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RESEARCH NOTE

EARLY COLOUR DEPRIVATION IN A MONKEY (*MACACA FASCICULARIS*)

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Abstract—Various forms of selective visual deprivation are known to affect the development of the monkey visual system. In the present study a monkey was born and spent the first three months of its life under red illumination. Despite this colour deprivation, the young monkey learnt to distinguish between colours. Furthermore, the monkeys' increment threshold spectral sensitivity was not affected by the deprivation.

Development Colour vision Monkey Deprivation Spectral sensitivity

INTRODUCTION

The fovea of the newborn human infant is morphologically immature (Abramov *et al.*, 1982) and colour discrimination still has to develop during the first months of post-natal life (Hamer *et al.*, 1982). Young infants' failure to discriminate between colours are considered to be immaturities of neural processing rather than anomalies of the cones themselves (Hamer *et al.*, 1982). Although the way in which various forms of selective visual deprivation affect the development of the visual cortex is being studied extensively (for a review see Movshon and Van Sluyters, 1981), possible influences on the development of the retina are often neglected. An exception is a behavioural study in which the right eyelids of three (1-month-old) rhesus monkeys were surgically closed for various periods of time (Harwerth *et al.*, 1981). It was observed that the scotopic mechanism appeared to determine the increment-threshold spectral sensitivity of the deprived eye for a large range of light adaptation at which photopic mechanisms determined the sensitivity of the "normal" eye. The abnormalities found in the deprived eye were attributed to processes within the retina. In another study, however, a macaque was shown to have trichromatic colour vision although it was raised in continuous darkness from 2 weeks after birth until it was 3-months-old (Boothe *et al.*, 1975). Selective deprivation, however, is often known to influence visual development to a much greater extent than total visual deprivation (Movshon and Van Sluyters, 1981).

Selective colour deprivation has two advantages when compared to most other forms of visual deprivation. First of all it can be "non-invasive", so that the results are not confounded by effects of the deprivation procedure on sensory-motor development (Held, 1965). This is particularly relevant since it has been shown that modifications in the development of the kitten visual cortex due to selective visual deprivation depend on feed-back information about eye position and motility via the proprioceptive signals from extraocular muscles (Buisseret and Singer, 1983). The second advantage is that the interactions between the cone systems in primate colour vision are relatively well known, so that any effect of the deprivation may immediately indicate a mechanism by which the environment influences the synaptic connections established during early development.

We have previously reported that early colour deprivation in pigeons did not change either their spectral sensitivity or their capacity to discriminate between colours (Brenner *et al.*, 1983). However, the mechanisms underlying their colour vision are quite different from those of primates, so that we could not conclude that a similar deprivation would not affect a monkeys' colour vision. The crab-eating monkey, *Macaca fascicularis*, appears to be a good model for normal human colour vision: these monkeys partition the spectrum into the same four basic hue categories that humans do (Sandell *et al.*, 1979), and the microspectrophotometric data for their photoreceptors can be used to reconstruct human psychophysically determined cone sensitivities (Bowmaker *et al.*, 1980).

A female monkey (*Macaca fascicularis*) was born and spent the first 3 months of its life under red illumination. The young monkey (Femke) was kept together with her mother (Leonie) in a room that was well lit by four red lamps. The lamps (Philips TL 40 W/15, $\lambda_{max} = 654$ nm, half band width of approximately 20 nm) gave red light in which human observers could not distinguish between colours even after several hours of adaptation. In the "night" (20.00–8.00) one red "darkroom" lamp (Philips PF 712 B 15 W, cutoff wavelength at half height at about 655 nm) gave a very low level of illumination. Another monkey should have given birth at about the same time in a room lit by "normal" fluorescent lamps, but as it had a miscarriage we decided to use Leonie as the control. When Femke was 3-months-old the four red lamps were replaced by "daylight" fluorescent lamps (Philips TL 40 W/47). Leonie was so eager to "play" with us that Femke never had a chance to interfere while she was being tested. Femke was tested in a small cage that remained attached to the home cage. She entered this cage through an opening that was too small for her mother.

When Femke was 5-months-old we tested whether she could distinguish between objects on the basis of differences in their colour. Using artificial food colouring we made red, yellow, green and blue jelly puddings. Sugar was added to the green puddings and salt to the others. After an initial learning phase the monkeys' first choice was observed when presented with various combinations of puddings of the four colours. By the colour we obviously only refer to our subjective experience. The puddings' actual spectral absorption curves are very irregular and cover all of the visible spectrum. A combination of brightness and saturation of the colour was varied considerably between presentations by changing the amount of food colouring independently for each pudding, making it practically impossible to choose the correct pudding only on the basis of brightness. Even more so since the puddings were of very irregular shapes and sizes. The mother selected the green pudding without difficulty (150 correct out of 150 trials). A human deuteranope also had no difficulty in selecting the green pudding under the same conditions. Although Femke did learn to take the green pudding, she often chose the blue pudding, tasted it, and then threw it away. She chose the yellow pudding three times, all during one session of eleven presentations, and never chose a red pudding (164 green, 33 blue and 3 yellow in 200 trials). The fact that Femke never took a red pudding but quite often took a blue one suggests that the task itself is not too difficult but that the deprivation has affected her colour vision. We cannot, however, exclude the possibility that the mistakes are due to the young monkeys' age and "playfulness", or to its lack of experience with colours.

About a year later the monkeys' relative spectral sensitivities were determined. The "increment-threshold" method was used as it reveals the interactions between the cone systems (Sperling and Harwerth, 1971). The procedure was as follows: a circle of light (2.5 cm diameter) was projected onto one of two semi-transparent (white, 8 cm diameter) plastic keys, which were part of a white panel that was attached to the wiring of the monkeys' cage (illumination of the panel was approximately 17 lx). The monkeys' heads were generally about 15 cm from the keys during stimulation. The monkey was rewarded with apple juice (and similar beverages) if it pressed the illuminated key. After either of the keys was pressed the stimulus was "off" for several seconds before a new stimulus appeared. We used Balzers interference filters (B-40, with half band widths between 7 and 13 nm) to produce stimuli of different spectral compositions (colours). The stimulus intensity was calculated from the absorbances of the neutral-density filters (see below) and of the plastic keys at each wavelength, and direct measurements (with a calibrated selenium cell) of the relative radiant quantum flux of the beam that illuminated the key for each colour filter. In each session one colour was tested and each colour was tested in three separate sessions. Each session was started at a clearly visible intensity. Once the monkey made ten consecutive correct responses (criterion), the intensity of the light was reduced by adding neutral density filters (in steps of about 0.1 density, depending on the filters' actual value at that wavelength). If the monkey made ten incorrect choices before reaching the criterion, the previous intensity was taken to be the threshold. The lowest of the three threshold values for each colour is shown in Fig. 1.

The two monkeys' sensitivity curves are quite similar (they have been separated vertically for clarity), which implies that stimulating one class of cones to a much greater extent than the others does not prevent the development of "normal" interactions between the pathways of the different classes of cones (although selectively stimulating one eye did prevent this development in the closed eye; Harwerth *et al.*, 1981). At one and a half years of age Femke is just

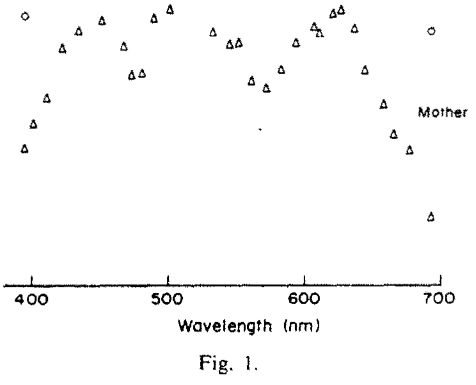

Fig. 1.

as sensitive as her mother in the blue-green range, although her "blue" and "green" (S and M) cones were not stimulated functionally (i.e. in a way that enables human colour vision) during the first three months of her life. Her "blue" cones were probably not stimulated by light at all during this period.

Since the procedure we used to determine the spectral sensitivity is not neccessarily based on a distinction on the basis of colour, the next step will be to critically test Femkes' sense of colour. The deprivation may have permanently affected Femkes' vision of "natural" colours (Zeki, 1983) without affecting her spectral sensitivity. However, although that would explain why she often chose the blue puddings, we must keep in mind that she did so two months after the deprivation was terminated. Femkes' colour vision could have been affected at that time, but have recovered completely since then. If so we may not find any effects in following experiments. We are not too worried about this, however, since we are interested in finding out to what extent sensory experience directs the normal development of the visual system, rather than in studying the effects of disuse due to prolonged sensory deprivation. A clear example of abnormal development due to selectively limited experience is the permanent shift in ocular dominance which occurs even after very short periods of monocular deprivation. As macaques (macaca nemestrina) have been shown to have trichromatic colour vision by two months of age (Boothe *et al.*, 1975), we think that a 3 month deprivation period should certainly be adequate for studying the organizing effects of experience on the development of colour vision.

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