).

The presented results of the spectral sensitivity functions of *L. lutea* offer a basis to investigate the use of UV vision in the visually guided behaviour of this bird species. The photopic sensitivity function is fundamental to future tests of wavelength discrimination and colour vision including the UV.

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