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EARLY COLOUR DEPRIVATION IN THE PIGEON

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SUMMARY

When cats and monkeys are deprived of specific stimuli during an early sensitive period the development of their visual system is known to be affected. In pigeons, pattern discrimination learning has been shown to be affected by monocular deprivation [2]. Our study was set up to examine whether colour discrimination learning could be affected by colour deprivation. Young pigeons were reared under restricted colour illumination for at least 3 months after hatching so as to obtain a group bred under red illumination, one bred under blue illumination and a control group. After this period several psychophysical tests were used to test the pigeons' sense of colour. No significant difference was found between the 'deprived' birds and the controls. The spectral sensitivity, determined with the help of the ERG, did not differ for the three groups. We conclude that early colour deprivation does not affect visual development in the pigeon.

INTRODUCTION

One method that is frequently used to examine the development of the visual system is based on selective deprivation from visual stimuli during the first stages of neonatal life. In cats and monkeys the effects of various forms of deprivation have been studied, leading to the conclusion that, in many respects, the visual system is irreversibly determined during an early (sensitive) period [1, 6].

Monocular deprivation has also been studied in pigeons [2] and owls [5] leading to the conclusion that early monocular deprivation affects the visual systems of these birds. It is suggested that monocular deprivation affects visual discrimination and interocular transfer in pigeons by inducing an asymmetrical development of the deprived eye's retino-thalamo-hyperstriatal projections due to binocular competition in the Wulst [2].

Colour discrimination is a result of the way in which responses of the different receptor cells are integrated in the neural part of the visual system. Some neurons receive excitatory synapses from certain sorts of receptors and inhibitory synapses from other receptors. If one set of receptors is not stimulated during the development of the visual system, one can expect this to have an effect on the competition between the synapses of the different receptors for arborization sites on neurons throughout the visual system.

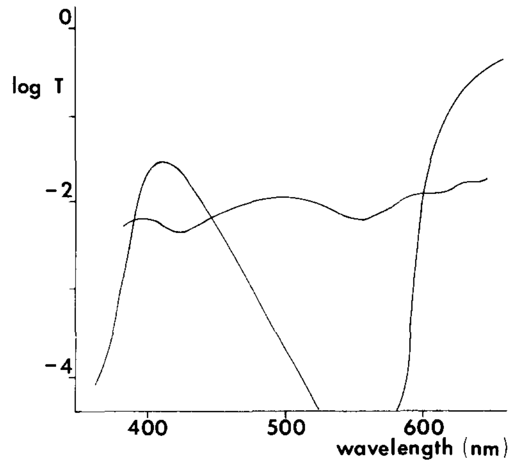
One of the advantages of using colour to examine visual development is that colour can be restricted relatively easily without any additional restrictions being imposed upon the experimental animals. Our hypothesis, therefore, was that selective colour stimulus deprivation would prevent the development of a normal sense of colour. Pigeons were chosen as the experimental animals, as they are known to have a well developed sense of colour based on the interactions of four types of cones [4].

GENERAL METHODS

Nine pairs of adult pigeons were distributed between three compartments of a pigeon-house provided with breeding accommodation. The ceiling of each compartment contained a glass window (60 × 120 cm) with filters to absorb large parts of the spectrum of the sunlight (Fig. 1). Human subjects could not distinguish between colours in the compartments used for deprivation even after their visual system had adapted; colour magazines looked black and white to them, although the light intensity was clearly photopic. With these arrangements we were able to obtain a group of nestling bred under red illumination, one bred under blue illumination and a control group. The young pigeons were kept in these compartments and were not allowed to see any other light for 3 months before the psychophysical training was started.

The training sessions were conducted in three computer-driven (Apple II) pieces of apparatus. Half an hour before their 30 min training session the pigeons were transported in dark cages to the room in which the training was to take place. This was to allow their visual system to adapt to the illumination of the training room (photopic illumination by indirect light from several 60 W tungsten light bulbs). The pigeons were not allowed access to food except during the half hour they spent in the training apparatus. Water and grit, however, were continuously available in the pigeon-house.

When in the training apparatus the pigeon was in a wire-mesh cube with



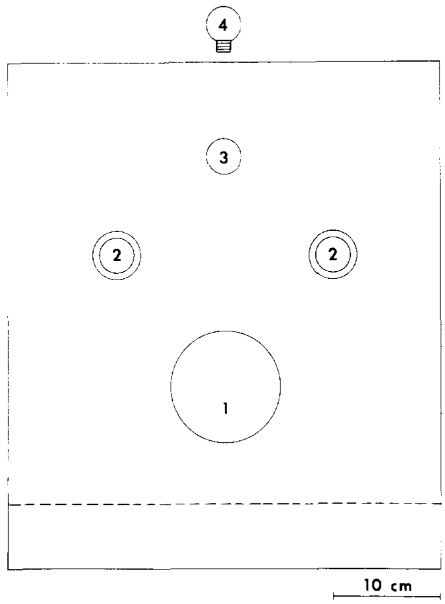


Fig. 1. Log spectral transmittance of the filters used for the breeding illumination.

Fig. 2. The front-panel of the training apparatus. Feeding unit (1), pecking keys (2), reference key (3) and lamp (4). The pigeon stands on a rubber mat at the level indicated by the dashed line.

sides of 40 cm, with one wooden panel (Fig. 2) containing two semi-transparent pecking keys (diameter, 3 cm), one on either side of an air-pressure-operated feeding unit (distance between keys, 20 cm). Various light stimuli provided by slides of various colour and intensity combinations (Fig. 3) were projected from behind on to the two pecking keys as well as on to a reference key above the feeding unit. The principle that the pigeons were supposed to learn was that they should choose the key of the same colour as the reference key. A correct choice was rewarded with 5–8 sec of access to grain. Following an incorrect choice a lamp above the apparatus was switched off and no stimulus was shown for 6–25 sec (depending on the stage in the training procedure). Each pigeon was first trained with black (dark) and white stimuli in order to make sure that it was capable of learning the above principle in our apparatus (see also refs. 8, 9).

After confronting the pigeons with the apparatus, the feeding system and the pecking keys, we taught them to look at the reference key by varying its illumination while the illumination of the other two keys remained constant. The training was then slowly elaborated and it continued until we were confident that the pigeons could respond adequately.

All 23 pigeons proved able to learn this task. They were, however, incapable of generalizing the task so the training procedure had to be repeated for the colour stimuli.

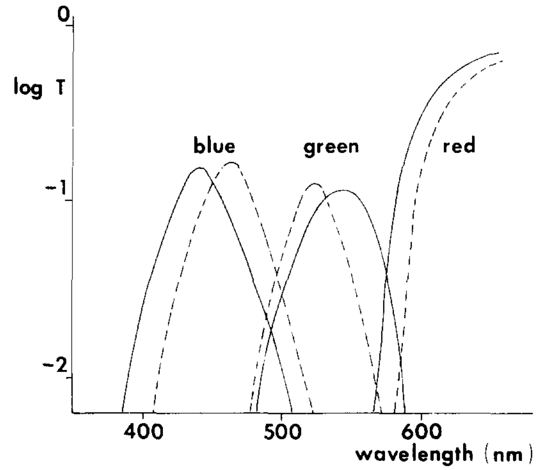


Fig. 3. Log spectral transmittance of the filters used for the stimuli of the psychophysical tests (arbitrary intensities). The dashed curves show the additional negative stimuli of the second and third experiments.

EXPERIMENT 1

Methods

The training was repeated for 13 of the pigeons (5 controls, 4 each from the other groups), using arbitrary (but clearly photopic) intensities of the three colours: red, green and blue (continuous curves in Fig. 3). Each set of stimuli consisted of one of these three colours as the positive stimulus (reference and one pecking key) and either of the other two colours as the negative stimulus (other key), all shown simultaneously. When the condition of over 80% correct choices on all (six) colour combinations was satisfied (total number of choices (n) > 100), the intensities of all stimuli except the reference stimuli were varied in large steps so that the pecking keys could be 0.9 D darker than, equal in intensity to, or 0.9 D brighter than the reference key. This was done in order to make sure that the pigeons were making the distinction on the basis of colour and not on the basis of intensity. Training was to be continued until the same condition was satisfied in tests with varying intensities.

Results

One pigeon of the group with the 'blue' experience learnt the initial problem in 58 sessions, and satisfied the criterion in tests with varying intensities in another 36 sessions. The rest of the pigeons did not learn the first step within 81–119 sessions. The large fluctuations in performance, even in the case in which the condition was satisfied, suggest that the task might have been too difficult. The tasks that pigeons were shown to be capable of learning in similar experimental situations [8, 9] differ from the task in our experiment in that in our experiment the pigeons did not trigger the appearance of the stimulus by pecking on the reference key. Also, the difference in either the configuration of the keys or just in the distance between the keys may affect the pigeons' performance. We observed that all the pigeons much more readily learnt the difference between red and one of the other colours than the difference between green and blue. This may be due to the fact that our 'green' stimulus had its maximum at the wavelength of a transition-point of pigeon 'colour-naming' experiments [8]. The pigeons proved capable of making the distinction (Experiments 2 and 3), but they may have had more difficulty in distinguishing between blue and green than between either of these and red because the 'blue' and the 'green' stimulus may be experienced by the pigeons as shades of the same 'colour', whereas they would experience the 'red' stimulus as a different 'colour'.

The fact that the pigeon that did learn the task is from the 'blue group' and not from the controls suggests that this form of colour deprivation did not restrict colour vision acquisition.

EXPERIMENT 2

Methods

The other 10 pigeons (4 controls, 3 each from the other two groups) were trained in the same apparatus, but the reference colour remained constant, so they had to learn to peck at only one colour. After the pigeon was trained with a stimulus of an arbitrary intensity, the intensities were varied as in Experiment 1. When the pigeon scored above 90% with either of the other two colours as the negative stimulus ($n > 100$), a new negative stimulus (dashed curve closest to the positive stimulus in Fig. 3) was introduced in approximately a third of the stimulus combinations, with the same variations in intensity. If the pigeon scored over 80% on the comparison between the positive stimulus and the corresponding negative stimulus in three consecutive sessions ($n > 100$), the distinction between the two stimuli was accepted as being within its visual capacity. A difference of approximately 20 nm between the peaks of the two filters was chosen as this was shown to be well above the threshold of wavelength discrimination at the wavelengths used in our experiments [3]. The procedure was repeated for each pigeon for all three colours.

Results

In this experiment, all pigeons met the criterion on all three colours, a task that a mildly red/green deficient (protanope) human subject (J.P.S.) was incapable of performing. The number of sessions required for meeting the criterion (minimum of 3) is shown in Fig. 4. *t*-Tests were used to examine whether there was a significant difference in the learning rate of the groups. The null-hypothesis of no difference in learning rate was rejected if the test showed an under 5% chance that the learning rate was unaffected. There was a clear difference in the number of sessions the pigeons needed to meet the criterion for the different colours, but for each colour no significant difference was found between the deprived groups and the controls. The 'blue group', however, did learn the distinction between the blue stimuli significantly faster than the 'red group' (t = 4.90, df = 4).

EXPERIMENT 3

Methods

The pigeons of Experiment 1 (4 of each group) were later trained in the same apparatus, but with only one pecking key visible. The colours used were the same as in Experiment 2, but the task was a 'go–no go' problem. The pigeons had to learn to peck at the key only if the appropriate stimulus was shown. This process was continued until three pigeons from each breeding group had been trained with each colour.

Results

The results are shown in Fig. 5. The 'blue group' did take significantly longer to distinguish between the red stimuli than did the controls (t = 2.84, df = 4). However, no other significant breeding-group differences were found.

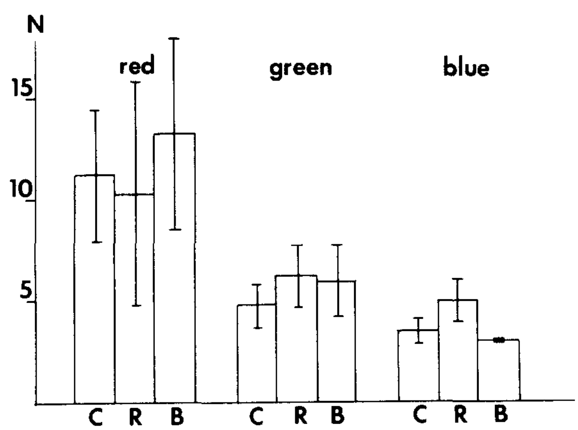
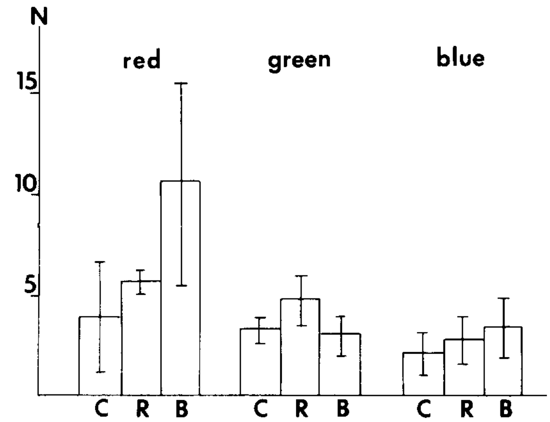


Fig. 4. Mean number of sessions (N) required for satisfying the criterion for each of the three colours in Experiment 2 (with standard deviations) for the three groups with different early colour experience (C, controls (n = 4); R, red group (n = 3); and B, blue group (n = 3)).



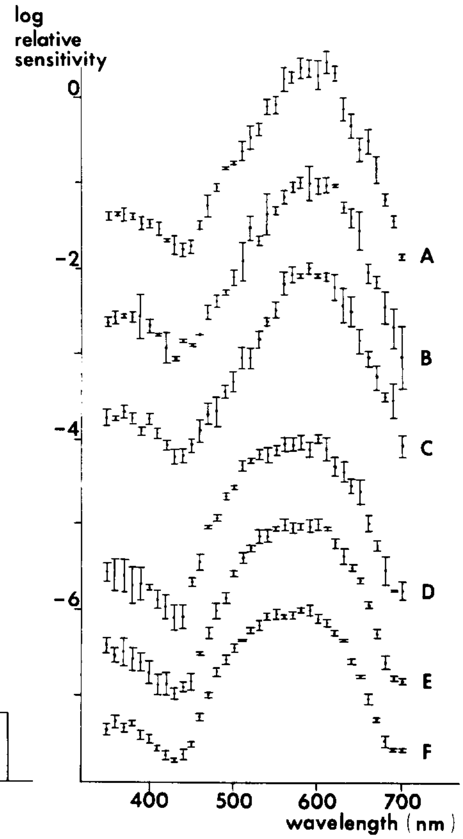


Fig. 5. Mean number of sessions (n) required for satisfying the criterion for each of the three colours in Experiment 3 (with standard deviations) for the three groups with different early colour experience (C, controls (n = 3); R, red group (n = 3); and B, blue group (n = 3)).

Fig. 6. Relative spectral sensitivity of the pigeons with different breeding conditions. Red retinal fields of the blue group (n = 3), of the red group (n = 2) and of the controls (n = 4) are denoted as A, B and C, respectively. The yellow retinal fields of the blue group (n = 4), of the red group (n = 4) and of the controls (n = 5) are denoted as D, E and F, respectively.

Spectral sensitivity

Heterochromatic flicker photometry based on ERG responses was used to obtain spectral sensitivity curves of the yellow as well as the red fields of the retinas of several anaesthetized pigeons of the different groups. A monochromatic test light was alternated with a constant reference light with a frequency of 30 Hz. At each wavelength the intensity of the test light was determined which gave a minimal amplitude of the ERG. The relative spectral sensitivity is proportional to the inverse of the number of test light quanta (for a more detailed description of the method used see ref. 7). The results are shown in Fig. 6. Here too, no difference was found between the groups with different early experience.

DISCUSSION

The experiments show that all pigeons developed a normal sense of colour. This means that our hypothesis has to be rejected: apparently selective colour stimulus deprivation during the first three months does not affect the colour discrimination learning capacity of pigeons. The differences in learning rate suggest that the pigeons learn slightly faster if they have experience with that colour. The individual differences between the pigeons are, however, also very large (Fig. 4, 5), so a conclusion of this kind must be regarded with some caution.

The ERG-data show that the spectral sensitivity of the retina was not affected by the deprivation. This implies that the deprivation did not influence the development of the photoreceptors, as the spectral sensitivity, as measured with a high flicker frequency, is considered to be the sum of the sensitivities of the various receptors. From the psychophysical data it was evident that the capacity to discriminate between colours was also unaffected.

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