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Development of the Brain Depends on the Visual Environment

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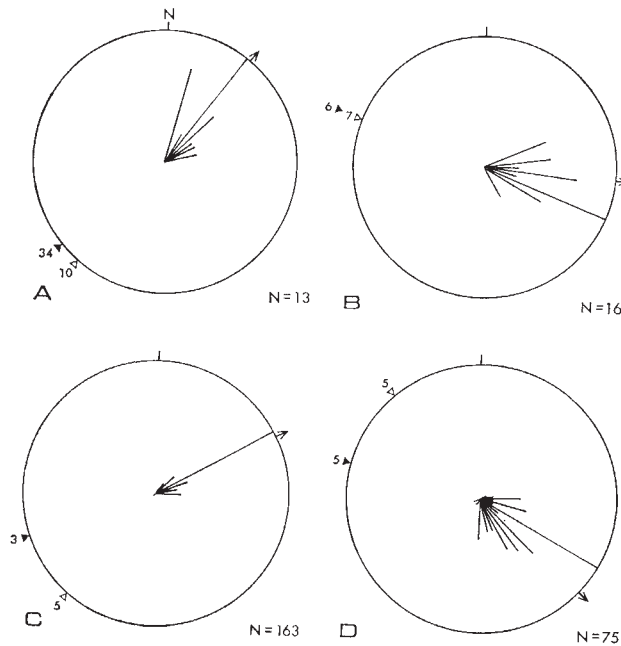


Fig. 3. Diagrams showing bird directions on two nights when winds shifted. May 10-11: A, 0240-0252 GMT; B, 0620-0645; September 22-23: C, 0120-0135; D, 0615-0645. Vector diagrams are plotted so that the radius equals the greatest number of birds in any 7.5° sector. The arrowhead is the mean direction, and the open and solid triangles represent surface and 305 m winds, respectively.

of migrants that the authors concentrated more on discrete dot echoes than on the dense pattern of fine echoes attributed to songbirds^{1,16,17}. This practice has probably resulted in the selection of larger birds, flocks of birds and birds at higher altitudes. Furthermore, most radars give an inadequate representation of the migration at low altitudes (below 700 m) where most passerines fly⁸. Although our data show that small passerine nocturnal migrants often do not compensate for wind drift, preliminary results indicate that ducks, geese and shorebirds can do so at night when unfavourable winds are light to moderate. These findings support Pennycuik's assertion that crosswinds of moderate strength deflect slow birds through a large angle, but have less effect on faster birds. In general, the slower (and thus smaller) the bird, the more it is affected by unfavourable winds¹⁸. Our finding that songbird migrants often fly downwind regardless of the direction of the wind in the southern United States accounts for such phenomena as reversed migrations (a general movement in the direction opposite to that normal for the season) and the appearance of migrants far from their normal migration routes. The importance of proposed stellar orientation mechanisms must be re-evaluated in light of the influence of wind direction on the direction of nocturnal passerine migration.

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S. A. GAUTHREAUX, jun.*
K. P. ABLE

Department of Zoology,
University of Georgia.

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* Present address: Zoology Section, Division of Biology, Clemson University.

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Development of the Brain depends on the Visual Environment

In a normal cat, neurones of the visual cortex are selective for the orientation of lines and edges in the visual field, and the preferred orientations of different cells are distributed all around the clock¹. Hirsch and Spinelli² have recently reported that early visual experience can change this organization. They reared kittens with one eye viewing vertical stripes, the other horizontal, and found that out of twenty-one neurones with elongated receptive fields all were monocularly driven, and in all but one case the orientation of the receptive field closely matched the pattern experienced by that eye.

We began a related project about a year ago and this is a preliminary report of our results. Our approach was rather different from that of the group at Stanford. We allowed our kittens normal binocular vision in an environment consisting entirely of horizontal or vertical stripes. The kittens were housed from birth in a completely dark room, but from the age of 2 weeks they were put into a special apparatus for an average of about 5 h each day. The kitten stood on a clear glass platform inside a tall cylinder the entire inner surface of which was covered with high-contrast black-and-white stripes, either horizontal or vertical (Fig. 1). There were no corners to its environment, no edges to its floor and the upper and lower limits to its world of stripes were a long way away. It could not even see its own body, for it wore a wide black collar³ that restricted its visual field to a width of about 130°. The kittens did not seem upset by the monotony of their surroundings and they sat for long periods inspecting the walls of the tube.

We stopped this routine when the kittens were 5 months old, well beyond the "critical period" in which total visual deprivation causes physiological deficits⁴. From that time the cats were taken for several hours each week from their dark cage to a small, well-lit room, furnished with chairs and tables, where we watched their visual reactions.

At first they were visually extremely inept, whether they had been exposed to vertical or horizontal stripes. Their pupillary reflexes were normal but they showed no visual placing when brought up to a table top and no startle response when an object was thrust towards them. They guided themselves mainly by touch and were frightened when they reached the edge of the surface they were standing on. But they quickly recovered from many of these deficiencies, which were probably visuomotor problems of the kind that Held and Hein described⁵. Within a total of about 10 h of normal vision they showed startle responses and visual placing, and would jump with ease from a chair to the floor.

On the other hand, some of their defects were permanent. They always followed moving objects with very clumsy, jerky head movements and they often tried to touch things moving on the other side of the room, well beyond their reach. Perhaps most telling of all, despite their

active, and as time went on increasingly frenzied, visual exploration of the room, they often bumped into table legs as they scurried around.

There were, moreover, differences between cats reared in horizontal and vertical environments. They were virtually blind for contours perpendicular to the orientation they had experienced. They showed no startle response for an approaching 'Perspex' ('Plexiglas') sheet covered with black stripes, nor would they visually place on such a pattern, if the stripes were of the inappropriate orientation. The differences were most marked when two kittens, one horizontally and the other vertically experienced, were tested simultaneously with a long black or white rod. If this was held vertically and shaken, the one cat would follow it, run to it and play with it. Now if it was held horizontally the other cat was attracted and its fellow completely ignored it.

We moved on from behavioural studies to neurophysiology when the cats were 7-5 months old. They were anaesthetized with nitrous oxide and paralysed with succinyl choline while we recorded from single neurones in the primary visual cortex, using sodium chloride filled micropipettes. The refractive states of the eyes was corrected with contact lenses, spectacle lenses and 3 mm artificial pupils. There was no evidence of severe astigmatism, which might have explained our behavioural findings.

We used thin bright slits or edges to plot receptive fields on a screen 114 cm from the cat. The luminance of the background was about 5 cd. m⁻² and of the bright target about 17 cd. m⁻². Our initial procedure was to make one long penetration deep into the medial edge

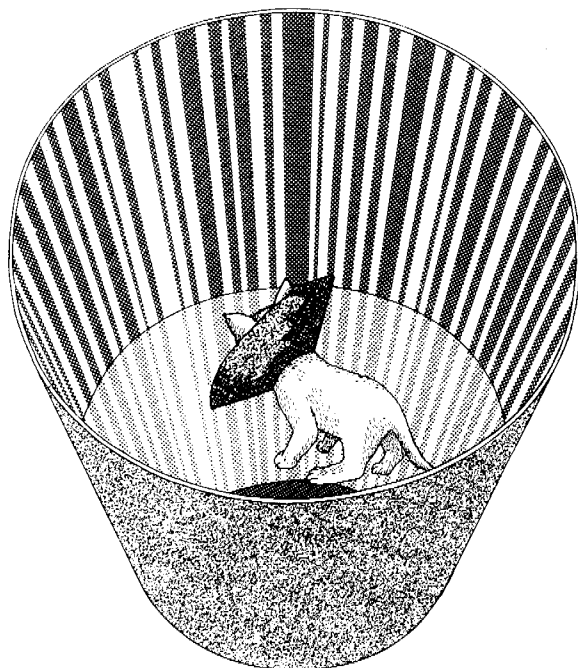


Fig. 1. The visual display consisted of an upright plastic tube, about 2 m high, with an internal diameter of 46 cm. The kitten, wearing a black ruff to mask its body from its eyes, stood on a glass plate supported in the middle of the cylinder. The stripes on the walls were illuminated from above by a spotlight. The luminance of the dark bars was about 10 cd. m⁻² and of the bright stripes about 130 cd. m⁻²; they were of several different widths. For this diagram the top cover and the spotlight have been removed from the tube.

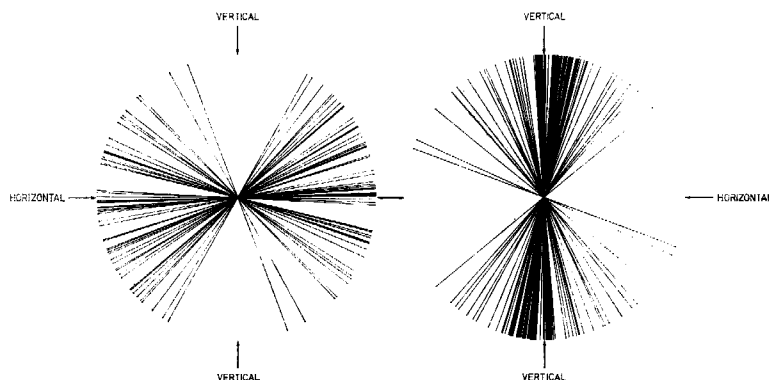


Fig. 2. These polar histograms show the distributions of optimal orientations for fifty-two neurones from a horizontally experienced cat on the left, and seventy-two from a vertically experienced cat on the right. The slight torsion of the eyes, caused by the relaxant drug, was assessed by photographing the pupils before and after anaesthesia and paralysis. A correction has been applied for torsion, so the polar plots are properly orientated for the cats' visual fields. Each line shows the optimal orientation for a single neurone. For each binocular cell the line is drawn at the mean of the estimates of optimal orientation in the two eyes. No units have been disregarded except for one with a concentric receptive field and hence no orientational selectivity.

of the post lateral gyrus, studying every single neurone encountered. We found units on the average about 80 μ m apart, so presumably our electrode was not specially selective for the cells from which it recorded. After the long penetration we moved the electrode to other positions in area 17 and sampled just a few neurones at each place. Our exploration thus covered many cortical columns¹ and quite a large area of the visual field around the area centralis.

So far we have studied 125 neurones from two cats, one horizontally, the other vertically experienced. Of all these units, only one did not have distinct orientation selectivity and it had the action potential waveform and concentric, monocular receptive field of a projection fibre from the lateral geniculate body. About 75 per cent of cells, in both cats, were clearly binocular and in almost every way the responses were like those in a normal animal. The distributions of preferred orientation, however, were totally abnormal (Fig. 2). Not one neurone had its optimal orientation within 20° of the inappropriate axis and there were, *in toto*, only twelve within 45° of it. This anisotropy is highly significant ($P < 0.00001$; chi-squared test).

Evidently the visual experience of these animals in early life has modified their brains, and there are profound perceptual consequences. But we do not think that there is merely passive degeneration of certain cortical neurones because of under-activity. For we did not notice any obvious large regions of "silent" cortex, corresponding to the "missing" cortical columns. It seems instead that the visual cortex may adjust itself during maturation to the nature of its visual experience. Cells may even change their preferred orientation towards that of the commonest type of stimulus; so perhaps the nervous system adapts to match the probability of occurrence of features in its visual input.

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COLIN BLAKEMORE
GRAHAM F. COOPER

The Physiological Laboratory,
University of Cambridge,
Cambridge CB2 3EG.

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