1 N.K. thanks the U.G.C. for the award of a research fellowship.
2 Bailey, C.J., and Matty, A.J., Horm. Metab. Res. *4* (1972) 266.
3 De Vlaming, V.L., Shing, J., Paquette, G., and Vuchs, R., J. Fish Biol. *10* (1977) 273.
4 De Vlaming, V.L., Vodicnik, M.J., Bauer, G., Murphy, T., and Evans, D., Life Sci. *20* (1977) 1945.
5 Khoo, K.H., Can. J. Zool. *57* (1979) 617.
6 Wallace, R.A., The Vertebrate Ovary. Plenum Press, New York 1978.
7 Nelson, N., J. biol. Chem. *153* (1944) 375.
8 Zlatkis, A., Zak, B., and Boyle, A.J., J. Lab. clin. Med. *41* (1953) 486.
9 Novak, M., J. Lipid Res. *6* (1965) 431.
10 Zilversmit, D.B., and Davis, A.K., J. Lab. clin. Med. *35* (1950) 155.
11 Oser, B.L., Hawk's Physiological Chemistry. McGraw Hill, New York 1965.
12 Seifter, S., Dayton, S., Novic, B., and Muntwyler, E., Archs Biochem. *25* (1950) 191.
13 Lewander, K., Dave, G., Johannson, M.L., Larson, A., and Lidman, U., Comp. Biochem. Physiol. *47B* (1974) 571.
14 Takashima, F., Hibiya, T., Nagan, P.V., and Aida, K., Bull. Jap. Soc. scient. Fish. *38* (1972) 43.
15 De Vlaming, V.L., Delahunty, G., Prack, M., and Bauer, G., Copeia *4* (1979) 749.
16 Anand, T.C., and Sundararaj, B.I., Gen. comp. Endocr. *22* (1974) 154.

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The pigeon's sensitivity to ultraviolet and 'visible' light[1]

J. Emmerton and M. Remy

Ruhr-Universität Bochum, Psychologisches Institut, D-4630 Bochum 1 (Federal Republic of Germany), January 24, 1983

Summary. The pigeon's spectral sensitivity, determined behaviorally between 320 and 640 nm, was maximal at 580 nm. Sensitivity extended into the near-ultraviolet but was, in contrast with previous findings, relatively low at these wavelengths. The discrepancy in results in the UV may be based on functional differences arising from the pigeon's retinal specialization.

Not only invertebrates[2] but also aphakic humans[3] and some amphibians[4-6], reptiles[7] and birds[8-10] can detect UV-light (wavelengths below 400 nm). One avian species for which this has been demonstrated behaviorally is the homing pigeon *(Columbia livia)*[11]. The optic media of this bird, unlike those of humans and many other vertebrates[12], are also relatively transparent in the UV[13]. To date, spectral sensitivity at both UV and 'visible' wavelengths has been measured in a single pigeon using a heart-rate conditioning technique[14]. Sensitivity to UV was reported to be exceptionally high, both for this animal and others tested in less detail. Using a simple behavioral method we have now determined the spectral sensitivity of pigeons in a food-seeking situation and find lower UV-sensitivity in this context.

Four pigeons, deprived to 80% of their ad-libitum body weight, were tested in their home-cages from which they could reach a 6 × 11 cm^2 quartz diffusing plate that was evenly illuminated from below to provide a colored background field. Chromatic stimuli were produced by interference filters (Balzers and Schott, half-bandwidths 8-14 nm). The quartz optics included a neutral density wedge to vary stimulus energy. Two different 150 W xenon light sources were employed (Müller 1530, and Bausch and Lomb). The optics were screened so that only the illuminated diffusing plate was visible. Stimulus energy was measured with a calibrated Oriel 7062 photomultiplier. The experiment was conducted in a darkened room, lit between trials for 1 min by a 100 W tungsten lamp next to the cage in order to keep the pigeons light adapted during an approximately 25 min session.

Within each 30-sec trial a pigeon was presented with 20 grains of corn scattered on the diffusing plate, and the number of grains eaten was counted. In daily sessions, starting at a stimulus intensity at which approximately 90% of grains were located, intensity was reduced between trials by 0.1 log units until the bird's performance fell below 50%. On average 14 trials were completed per day. Data were collected at each wavelength over 3 sessions and wavelengths were presented in a quasi-random order.

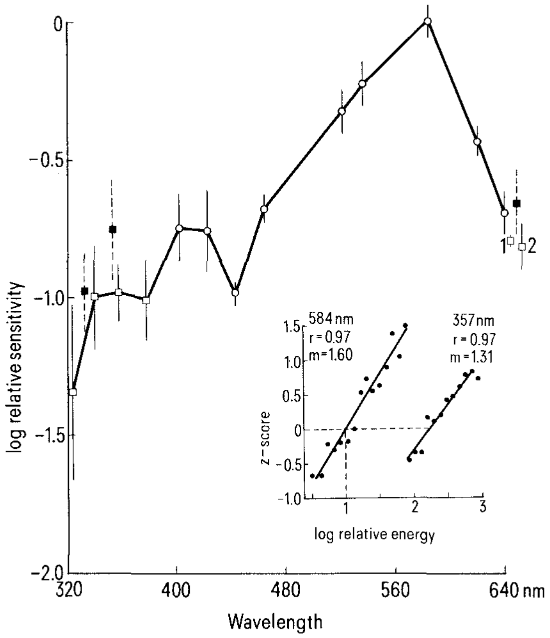

Figure 1. Means and SD of log relative sensitivity expressed on a quantal basis. Circles (○) and squares (□) refer to data obtained using Müller or Bausch and Lomb xenon lamps respectively. Black symbols indicate results using stained seeds. Points 1 and 2 are from test repetitions after exchanging the lamps and at the end of the experiment. Points at the same wavelength are displaced for clarity. Inset are 2 sets of psychophysical data, fitted by linear regression (r, correlation coefficient; m, slope), at UV and 'visible' wavelengths for 1 bird. Performance is expressed as z-scores against an arbitrary log relative energy scale on which 1 log unit corresponds to a stimulus luminance at 584 nm of 0.051 cd/m^2, measured at 6 cm above the quartz plate (the 'fixation') distance before a pigeon finally pecks[21]).

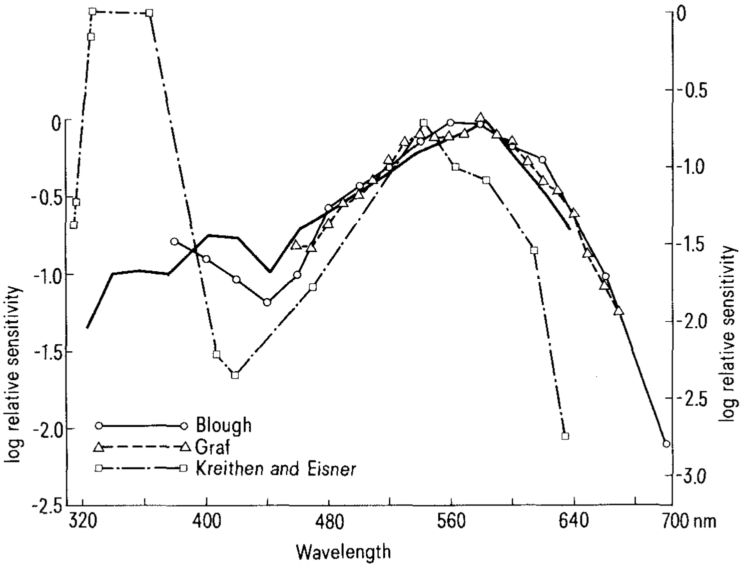

Figure 2. Mean sensitivity curves from this and from other behavioral studies. The present data (solid line) correspond closely in the 'visible' spectrum with the results of Blough[15] using a staircasing method of stimulus presentation and of Graf[16] using flicker photometry. Sensitivity in these experiments is expressed on the left ordinate. The data are also compared with Kreithen and Eisner's[14], whose sensitivity curve has been displaced so that its maximum in the 'visible' spectrum coincides in height with the maximum in the present experiment. For their results, sensitivity relative to the UV-maximum is shown on the right ordinate.

For each wavelength the mean percentages of grains eaten by each bird for trials at the same intensity settings were calculated. These data were transformed to z-values. Linear regressions were computed of z-values against neutral density wedge settings (proportional to log stimulus energy). The psychophysical functions were highly linear with correlation coefficients mostly exceeding 0.9 (see inset, fig. 1). Neutral density wedge settings corresponding to a threshold criterion of 50% grains eaten were calculated and the stimulus energies at threshold were measured.

A mean relative spectral sensitivity function (fig. 1) was calculated from these threshold values. In the 'visible' part of the spectrum sensitivity is maximum at about 580 nm and there is a small subsidiary peak at 400-420 nm. At UV-wavelengths the intensities provided by the Müller lamp were insufficient for reliable testing. This lamp was therefore replaced by a Bausch and Lomb model. Repeated threshold measures at 639 nm showed only small variations of about 0.1 log units (fig. 1). Spectral sensitivity at UV-wavelengths is therefore expressed without further adjustment in the data. Sensitivity in the UV is relatively low and declines towards 320 nm. At this point the data for only 3 birds are included since the correlation coefficient for the psychophysical function of the 4th bird was very low. The birds showed little or no response at 300 nm where transmission of the pigeon's optic media also declines sharply[13].

Although we could detect no fluorescence with the naked eye under the present experimental conditions, the food grains fluoresced under strong UV-illumination. This fluorescence could be eliminated by staining the seeds with black Indian ink. These seeds were neither preferred nor avoided by the birds. The results were compared for black-stained and unstained seeds at UV-wavelengths 357 and 340 nm and at 639 nm. The stained seeds were detected as easily or, perhaps due to their enhanced contrast, even more easily than the unstained seeds. This indicates that the pigeons could form a focused retinal image in the UV-independent of any grain fluorescence.

The low sensitivity to UV which we found contrasts with the results of Kreithen and Eisner[14] who reported greater sensitivity in this part of the spectrum than in the 'visible' range (fig. 2). In spite of methodological differences, our own data at 'visible' wavelengths correspond closely with previous sensitivity functions for the pigeon[15, 16] (fig. 2). Discrepancies between our own and Kreithen and Eisner's functions within this spectral range might simply be due to individual sensitivity variability, since their function refers to only one subject. However, the large discrepancies, of the order of several log units, within the UV-spectrum may relate to the different retinal regions stimulated in the 2 experiments and may have a functional significance.

The pigeon's retina is inhomogeneous, consisting of a dorso-temporal 'red' and a remaining 'yellow' field. These fields differ in the type and distribution of colored oil-droplets and visual pigments in their cone receptors[17]. The laterally presented stimuli in Kreithen and Eisner's experiment probably stimulated the yellow field, whereas those in our own experiment, which were presented in front of and below the birds, would have fallen on the red fields. The yellow retinal field serves the lateral and upper visual field whereas the red fields, normally associated with the pecking response, project frontally and binocularly. Previous investigations[18, 19] comparing spectral sensitivity of the red and yellow fields have found similar discrepancies for blue light, with reduced sensitivity in the red field.

The adaptive significance of the discrepancies we discuss here remains speculative. However, high UV-sensitivity in the portion of the retina which projects to the sky might correlate with the pigeon's ability, particularly associated with the yellow field, to discriminate the axis orientation of polarized light[20]. The high UV-sensitivity of the yellow field could aid the detection of natural skylight polarization patterns and thus be involved in the pigeon's homing ability. The relatively poor UV-sensitivity of the red field suggests that this sensitivity may be of little value in foraging and locating grains. However, too little is known at present about the spectral characteristics of the pigeon's natural environment to decide this issue.

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2 Silberglied, R.E., A. Rev. Ecol. Syst. *10* (1979) 373.
3 Wald, G., Science *101* (1945) 653.
4 Dietz, M., Naturwissenschaften *59* (1972) 316.
5 Govardovskii, V.I., and Zueva, L.V., Vision Res. *14* (1974) 131.

6 Kimeldorf, D.J., and Fontanini, D.F., Envir. Physiol. Biochem. *4* (1974) 40.
7 Moehn, L.D., J. Herpetol. *8* (1974) 175.
8 Huth, H.-H., and Burkhardt, D., Naturwissenschaften *59* (1972) 650.
9 Goldsmith, T.H., Science *207* (1980) 786.
10 Parrish, J., Benjamin, R., and Smith, R., Auk *98* (1981) 627.
11 Wright, A.A., J. exp. Analysis Behav. *17* (1972) 325.
12 Muntz, W.R.A., in: Handbook of Sensory Physiology, vol. VII/1, p. 529. Ed H.J.A. Dartnall. Springer, Berlin 1972.
13 Emmerton, J., Schwemer, J., Muth, I., and Schlecht, P., Invest. Ophthalmol. Vis. Sci. *19* (1980) 1382.
14 Kreithen, M.L., and Eisner, T., Nature, Lond. *272* (1978) 347.
15 Blough, D.S., J. opt. Soc. Am. *47* (1957) 827.
16 Graf, V.A., Psychon. Sci. *17* (1969) 282.
17 Bowmaker, J.K., Vision Res. *17* (1977) 1129.
18 King-Smith, P.E., cited in Muntz, W.R.A., see Muntz[12].
19 Martin, G.R., and Muntz, W.R.A., Nature, Lond. *274* (1978) 620.
20 Delius, J.D., Perchard, R.J., and Emmerton, J., J. comp. physiol. Psychol. *90* (1976) 560.
21 Hodos, W., Leibowitz, R.W., and Bonbright, J.C., J. exp. Analysis Behav. *25* (1976) 129.

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Diurnal and seasonal rhythms of stridulatory activity in the water boatmen *Corixa dentipes* and *Corixa punctata*

J. Theiss[1]

Institut für Zoologie, Universitätsstrasse 31, D-8400 Regensburg (Federal Republic of Germany), November 15, 1982

Summary. Two species of water boatmen which live sympatrically in Central Europe, begin stridulatory activity in the autumn. But whereas the activity of *C. punctata* is maximal during autumn, the peak activity of *C. dentipes* occurs in the spring.

The water boatman *Corixa punctata*, like *C. dentipes* and most other Corixidae, reportedly produce stridulatory sounds mainly in the spring, during the reproductive period, and mainly in the twilight hours[2-4]. Although some data on the diurnal and seasonal periodicity of stridulatory activity are available[5-7], no detailed long-term study of the Central European corixids has previously been published. Whereas *C. punctata* males have only 1 song, *C. dentipes* males have a repertoire of 4 different songs (songs A–D)[8]. The mechanism that enables the corixids to produce their acoustic signals under water has been described elsewhere[8,9]. Comparison of the diurnal and seasonal periodicities of stridulatory activity in the 2 species considered here, should be interesting because a) they live sympatrically in Central Europe and b) they use the same frequency band for acoustic communication[9].

For the first experiments, adult animals were caught in the vicinity of Regensburg in the autumn of 1979. Separated by species and sex, the animals were kept in cages in an atrium of the University of Regensburg and fed chironomid larvae. The wire cages had a floor area of 0.6 × 0.6 m; they were placed in water 0.5 m deep, in 2 concrete tanks each containing about 25 m^3 of water. Each tank housed males and females of only one species; the 2 sexes were not acoustically isolated from one another. The water temperature, light intensity and stridulatory activity were continually monitored electronically beginning at the end of February, and were displayed on a 4-channel pen-writer. The stridulatory sounds were recorded by modified condenser microphones and displayed on the pen-writer after filtering, rectification and integration. Exact numerical data on stridulation activity are given for *C. dentipes* only, because it was uncertain, whether some of the fainter stridulatory signals of *C. punctata*[8] could have been lost in the background noise or that of the recording system.

Surprisingly, most of the *C. punctata* males died during the winter of 1979. From the few males still surviving in the spring, only weak, irregular stridulatory sounds could be recorded. Examination of the females of this species, which had been kept in isolation from the males since November, showed that the seminal receptacle of some of them was already full. Evidently, in contrast to other reports[2,4], the reproductive phase of *C. punctata* in our latitudes already begins in the autumn. The *C. dentipes* males stridulated as soon as the recording of activity was begun, at a water temperature of 4–5 °C at the cage floor. A high noise level caused by falling snow or rain appears to have no appreciable effect on stridulatory activity. In March 1980 the main activity phase occurred during the day (fig. 1,a). The minimum in the stridulation curve often observable in the early afternoon resulted from an increase in the animals' swimming activity at this time of day. The daily stridulatory activity became maximal in April (fig. 1,b) when it was uniformly distributed throughout the 24 h. The presence of special activity peaks during the morning and evening twilight could not be confirmed. By the end of June all of the *C. dentipes* males had died.

In the field, imagines of the new generation of both species begin to appear in August. In a 2nd experiment, the stridulatory activity of the 2 species was recorded under the same conditions as previously described, from August 1980 to May 1981. *C. punctata* males began to stridulate in September. The activity reached a prominent peak in this month, and then decreased until December. Some slight stridulatory activity then persisted throughout the entire winter, even though the tanks containing the cages were completely covered with ice for at least 3 months and the water temperature at the floor of the cage at times fell to +2 °C. Stridulation activity remained low in the spring of 1981. No clear activity maxima at particular times of day could be observed. *C. dentipes* males also occasionally stridulated as early as September. But in contrast to *C. punctata* the stridulation rate remained low in autumn, and in October and November it was about half as high as in the 2nd week of March 1981 (fig. 2). In autumn all 4 songs are produced mainly at night, song A being most common. The stridulatory activity ceased as soon as the water temperature fell below 5 °C.

The observations of *C. dentipes* in spring of 1980 were repeated in the following spring with males that had been kept in the same cage with females. In a 2nd tank, *C. dentipes* males were kept without females, and their stridulation was also recorded. The frequency of occurrence of the 4 songs was plotted separately (fig. 2). The first stridulations