Unexpectedly low UV-sensitivity in a bird, the budgerigar

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1. Introduction

Photoreceptor adaptation ensures appropriate visual responses during changing light conditions and contributes to colour constancy. We used behavioural tests to compare UV-sensitivity of budgerigars after adaptation to UV-rich and UV-poor backgrounds. In the latter case, we found lower UV-sensitivity than expected, which could be the result of photon-shot noise corrupting cone signal robustness or nonlinear background adaptation. We suggest that non-linear adaptation may be necessary for allowing cones to discriminate UV-rich signals, such as bird plumage colours, against UV-poor natural backgrounds.
UV-poor conditions [9], our study offers the first experimental data on the selective adaptation of UV cones.

2. Material and methods

Experiments were carried out using the same experimental set-up, procedures and animals as in an earlier study [8]. For a detailed description of methods see the electronic supplementary material.

(a) Animals and experimental set-up

We used three male budgerigars kept in a room illuminated by fluorescent tubes set to a 12 L:12 D cycle. We trained and tested the birds in a cage illuminated from above by light-emitting diodes (LEDs). One cage wall was made from UV-transparent Perspex board (845 mm wide, 652 mm high) covered with white diffusers, and this functioned as adaptive background. The monochromatic stimuli were projected on the left or right side of that background, above two feeders with perches and removable lids. The Swedish Board of Agriculture granted the experiments (M68-11).

We used two channels of a 175 W dual power supply (CPX200, Thurlby Thandar instruments Ltd., Huntingdon, England) to control four white LEDs (LZC-00NW40, LED Engin Inc., San Jose, CA, USA) and four UV LEDs (LZ4-00U600, LED Engin Inc.). The white LEDs always generated a luminance of $6.3 \times 10^5$ cd m$^{-2}$ ($4.9 \times 10^{10}$ photons cm$^{-2}$ s$^{-1}$ sr$^{-1}$), while UV LEDs were switched on ($1.6 \times 10^{12}$ photons cm$^{-2}$ s$^{-1}$ sr$^{-1}$) or off to create UV-rich and UV-poor test conditions (figure 1a).

(b) Stimuli

Monochromatic stimuli generated by a monochromator (TILL Polychrome V software POLYCON v. 3.0 v. 3.0.12, Till Photonics GmbH, Germany) were projected onto the background from behind by two light guides (1000 μm, Ocean Optics). The resulting circular stimuli had approximately Gaussian intensity distributions with a full width at half maximum (FWHM) of 50 mm, they were separated by 280 mm, and 775 mm away from the starting perch. The spectral bandwidth (FWHM) of stimuli was 10 nm except for the stimulus at 415 nm (15 nm FWHM). We measured stimulus (without background illumination) and background radiance (without stimulus) using a spectroradiometer (RSP900-R; International Light, Peabody, MA, USA) aimed at the stimulus centre from 40 mm distance.

(c) Behavioural procedure

Birds adapted to the cage conditions for 5 min, and each trial was started by an auditory two-tone signal after which the stimulus was presented. Flights from the starting perch to the feeder at the presented light were counted as correct choices and reinforced with 2–4 s access to food. Incorrect choices (flights to feeder with no presented light) were not punished. After each trial, the bird had to return to the starting perch to initiate a new trial. We determined thresholds using a 2-down/1-up staircase procedure with equal step sizes and each staircase comprised 40 trials. We calculated the thresholds as the average intensity of all reversals during the last 20 trials and spectral sensitivity as the inverse of these thresholds.

The spectral sensitivity determined under the UV-rich condition (nine stimuli between 355 and 640 nm) has already been reported [8]. Here, we present new results for subsequent tests during UV-poor conditions, with stimuli at 355, 370, 415 nm, and one control at 575 nm. The birds were first tested for all four wavelengths, and this procedure was repeated until each bird completed four repetitions at each wavelength.

Figure 1. Spectral sensitivity of budgerigars after spectral adaptation. (a) UV-rich (dashed line) and UV-poor (solid thick line) illumination, normalized budgerigar cone sensitivities (thin lines). (b–d) Sensitivity of three birds in UV-rich (black) and UV-poor (grey in print, blue online) condition given as inverse of detection threshold, mean of 4 staircase runs ± s.d. (see the electronic supplementary material for tabulated data). (Online version in colour.)
4. Discussion

(a) Unexpectedly low sensitivity in UV-cones

Our results are not consistent with Weber’s law, which would predict a linear correlation between background intensity and spectral sensitivity (with a slope of $-1$ for log units, figure 2b). We conclude that either one or other of the assumptions of (i) linear von Kries adaptation or (ii) invariant SNR is erroneous.

We use UV-cone quantum catch to describe background intensity and because the conclusions are similar for all test stimuli (figures 1 and 2), we focus our discussion on the result for $370 \text{ nm}$ to simplify the argument. The decrease in quantum catch between the UV-rich and the UV-poor backgrounds was $1.3 \text{ log units}$, but the corresponding average increase in UV-sensitivity at $370 \text{ nm}$ was only $0.36 \text{ log units}$ and thus lower than expected from Weber’s law by $0.94 \text{ log units}$ (figure 2a,b).

In the preceding study of spectral sensitivity in budgerigars for backgrounds of different intensity (but invariant UV-rich spectrum), we found that a $1.17 \text{ log unit}$ decrease in UV-cone quantum catch produced an average sensitivity increase of $0.92 \text{ log units}$ at $370 \text{ nm}$, thus $0.25 \text{ log units}$ less than expected ([8]; figure 2a,b). We suggested that low UV-sensitivity was the result of photon-shot noise that give lower SNR and signal robustness in dimmer light (lower quantum catch) ([8]).

Both studies were performed on the same animals following the same experimental methods and similar differences in UV-cone quantum catch between test levels (1.3 versus 1.17 log units). We find no learning effects (see the electronic supplementary material) and no difference in sensitivity at $375 \text{ nm}$ (figures 1b and 2a), which strongly suggests invariant test conditions. The independence of the behavioural sampling could have been further ensured with interleaved rather than subsequent tests with UV-rich and UV-poor backgrounds, and the possible effects of such methodological differences may be evaluated in future studies. Here, we conclude that the deviation in sensitivity from the Weber’s law predictions is larger in the tests with backgrounds differing

3. Results

In tests with UV-poor compared with UV-rich background condition, spectral sensitivity was higher by $0.18–0.44 \text{ log units}$, with averages for all birds of $0.22, 0.36$ and $0.38 \text{ log units}$ at $355 \text{ nm}, 370 \text{ nm}$ and $415 \text{ nm}$, respectively (figures 1b–d and 2a). We found no differences for the control at $575 \text{ nm}$ (figures 1b–d and 2a).

(d) Receptor adaptation

The intensity difference between background and stimulus equals the intensity of the monochromatic light. In terms of quantum catch, this difference $\Delta q_i$ can be expressed as

$$\Delta q_i = k_i R_i(\lambda)I_b(\lambda),$$

where $R_i$ is the sensitivity of receptor $i$ ($i = \text{UV}, \text{S}, \text{M}, \text{L}$) and $I_b$ is the intensity of the monochromatic light. Receptor sensitivities were modelled using the Govardovskii template [10] while accounting for oil droplet and ocular media transmittance ([8]; electronic supplementary material). Receptor adaptation $k$ is described by von Kries transformation

$$k_i = \frac{1}{I_b} \int_{\text{UV}}^\infty R_i(\lambda)I_b(\lambda)d\lambda,$$

where $I_b$ is the background intensity. We model spectral sensitivity assuming that detection thresholds are set by receptor noise [11]

$$S^2 = \frac{(\omega_{\text{UV}}\omega_{\text{S}})^2(\Delta q_L - \Delta q_M)^2 + (\omega_{\text{UV}}\omega_{\text{L}})^2(\Delta q_L - \Delta q_S)^2 + (\omega_{\text{S}}\omega_{\text{L}})^2(\Delta q_M - \Delta q_S)^2}{(\omega_{\text{UV}}\omega_{\text{S}})^2 + (\omega_{\text{UV}}\omega_{\text{L}})^2 + (\omega_{\text{S}}\omega_{\text{L}})^2}.$$

Contrast $S$ is expressed in the unit of just noticeable difference (JND), where one JND corresponds to threshold noise. This is treated as limiting Weber fractions, $\omega$, set to $0.210, 0.121, 0.103$ and $0.105$ for the UV, S, M and L cones, respectively, as estimated in [8].

Figure 2. (a) Measured average spectral sensitivity of all budgerigars. Lines indicate model predictions and data points indicate measured sensitivity for different backgrounds; black squares: UV-rich bright light; grey squares and dashed line (blue online): UV-poor bright light; UV-rich dim light (4.3 cd m$^{-2}$, data from [8]). (b) Spectral sensitivity at 370 nm as a function of the quantum catch of the UV-cone. Weber’s law predicts a linear relationship with a slope of $-1$, but we find shallower slopes for the measured data. The light grey open square (light blue online) indicates the relative shift in estimated quantum catch that results from the alternative approach of modelling a 5 nm red-shifted visual pigment using the Lamb-template (see §4). Error bars indicate minimal and maximal individual spectral sensitivity (averages in figure 1). (Online version in colour.)
in UV-composition compared with the tests with different background intensities [8]; figure 2a,b).

A possible explanation of our results could be that we have underestimated the UVS cone quantum catch for the UV-poor condition. We used a template suggested by Govardovskii et al. [10] to model a visual pigment with peak sensitivity at 371 nm (see §2). It is challenging to estimate pigment sensitivity at short wavelengths below 400 nm, and the template for UV-pigments is less robust than those for pigments sensitive to longer wavelengths [10]. If we instead use a visual pigment template suggested by Lamb [12] and a UV-pigment red-shifted by 5 nm (see the electronic supplementary material for details), UV-cone sensitivity increases at longer wavelengths. This reduces the difference in UV-cone quantum catch between UV-rich and UV-poor conditions to 0.73 log units, which is only 0.37 log units less than expected and close to the deviation measured in the preceding experiments [8]. With these assumptions, all deviations from Weber’s law, in both the preceding [8] and present tests, could be explained by a decreasing SNR resulting from photon-shot noise in UV-poor test conditions. Previously, it has been shown that small variation in visual pigment sensitivity has little effect on colour vision modelling under most conditions [13]. The modelling of spectral sensitivity for a UV-poor background is unusual because the predictions change substantially from subtle variation in how pigment sensitivity is estimated (either by Govardovskii or the Lamb-template).

However, if we stay with the initial, and more conventional estimation of UV-cone absorbance, we reach the conclusion that UV-cone adaptation is not consistent with linear independent von Kries adaptation; it is weaker when under spectral changes compared with intensity changes. Could there be any functional advantages of low UV-sensitivity in UV-poor conditions?

References