Pattern discrimination in the near-ultraviolet by pigeons

JACKY EMMERTON

Ruhr-Universität Bochum, Bochum, Federal Republic of Germany

Four pigeons were tested, using an operant conditioning method with successive stimulus presentation, on a pattern discrimination task to determine whether or not they could distinguish patterns that were illuminated by near-ultraviolet (UV) light. Tests at red, green, and UV wavelengths showed that they could significantly discriminate not only the chromatic stimuli that were visible to human observers but also the UV-illuminated patterns that humans could not see. In control sessions, the birds' performance deteriorated to chance levels when these UV wavelengths were blocked by additional filters. Their discrimination of UV patterns precludes that the pigeon's known sensitivity to UV is mediated by a preretinal fluorescence, as is probably the case in some other animals, since such a fluorescence does not permit a focused retinal image. Possible retinal mechanisms mediating their UV detection are discussed.

Humans are normally blind to ultraviolet light (UV, wavelengths below 400 nm) but aphakic (lensless) individuals are able to see these wavelengths (Wald, 1945). Thus, humans possess a retinal mechanism for UV detection, but these short wavelengths are strongly absorbed by the yellow-pigmented lens (Said & Weale, 1959). Similarly, the cornea or lens of several other diurnal vertebrate species absorbs UV (see Muntz, 1972). Indeed, based on the finding that preretinal absorption of short wavelengths is widespread among those animals that are exposed to solar UV in their natural environments, it was previously supposed that all vertebrates were, like man, blind to UV light. However, this overgeneralization has been disproved for some amphibian and avian species (Dietz, 1972; Goldsmith, 1980; Huth & Burkhardt, 1972; Kimeldorf & Fontanini, 1974; Zipse, 1935), which have been shown in behavioral experiments to respond visually to UV light. Nevertheless, the basis for this detection has not been satisfactorily clarified. In some species (e.g., newts: LaTouche & Kimeldorf, 1979), UV detection seems to be mediated by fluorescence of the ocular media, in particular the lens. That is, UV is absorbed by lenticular substances and re-emitted as longer, visible wavelengths directly initiating transduction processes in receptors containing a UV-sensitive visual pigment.

One species for which behavioral evidence of UV sensitivity is available is the pigeon (Emmerton & Remy, 1983; Kreithen & Eisner, 1978; Wright, 1972). Spectrophotometric measures of this bird's ocular media show them to be remarkably transparent, with a high transmission down to about 310 nm in the UV and revealing no signs of fluorescence (Emmerton, Schwemer, Muth, & Schlecht, 1980). Lens fluorescence in the domestic chicken (*Gallus gallus*), when its lens was intensely illuminated with UV, was estimated to be very low in comparison with the fluorescence in other species (Brolin & Cederlund, 1958). This finding should not, however, be generalized to all avian species (Merker, 1934). The UV sensitivity of pigeons could be mediated by intraocular fluorescence, a possibility that could be decided in a behavioral experiment.

When UV stimulation causes some component of the ocular media to fluoresce, a secondary, scattered light source is formed within the eye and a visible "blue-haze" is cast on the retina (Muntz, 1972). Under these conditions, no sharply focused retinal image of a patterned, extraocular stimulus can be formed. Thus, a discrimination of UV-illuminated patterns would not be possible. To determine whether or not UV detection could be attributed to such preretinal fluorescence, an experiment was undertaken using pigeons and a pattern discrimination task.

METHOD

Subjects

Four naive adult homing pigeons (*Columba livia*) of local stock and unknown sex were used. They were housed under artificial daylight illumination (Sylvania Cool White ES Deluxe) and were maintained at 80% of their ad-lib body weights throughout the experiment.

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Apparatus

The pigeons were trained and tested in a two-key Skinner box (Figure 1) that was dimly lit by a 1-W houselight, shielded to provide an average luminance of 0.02 cd/m^2 on the walls and ceiling. The right-hand key, made of ground Plexiglas, was transilluminated with white light from a 1.2-W tungsten bulb. The left-hand key was made of a UV-transmitting Plexiglas (Röhm, Type 218), also with a matt surface. During the main part of the experiment, the stimulus patterns, a circle or a triangle of virtually equal area (50 mm^2), were projected onto the latter key.

Stimulus illumination was provided by a 75-W mercury lamp (Hanau Höhensonne Model 100, without the infrared elements). Light scatter was restricted by a black metal tube fitted to the lamp housing in front of the mercury bulb and by additional baffles surrounding the optical path. The spectral content and intensity of the stimuli were altered by filters inserted in the light path. The stimuli were switched on or off by a shutter that was driven by a rotating solenoid. Immediately in front of this shutter and behind the pecking key was a vane bearing the cutout circular and triangular stimulus shapes, which were also switched by activation of a rotating solenoid. A dummy vane, operated between trials when the stimuli were not switched, counteracted artifactual auditory cues. The Skinner box and stimulus projection system were placed inside a sound-attenuating box with an observation window. Experimental events were controlled and registered by conventional modular programming equipment. Stimuli were calibrated with an Oriel photodiode (7054) and a Mavolux luxmeter.

Procedure

After preliminary shaping, the pigeons were trained and tested on a successive discrimination task using a modified go/no-go procedure (Deliuss & Nowak, 1982). The white-illuminated right-hand key functioned as a "calling" key. A single peck darkened it and switched on the stimulus on the other key. For two birds, a circle was the positive ($S+$) and a triangle the negative ($S-$) stimulus. For the other two pigeons, this designation was reversed. Stimuli were presented in quasi-random order (Gellermann, 1933). An $S+$ was presented for 6 sec, during which time pecks to it were counted and were rewarded with 3-sec food access on a VI schedule. An $S-$ was presented for a minimum of 6 sec. Pecks to it were not reinforced, but each peck initiated a 10-sec extension of stimulus presentation, thus delaying the start of the next trial. Only those pecks during the initial 6 sec of $S-$ duration were counted. Each trial was separated by a 3-sec intertrial interval before the "calling" key was illuminated again. Fifty trials were given in each daily session, which lasted approximately 10-15 min.

Training

At the start of discrimination training, the stimuli were illuminated with "white" light from the mercury lamp from which most of the high-intensity UV had been attenuated by a Kodak Wratten 2B filter (see Table 1). During the 24 sessions of training, the VI schedule was gradually lengthened to 25 sec, which meant a delivery of only about nine reinforcements per session. Thus, very little of the $S+$ time was occupied by reward. The duration of $S-$ extension, contingent upon each incorrect peck, was also gradually increased to 10 sec. The intensity of the stimuli was decreased, using quartz neutral-density filters, by 1.5 log units to a luminance of 1.45 cd/m^2 during the course of training.

Habituation

The pigeons were next habituated to a color change, which was accomplished by inserting a Corning filter (No. 7-54, see Table 1) in the light path. This filter transmits a broad band of wavelengths in the UV but also leaks some red light (see Table 1). The stimuli appeared deep violet to a human observer. The reinforcement schedule was initially increased to VI 15 sec, to provide more frequent reward, and subsequently reduced again to VI 25 sec. For three birds, this habituation phase lasted 15 sessions. The fourth bird, however, ceased responding when the stimulus illumination was changed; it had to be extensively retrained during 43 sessions using a "fading" technique (white light of decreasing intensity from a small tungsten bulb was mixed first with broad-band and then with narrow-band UV, see below).

A similar habituation procedure was used when stimuli were illuminated with narrow-band UV from a Balzers interference filter (Table 1). Without additional attenuation by neutral-density filters, the stimuli appeared to human observers to have a dim bluish illumination. During this second habituation phase, the reinforcement schedule was again decreased from VI 15 sec to VI 25 sec and the stimulus intensity gradually reduced by 2 log units. At this intensity, the stimuli were invisible to three independent human observers.

Testing

To make sure that the pigeons were responding to the UV-illuminated stimuli and were not basing their discrimination on any artifactual cues, eight test sessions were run. On alternating sessions, the stimuli were illuminated with narrow-band UV, either at the intensity used at the end of habituation or with a UV-blocking (Kodak Wratten 2B) filter added.

Subsequently, the animals were tested with red (662 nm) and green (536 nm) stimuli, and then retested with UV (357 nm) stim-

Figure 1 (A) Two-key Skinner box used for training and testing. (B) Projection system for illuminating the stimulus key. Spectral content and intensity of the stimuli were altered by means of filters. (C) Circular or triangular stimuli of equal area were projected onto the stimulus key. For further explanations see text.

Table 1
Filters Used for Chromatic and Achromatic Stimuli

Stimulus	Filter Type	Transmission Characteristics	Remarks
UV (broad band)	Corning 7-54	$\lambda_{\max}(\text{UV}) = 320 \text{ nm}$ $T_{\max}(\text{UV}) = 85\%$ $\text{HB} = 130 \text{ nm}$ $\lambda_{\max}(\text{R}) = 730 \text{ nm}$ $T_{\max}(\text{R}) = 40\%$ $\text{HB} = 60 \text{ nm}$	UV transmission Red sideband
UV (narrow band)	Balzers R-UV	$\lambda_{\max} = 357 \text{ nm}$ $T_{\max} = 35\%$ $\text{HB} = 16 \text{ nm}$	
Green	Balzers B-40	$\lambda_{\max} = 536 \text{ nm}$ $T_{\max} = 40\%$ $\text{HB} = 9 \text{ nm}$	
Red	Balzers B-40	$\lambda_{\max} = 662 \text{ nm}$ $T_{\max} = 40\%$ $\text{HB} = 9 \text{ nm}$	
UV block	Kodak Wratten 2B	$T = < 0.1\%$ below 390 nm $T = > 90\%$ above 500 nm	Cutoff filter absorbing UV and transmitting visible wavelengths
Brightness Attenuation	Balzers quartz neutral density filters	0.5, 1.0 optical density 200 nm – 2.5 μ	Attenuate light intensity at UV and visible wavelengths

Note— $\lambda_{\max}$ = maximally transmitted wavelength; $T_{\max}$ = maximal percentage transmission; HB = half-bandwidth.

uli that were approximately matched in brightness for the pigeon (Emmerton & Remy, 1983) to the intensity of the UV stimulus. The luminance of the green stimulus was 0.14 cd/m². The order of testing varied among birds. Six sessions were completed at each wavelength.

RESULTS

By the end of the training phase with white light, all birds were responding stably at a level of more than 90% of the total number of pecks being made to the S+. In the final sessions of the habituation phase with broad-band UV illumination, the three birds that did not need additional training with a fading technique were responding at 80%-95% correct. For the fourth bird, fading was continued into the second habituation phase with narrow-band UV stimuli. At the end of these sessions, all birds were performing at a level of 80%-95% correct.

The mean results of the test sessions using three different stimulus wavelengths are shown in Figure 2. There were no systematic differences related to the shapes used as S+ and S-. For all three color conditions, performance is well above chance, although the scatter of results is slightly greater for UV stimuli than for the other hues used. In control tests with UV illumination, mean performance fell to chance levels when, on alternate sessions, the UV-blocking filter was inserted in the light path. The mean number of pecking responses made when the blocking filter was added was also very low, but this mean was generated mainly by the responding of one already overtrained bird which tended to peck the stimulus key indiscriminately, regardless of whether an S+ or an S- was being presented. Nevertheless, t tests

confirmed that the differences between the presence and absence of a blocking filter were significant ($p < .01$), both for the percentages and numbers of correct responses.

DISCUSSION

Once the discrimination task had been mastered, the pigeons maintained a high level of correct performance, not only at green and red wavelengths, which were visible to human observers, but also when the stimuli were illuminated with UV, which humans could not see. The pigeons' discrimination at UV wavelengths was confirmed in control tests in which their performance broke down when a UV-blocking filter was inserted in the optical system.

In spite of a considerable amount of pretest experience with UV-illuminated stimuli, performance in the test sessions at these wavelengths shows a larger amount of variance than was the case for tests with red and green stimuli (see Figure 2). This variance, which was generated mainly by one bird, might be due to interindividual differences in spectral sensitivity, which tend to be greater at shorter wavelengths (Emmerton & Remy, 1983; Graf & Norren, 1974). The UV stimuli might thus have appeared dimmer and were perhaps less easy to discriminate for the one bird. Nonetheless, the pigeons' high level of discrimination of UV-illuminated patterns indicates that UV sensitivity in the pigeon is not based on the detection of preretinal fluorescence but must instead rely on a retinal mechanism.

There are several possible mechanisms that could mediate UV detection. There is evidence that the

Figure 2. Results of test sessions (top) performed at each of three stimulus wavelengths, which were approximately equal in brightness for the pigeon. Mean percentage scores and standard deviations are presented. Data, in terms of mean percentage scores and numbers of correct responses, from control sessions with UV illumination are shown at bottom. In all sessions, a narrow-band UV (357 nm) filter was used and on alternate sessions (X) a UV-absorbing (Wratten 2B) filter was added. For further explanations see text.

pigeon has, in addition to red-, green-, and blue-sensitive photopigments (Bowmaker, 1977), a pigment with maximal sensitivity at about 400–415 nm (Govardovskii & Zueva, 1977; Graf & Norren, 1974; Norren, 1975), which would also be sensitive to the near-ultraviolet. Recent measures of the visual pigments in the human retina show that the "blue" pigment has its peak sensitivity at about 420 nm (Bowmaker & Dartnall, 1980). The effective sensitivity of the "blue" receptors is shifted due to the filtering action of the yellow-tinted lens to about 440 nm, the spectral peak that was previously reported for the blue pigment. Presumably, it is mainly these receptors that mediate UV detection in aphakic humans, for whom UV has a color quality indistinguishable from blue or violet (Wald, 1945). On the other hand, there is some evidence from a determination of the wavelength discrimination function that pigeons may distinguish the near-ultraviolet from the blue-violet part of the spectrum (Emmerton & Delius, 1980).

In addition to a characteristic region of maximal spectral sensitivity, all visual pigments exhibit a second minor peak, the β -band, which absorbs shorter wavelengths (Wald, 1958). For most visual pigments, the β -band occurs in the near-UV (Wolbarsht, 1976) and contributes to the aphakic human's vision in the UV (Tan, 1971). However, most of the cone cells in the pigeon's retina contain variously colored oil droplets, which act as cutoff filters that differentially absorb shorter wavelengths before light reaches the visual pigments (Bowmaker, 1977). UV detection, whether mediated by a "violet" (400 nm) pigment or the β -band of another pigment, is presumably asso-

ciated with the more infrequent and scattered receptors that either contain a colorless oil droplet or lack an oil droplet (Bowmaker, 1977). Another possibility, open to similar restrictions, is that an intermediate breakdown product of a visual pigment (e.g., metaiodopsin II: Yoshizawa, 1972) is UV-sensitive. Alternatively, it could be that, as in insects (Hardie & Kirschfeld, 1983), UV sensitivity in the pigeon is mediated by a sensitizing pigment (Kirschfeld, Note 1).

It is also conceivable that the retina itself fluoresces when illuminated with UV, which would permit perception of a focused retinal image. Thus, the oil droplets, or even the visual pigments themselves or their breakdown products, could fluoresce. Fluorescence of yellow oil droplets has been reported by Marc (cited in Donovan, 1978). However, relatively intense illumination would seem to be necessary if such intraretinal fluorescence were to play a functional role.

Precisely what retinal mechanisms subserve UV sensitivity in the pigeon can be clarified only after further investigations, using, for instance, microspectrophotometric or pigment-extraction techniques. However, the present experiment, demonstrating UV image formation, eliminates lens fluorescence as a basis for a sham sensitivity to UV and confirms Wright's (1972) arguments, following a somewhat more complex operant conditioning experiment, that pigeons have a retinal mechanism for UV detection.

REFERENCE NOTE

1. Kirschfeld, K. Personal communication, October 1982.

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