Small Passerines Can Discriminate Ultraviolet Surface Colours

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Hollow-dwelling passerine birds were tested for UV surface colour discrimination by using the instinct to bring food to nestlings that makes a bird search for the nest under changing conditions. The experiments were carried out on breeding pairs of pied flycatcher (*Muscicapa hypoleuca*), great tit (*Parus major*) and tree sparrow (*Passer montanus*) in the wild by the method of alternative choice of entrance into a double nesting-box with the nestlings in one or the other section. The entrances were marked with sheets of painted papers that had different reflectances in UV. For a human observer, all marks looked achromatic. Birds were trained to discriminate the mark coloured with UV-absorbing paint from a neutral one (with equal reflectance throughout the spectrum). Birds easily learned to search for the UV-absorbing mark, and transferred the acquired habit when tested with new marks that differed only slightly from the initial ones in lightness to eliminate brightness cues.

Ultraviolet sensitivity   Colour vision   Birds   Behaviour   Passerines

INTRODUCTION

UV vision means above all the ability to distinguish objects by their different reflectances in UV not just mere UV sensitivity. An appreciable sensitivity to UV light exists even in those animals that lack a special type of UV-sensitive photoreceptor if their ocular media are sufficiently transparent to UV (Govardovskii & Zueva, 1974). But such sensitivity alone cannot provide discrimination of objects by their UV patterns because inevitable surface reflectance in the main band of photopigment sensitivity will overwhelm the contribution of the UV region in natural lighting conditions. Therefore the behavioural experiments that use as stimuli narrow band UV light sources instead of coloured surfaces (Dietz, 1972; Goldsmith, 1980; Hawryshyn & Beauchamp, 1985; Reed, 1987; Arnold & Neumeyer, 1987) can demonstrate the presence of UV sensitivity but say little about the possibility of using it in visually guided behaviour in natural environments.

To investigate the behavioural significance of incorporating an UV channel into colour vision in birds, we used painted surfaces under daylight illumination as stimuli in a natural type of behaviour of a kind that is already known to use colour vision. This is the ability of hollow-dwelling small passerine birds to find their nests with nestlings using features of the surroundings that can

be changed in the experiment. This ability has been examined using a classical conditioning paradigm (Derim-Oglu, 1981). Derim-Oglu, Pavlova and Maximov (1987) demonstrated with this method that birds can easily be trained to discriminate coloured surfaces at least in the visible spectrum.

In the present study, in order to investigate the vision of birds in the UV range invisible to humans using coloured surfaces, we took advantage of a property possessed by some kinds of white paint of having different reflectances in UV—a property well known in painting that helps to reveal recent forgeries and distinguish them from the work of older artists.

MATERIALS AND METHODS

Subjects

The experiments were conducted in the mixed woodlands of the Moscow and Vladimir districts on breeding pairs of hollow-dwelling small passerine birds: pied flycatcher *Muscicapa hypoleuca* (two nests), great tit *Parus major* (two nests) and tree sparrow *Passer montanus* (one nest).

Procedure and apparatus

In spring, nesting-boxes were hung up on trees where the birds nested. When the nestlings hatched, the nesting-box with the nest was gradually lowered to a height convenient for experiments. Meanwhile, the birds were accustomed to the presence of the experimenters. During an experimental session, the nesting-box was replaced by a special experimental box that consisted of two sections

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with separate entrances and a mobile tray with an artificial nest, to which the nestlings were transferred. The tray could be moved from one section to the other. The sections were marked outside with coloured stimuli attached to the front panel of the box around the entrances.

Experiments were conducted with breaks during daylight hours over a period of a few days. Between the experimental sessions, the nestlings were returned to their native nesting-box.

Stimuli

Stimuli were made from papers evenly painted with glue colours based on zink white (UV-absorbing stimuli) or chalk (UV-reflecting stimuli), with or without the addition of a small amount of black paint thus producing light grey (approx. 60% reflectance in the visible spectrum), or white (approx. 85% reflectance) papers. As a result we had four types of stimuli. For simplicity, we will code the names for the stimuli with two letters: UW, NW, UG and NG. The first letter denotes the spectral properties of the paper in the UV region (U for UV-absorbing papers, and N for UV-reflecting papers with uniform reflectance throughout the spectrum). The second letter denotes how the stimuli look to human observers based on their reflectances in the visible spectrum (W for white papers, and G for grey ones). Spectral reflectances of the papers were measured with LOMO SF-10 and Shimadzu MPS-5000 spectrometers and are given in Fig. 1. Stimuli were $10 \times 10\,cm^2$ squares with a central hole, 3.2 cm in dia, for the entrance.

When attached to the entrances, the stimuli were in equal lighting conditions. The total illumination depended on the position of the nest in the wood and changed according to time of day and weather, varying between 1000 and 50,000 lx.

Training

In all five nests, the birds were trained to discriminate one of the UV-absorbing stimuli, reinforced by access to the nestlings, from one of the neutral stimuli as a reference. From time to time the tray with the nestlings

FIGURE 1. Spectral reflectances of the stimuli used in the experiments.

was moved to the adjacent section, the stimuli being exchanged on the entrances to prevent the birds from developing a position habit. For convenience in viewing the stimuli, a special perch was fixed at a distance of 1.5–2 m in front of the experimental box where the birds used to sit before making a choice.

During the session, the experimental box was watched continuously with binoculars from a distance of 5–10 m. The choices of each nursing parent were registered separately. When, in the trial, a bird flitted from one entrance to another, only the first visit was taken into account. Once it became clear (see Results) that a bird had learned to fly to the UV-absorbing stimulus despite the changes in its position, the last training session(s) was carried out to score the bird's final performance. In some experiments, the pair of training stimuli for this session was replaced with a new one made from the same papers to exclude cues other than colouration.

Testing

Testing was conducted with a pair of stimuli, each of which (both positive and negative) was different from the initial ones either in brightness or in UV spectral properties (or in both these features simultaneously). This made it possible to find out which one of these cues was being used by the bird in discrimination. The test sessions were not tests in the usual sense in which neither stimulus was reinforced. Since one cannot deprive parents of the possibility of feeding their nestlings during the experiments, one of the stimuli was always reinforced during the tests as well. However, these remain an adequate test of the bird's response criterion, since well-trained birds continue to use the former cue for a long time after the changes of the meaning of the stimuli without any sign of being retrained (Derim-Oglu, 1981; Derim-Oglu et al., 1987).

Birds feed nestlings in a very irregular manner, spending 10 min on the average in search of food. Many external factors affected the length of experimental sessions (e.g. we failed to continue experiments with tree sparrows because the nestlings left the nest during the test session). As a result, the number of trials in sessions varied. This makes the results less uniform, but does not impede statistical analysis. For each session of a certain length, accumulated scores were analysed with the binomial test.

RESULTS AND DISCUSSION

Training

From the very beginning, the birds did not randomly choose which section of the experimental box to go to (Derim-Oglu, 1981). In the learning process, birds, like other animals (Krechevsky, 1932), attempt various cues until they finally hit upon the suitable one. Generally, this process began from one or another position habit.

The behaviour of the male great tit from nest 3 is demonstrative in this respect. Here, because of a period of very bad weather, the training process turned out long
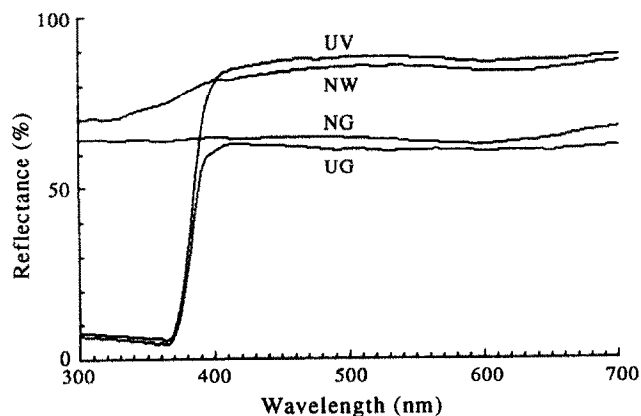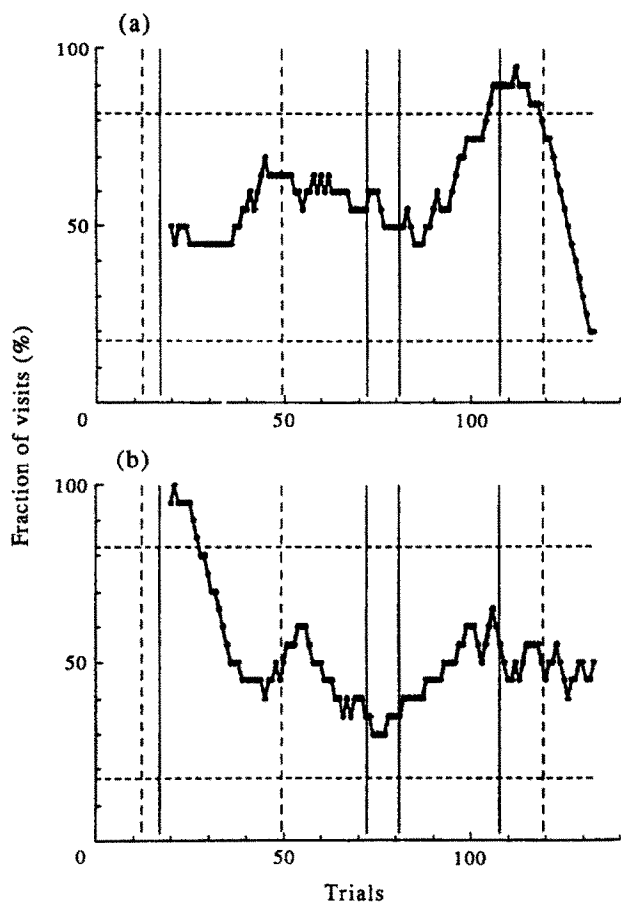
FIGURE 2. Learning curves for the male great tit from nest 3. The curves represent: (a) percent of successes in visiting the nestlings in 20 previous trials; (b) percent of visits to the right entrance. Vertical lines separate different sessions, solid ones indicating night intersession breaks. Horizontal dashed lines indicate the limits, above and below which the deviations from random choice are statistically significant at the 95% level of confidence.

enough to be divided into different stages. Figure 2 represents the process of training and subsequent testing for this experiment in two classical "learning curves" (Krechevsky, 1932) that show the change in frequency of visits to the section with nestlings (upper curve) and to the right-hand section (lower curve). For each trial (abscissa) starting from the 20th one, the data points show the fraction of corresponding choices in a sequence of 20 preceding trials. For the whole of the first training day and at the beginning of the second day, the bird mainly flew into the right entrance as is evident from Fig. 2(b). Then, the bird abruptly changed the habit to a left-going strategy, which results in a steep drop in the curve in Fig. 2(b), although the curve does not achieve the significance level for this strategy (lower dashed line). Since the location of the nestlings was always being changed, the fraction of successful visits remained at the level of 50% all this time, as is clear from the left part of the learning curve in Fig. 2(a). On the fourth day of training the bird discovered the necessary cue and began to fly into the section with the nestlings marked with UV-absorbing grey stimulus, as is evident from the rise in the learning curve in Fig. 2(a). Right up to the test

session the bird chose mainly the section with the nestlings in spite of the changes in their location.

Usually, one can recognize that the bird has learned the task not only by the discrimination performance but also by changes in its very behaviour. A bird that has not learned usually flies straight into some entrance from the wood. But after learning, it first settles on the perch and examines the entrances with the attached stimuli, and only from there makes the choice. So, in the experiments the bird was considered to have learned only when it began to use the perch. After that the last training session was started to score its performance.

As a rule, one parent from a breeding pair (either male or female) exceeds another in activity or in learning ability (Derim-Oglu et al., 1987), and it is the bird that learns faster that determines the course of the experiment. Therefore, we usually had reliable results for only one bird that had learned from each nest.

Discrimination of the UV surface colours

All the birds learned to discriminate the UV-absorbing colours from the neutral ones fairly quickly. They required for this approximately as much time as in the case of learning to make colour discrimination in the visible part of spectrum (Derim-Oglu et al., 1987). After the new (test) pair of stimuli was presented, birds continued to choose an UV-absorbing stimulus with confidence. But even for the experiments where exactly UV-absorbing stimulus was reinforced during the testing such choices could not be explained by fast retraining of the birds. The process of relearning of birds itself is generally well recognizable and consists of a series of clearly identified phases (Derim-Oglu, 1981; Derim-Oglu et al., 1987) Typically, the birds first choose an entrance using the former cue despite the absence of the nestlings in the corresponding section; only then do they each time flit to the necessary entrance. After some dozens of trials they abandon this habit, and adopt some position strategy as more simple for birds. And only after that do they begin to learn anew. In all our experiments the testing was confined completely to the time of the first phase. The results are summarized in Table 1.

In the table, the column "Stimuli" specifies the experimental conditions, i.e. the pair of stimuli presented during the session, "(+)" identifying the stimulus that

TABLE 1. The discrimination scores for the stimuli of the birds

Nest	Species	Sex	Stimuli	Scores
1	M. hypoleuca	M	UG(+):NG(−)	22:5
			UW(+):NW(−)	23:6
2	M. hypoleuca	F	UW(+):NW(−)	33:8
			UG(+):NG(−)	18:3
			UG(+):NW(−)	17:1
			UW(+):NG(−)	9:0
3	P. major	M	UG(+):NW(−)	13:3
			UW(−):NG(+)	14:0
4	P. major	M	UW(+):NW(−)	22:5
			UG(+):NG(−)	18:5
5	P. montanus	Both	UG(+):NW(−)	28:4
			UW(−):NG(+)	18:7

points the way to the nestlings. The next column contains the experimental results—the number of choices of these stimuli. We do not list separate statistical estimates for the results, since rates listed in the last column for all birds and sessions (except the last line in the table) show a reliable preference for UV-absorbing stimuli according to the binomial test at a significance level of $P < 0.01$. The first line for each nest indicates the training conditions and the resultant scores at the end of training. In the next line(s), the experimental conditions and results for test sessions are listed.

Thus, the male pied flycatcher from nest 1 was trained with the pair of grey stimuli (UG stimulus being reinforced), and after learning it chose the positive stimulus 22 times in 27 trials. After that it was tested with the pair of new (white) stimuli. Without additional training it chose UW stimulus 23 times but the neutral white one (NW) 6 times only. In contrast the female pied flycatcher from nest 2 was trained with the pair of white stimuli, and then tested with the pair of grey ones, and with other possible combinations of our stimuli. In all cases the bird demonstrated a statistically significant preference for the UV-absorbing papers irrespective of their lightness. This result is consistent with the well-known fact that birds usually disregard the brightness cues in colour discrimination (Goldsmith, Collins & Perlman 1981; Derim Oglu & Maximov, 1987; Peiponen, 1992). The male from the same nest 2 was also trained to discriminate white stimuli, but it was less active and did not accumulate a sufficient number of visits in tests sessions. Therefore, its data are not included in Table 1.

The rejection of brightness cues was clearer still in the experiments, where even the original stimuli in the training pair differed in the two features simultaneously: both in lightness and in spectral properties. This type of experiment was already used to estimate the influence of different cues (Derim-Oglu & Maximov, 1987). A male great tit from nest 3 was trained to discriminate the UV-absorbing grey stimulus from the neutral white one. Though the lightness might be used here as a guide as well, the bird preferred to be guided by the UV properties of colouration. Indeed, when in the test session the bird was offered a pair of stimuli in which one feature (UV-absorbing properties) was reversed, it clearly preferred the white (instead of grey) but also UV-absorbing stimulus. This behaviour was especially impressive for human observers (the experimenters themselves), who saw how a well-trained bird regularly visited the section of the nest-box marked with the grey stimulus, but in the test session began to fly to the white stimulus, rejecting the grey one.

Notice that in these experiments the nestlings were always placed in the section marked with grey stimuli (Table 1). So, in the test session the bird flew all 14 times into the section without nestlings, as is also evident from the abrupt drop in the "learning curve" during the last (test) session in Fig. 2(a). This means that neither lightness nor some unknown signals from the nestlings were used here. The only explanation for such a behaviour is the use of the UV-properties of the stimuli as

a cue. This result illustrates also the fact well known to ethologists that birds hardly ever learn anew after changes of the meaning of the stimuli (Derim-Oglu et al., 1987; Peiponen, 1992). They persist in choosing the colours which they have learned to connect with reinforcement. It is clear from the scores (see Table 1) that in this experiment the training of the male great tit to fly to the UV-absorbing stimulus had still not been extinguished by the end of the test session. As a rule, extinguishing the training of the bird takes one day of experiments or even more.

As to possible uncontrolled signals of nestlings, it should be mentioned that in experiments with hollow-dwelling birds, acoustical, olfactory and even visual cues given by the nestlings themselves do not help the birds to find the right entrance to the nest. When searching for their nest, birds nesting in hidden places are guided only by features of the surroundings and pay no attention to their own nestlings when they meet them at an inappropriate place (Derim-Oglu, 1964). Such a behaviour was also observed in our previous experiments with double nest-boxes (Derim-Oglu et al., 1987). Birds usually paid no attention to the grown-up nestlings, peeping out through the entrance marked with the wrong stimulus. They first brought the food to the section indicated with the proper mark, and only on finding no nestlings there did they go to the other entrance.

The same experimental scheme was used in experiments with the tree sparrow (nest 5). Here, the male was more active than the female, and learned to discriminate the stimuli in one session (less than 4 hr). But in this species the sex dimorphism is less marked, so in this experiment we sometimes failed to recognize with confidence which one of the parents flew into the entrance. Therefore in the column "Scores" the data for both birds were summed, which somewhat smoothed out the results. As in the case of the great tit, in the test session the tree sparrows flew mainly to the entrance marked with the white UV-absorbing stimulus, rather than to the nestlings. Although the difference between the scores is less marked here (see Table 1), the deviation from the chance is significant by the usual criteria ($P = 0.02$).

Thus, one may conclude that the investigated passerine species are not merely capable of seeing UV, but can also discriminate objects by the different spectral reflectances of their surfaces in this region of the spectrum, and can use this ability to orient themselves in the surroundings. As to the photoreceptor basis for such an ability, one has to expect that their retinas have a special type of UV-sensitive cone. This may be concluded from the fact that in our experiments we used white and light-grey papers with uniformly high reflectance in the visible part of the spectrum (for human beings). The discrimination of such stimuli cannot be explained by the short-wave band of sensitivity inherent to the usual cone mechanisms, for in the cones with $\lambda_{max} > 400$ nm the contribution of light reflected in the main band of sensitivity will greatly surpass the small difference between the stimuli in the UV region (even in cones lacking coloured oil droplets). The fact that an aphakic observer

(short-wave cones in the human eye have λ_{max} at 420 nm) did not see the difference between our neutral and UV-absorbing papers may serve as an experimental support of this statement.

The bird's environment is rich in UV surface colours both in the colouration of the birds themselves (Burkhardt, 1989), and in the colouration of such relevant objects as leaves, fruits, berries, and insects (Chen, Collins & Goldsmith, 1984; Loew & Lythgoe, 1985). This accounts for the demonstrated capacity to discriminate these colours in the visually guided behaviour of birds. Presence of a special type of UV-sensitive cone, necessary for this, was shown by electrophysiological methods in some related species of small passerines (Chen et al., 1984; Chen & Goldsmith, 1986).

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