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**The Role of Early Experience in the Development and  
Maintenance of Orientation Selectivity in the Cat's  
Visual Cortex: M. Stryker**

The role that early visual experience plays in the development of the selective response properties of cells in the visual cortex has been investigated extensively. Two prominent organizing properties of the visual cortex are the selectivity of the cells for the orientation of a bar or edge in visual stimulus and the propensity of the cells to respond to stimuli presented through one eye or the other (Hubel and Wiesel, 1974a,b, and Hubel, above, "Architecture of the Monkey Striate Cortex"). A discussion of the role of early visual experience in determining the eye preference of cortical cells is presented elsewhere (Hubel et al., 1976, 1977a; Wiesel, above, "Effects of Visual Deprivation on

Macaque Monkey Striate Cortex"). Stryker's report concerned the selectivity of cortical cells for edge orientation, offering an interpretation of experimental findings on the role of visual experience in the development and maintenance of this selectivity.

The most obvious experiment on the role of early experience is to examine cells of the visual cortex before the animal has acquired any visual experience. If the kinds of selectivity found in the adult animal are present, then experience is not required for their normal development. For the monkey the results of this experiment gave a conclusive answer: The cells of the newborn monkey's visual cortex responded with selectivity indistinguishable from that of the adult for the orientation of a bar or edge visual pattern (Wiesel and Hubel, 1974). Furthermore, the orderly arrangement of cells in the cortex according to preferred orientation was also present in the newborn monkey (see Wiesel, above). Hence visual experience is not necessary to guide or otherwise promote the establishment of the neural connections underlying the orientation-selective response properties that are evident in the adult visual cortex. However, this experiment leaves open questions regarding the extent to which these connections may remain plastic or modifiable by visual experience.

The cat is born with its visual system in a more immature state than that of the monkey; for the first week or more its eyes remain closed, and its originally cloudy optic media do not allow a clear image to be focused on the retina until the animal is 2 to 3 weeks of age (Thorn et al., 1976). It might be thought that this later development of the visual system would allow a greater role for early visual experience in the cat's normal development than was found for the monkey; but the immaturity of the optical parts of the young kitten's visual system and the generally fragile condition of these animals make the most obvious experiment, examining the kitten before visual experience is normally acquired, difficult to perform and interpret. An alternative experiment is to allow the kitten to grow until it is several months old while deprived of visual experience by being reared in darkness or with sutured eyelids. This experiment, though easier to perform, gave a clear result but an equivocal answer to our question. Most of the cells studied in such animals were found not to be selective for orientation; rather they were unresponsive or very poorly responsive to visual stimuli (Wiesel and Hubel, 1965b; Cynader et al., 1976). It was not clear from these results whether the cells had failed to develop normal selectivity or whether an original innate selectivity had deteriorated as a consequence of this long period of deprivation. Visual experience was neces-

sary, but whether to maintain an innate selectivity or to guide the development of selectivity was unresolved.

Thus, the experiment of looking at the very young, visually inexperienced animal required interpretation. Hubel and Wiesel (1963a) published the results of the first such experiment. Among the cells studied, they found examples of both simple and complex receptive fields with orientation selectivity. Some of the other cells responded abnormally, but this could have been due to abnormal recording conditions or poor optics. Barlow and Pettigrew (1971; Pettigrew, 1974), disputed these findings. In a group of visually inexperienced animals they studied, almost none of the cells showed selectivity for stimulus orientation. These findings were lent additional weight through the use of quantitative methods. For some cells, the investigators counted the number of spikes evoked by stimuli of different shapes and orientations and made graphs showing response as a function of stimulus orientation. Shortly thereafter, other workers reported similar results (Blakemore and Mitchell, 1973; Imbert and Buisseret, 1975).

An experiment on the role of specific kinds of early experience in the development of the visual cortex was reported at about the same time. Hirsch and Spinelli (1970, 1971) raised kittens with extremely restricted visual experience. Kittens wore opaque goggles whenever they were not in total darkness. Within the goggles, each eye of the kittens could see stripes of only one orientation, horizontal for one eye and vertical for the other eye. Hirsch and Spinelli studied the visual cortex of these animals using a novel automated method, the findings of which are somewhat difficult to relate to those of conventional receptive field plotting by hand. They found, however, that two-thirds of the cells studied did not appear to be selective for stimulus orientation. Most of the remaining selective cells were monocularly driven and responded optimally to the orientation to which the effective eye had been exposed. Two possible interpretations were offered for these results: (1) cells in the visual cortex were programmed to develop a preferred orientation according to the prominent features of the early visual environment (under this interpretation no particular explanation is offered for the two-thirds of the cells not selective for orientation); or (2) only the cells that received appropriate stimulation early in life could maintain their innate orientation selectivity; cells not stimulated at their innate, preferred orientation became unresponsive or nonselective.

The finding of Hubel and Wiesel (1963b) that many or most cells had an innate, preferred orientation, together with the results of many workers (Hubel and Wiesel, 1965; Cynader et al., 1976) that com-

plete pattern deprivation early in life causes most cells of the cortex to lose selectivity for orientation, favored the second alternative above. The work of Barlow and Pettigrew (1971) and other similar reports (Blakemore and Mitchell, 1973; Pettigrew, 1974; Imbert and Buisseret, 1975) favored the first alternative, that cortical cells may be programmed during normal development to acquire selectivity for the redundant features of the early visual environment.

Reports by Blakemore and co-workers (Blakemore and Cooper, 1970; Blakemore and Mitchell, 1973; Blakemore, 1974) supported the first alternative. They raised kittens with a somewhat less severe but perhaps more natural restriction of early visual experience by allowing them to see only when standing on a glass plate inside a vertically or horizontally striped drum and wearing a ruff collar that obscured view of the body. Most cortical cells studied were selective for orientations similar to that to which the kittens had been exposed. These workers did not note the presence of large numbers of unresponsive or non-selective cells. Thus, these results suggested that all cortical cells can develop selectivity for the orientations present in early visual experience and that, if they have any innate selectivity, this must be modifiable.

Barlow (1975 and this Work Session) offered an analogy between this second alternative scheme for cortical development and the phenomenon of imprinting in birds: Because of the difficulty of innately specifying the exact appearance of its mother, a baby duckling does not receive this information innately. Instead, it is innately programmed to follow and treat as its mother the most prominent large, noisy, moving object it encounters after hatching, allowing it the opportunity to learn its mother's appearance gradually, through experience. It was proposed that in a similar fashion the innate developmental program for the visual cortex might not be sufficiently detailed to specify the preferred orientation for each cell. Instead, each cell (or column of cells) might be programmed to use early visual experience with oriented edges to reinforce initially unspecified and random response biases. Thus it was proposed that just as all ducklings can be imprinted by a beach ball if their early experience is restricted to beach balls, so might all cortical cells become selective for the vertical orientation if early experience were restricted to vertical stripes rather than to a normal environment rich in orientations. This analogy incorporates an attractive teleological explanation for why orientation selectivity in the visual cortex should be modifiable by early experience.

Any abnormal physiological state associated with the trauma of microelectrode recording might conceivably cause innately selective

cells in the fragile cortex of young kittens to respond nonselectively, whereas it seems unlikely that cells might appear to respond selectively when they were in fact innately nonselective. Hence the reports showing no orientation selectivity in visually inexperienced kittens (Barlow and Pettigrew, 1971; Pettigrew, 1974) were not entirely persuasive when compared with the report of selectivity in such animals (Hubel and Wiesel, 1963a), even though the former studies used quantitative methods to study some cells. For this reason, Sherk and Stryker (1976) investigated the orientation selectivity of cells in visually inexperienced kittens using an automated, quantitative procedure for assessment of each cell encountered. One of their findings (shown in Figure 71) is from a kitten that had been dark-reared from birth except for a brief

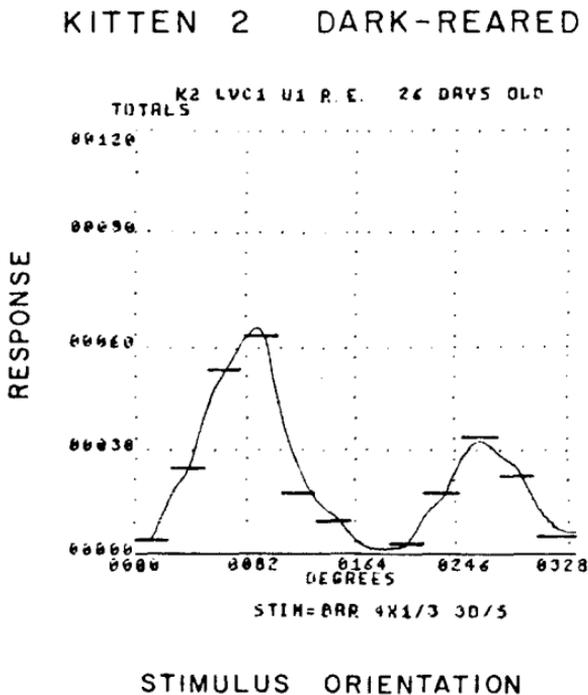


Figure 71. Photograph of orientation tuning histogram displayed on CRT screen for the first cell recorded in a 26-day-old dark-reared kitten. The kitten's eyes were opened for the first time immediately prior to compiling this histogram. Total number of spikes (*ordinate*) are plotted as a function of stimulus orientation (*abscissa*); stimulus was a bar of light that swept across the receptive field. Each of the 12 stimulus orientations tested appeared a total of five times, in random order except that no presentation of any one orientation was repeated more than twice in a row.  $0^\circ$  on the abscissa represents a vertical bar moving from right to left;  $90^\circ$  represents a horizontal bar moving down;  $180^\circ$  represents a vertical bar moving from left to right, etc. [Stryker]

period prior to the time of eye opening when its eyelids were sutured shut. At 3½ weeks of age, the kitten was removed from the dark and prepared for microelectrode recordings; its eyelids were opened less than 2 min prior to compiling the histogram illustrated. The selectivity shown by such a cell is unlikely to be due to only 2 min of visual experience. Most (more than 80%) of the cells in these visually inexperienced animals were selective for the orientation of a moving bar or edge stimulus. In addition, preferred orientation changed gradually and progressively across the cortical surface as the electrode moved from cell to cell. This arrangement of the cells in the cortex according to preferred orientation, characteristic of the adult animal, was striking in these visually inexperienced kittens. There are other reports of varying but considerable proportions of cells in similarly visually inexperienced kittens showing selectivity for orientation (Blakemore and Van Sluyters, 1974), confirming the earliest finding that, for many or most of the cells in the cat's visual cortex, orientation selectivity is innate (Hubel and Wiesel, 1963a).

If orientation selectivity is innate, the experiments on kittens reared in striped drums suggested that it must also be modifiable by visual experience (Blakemore, 1974). Stryker and Sherk (1975) repeated these experiments using a similar rearing procedure but different recording techniques. Employing a systematic sampling technique designed to examine the distribution of orientation preference across wide areas of the cortical surface, together with an automated assessment of preferred orientation for each cell studied and a blind procedure to guard against the effects of inadvertent experimenter bias, they did not find a biased distribution of preferred orientations in the visual cortex of the kittens. Instead, these kittens were like normal animals, with all orientations represented in the visual cortex and with preferred orientation changing gradually and progressively across the cortical surface. This finding is perhaps not surprising because the rearing procedure does not completely restrict kittens' visual experience to the orientation of the stripes within the drum. The animals may sometimes turn their heads from side to side or look up and down; and when they do this, the stripes may appear at many different orientations on their retina.

Fitting kittens with striped goggles does restrict their visual experience almost completely to contours of just one orientation (Hirsch and Spinelli, 1970, 1971). The recording techniques described above (Stryker and Sherk, 1975), from which the findings are closely comparable to those of conventional hand-plotting of receptive fields, were

able to demonstrate the main effects reported in such kittens. When the goggles showed horizontal stripes to one eye and vertical stripes to the other, most of the cells became quite abnormal in that they were unresponsive or nonselective for orientation (Stryker and Sherk, 1975). Most of the remaining selective cells had preferred orientations near horizontal or vertical and were monocularly driven by the eye whose early experience was nearer the cell's preferred orientation.

These results may be explained by theorizing that the role of early experience is only to maintain the responsiveness and selectivity of cells, each of which already has an innate selectivity for a particular orientation. The results would come about as follows: Cells whose innate preferred orientations were oblique would not be stimulated by the pattern shown to either eye. These cells would effectively be binocularly deprived, somewhat like all cells in cats raised in the dark or with both eyelids sutured shut. In these latter circumstances, it is known that most of the cells would lose their responsiveness or selectivity (Hubel and Wiesel, 1965; Cynader et al., 1976). For the cells whose innate, preferred orientations were near horizontal or vertical, a different known mechanism, similar to that of monocular deprivation, would come into play. The eye that experienced vertical would tend to take over all the cells whose preferred orientations were near vertical because these cells, like all the cells in the cortex of a monocularly eyelid-sutured cat, are stimulated by only one eye. The same mechanism would cause the cells whose preferred orientations were near horizontal to come to be driven exclusively by the eye that had seen horizontal stripes in early life. Such an orientation-selective shift in eye dominance is known both in the cat (Cynader and Chernenko, 1976\*) and in the monkey (Wiesel, 1977): When animals were reared viewing vertical stripes through one eye and either all orientations (in the cat) or nothing (in the monkey) through the other eye, cells selective for the orientations seen by both eyes or by neither eye were shared equally between the two eyes, while most of the cells selective for the orientation seen by only one eye were taken over by that eye. Thus, for the cats discussed above reared with one eye viewing horizontal and the other eye viewing vertical, mechanisms like those of two known phenomena, the one similar to that of binocular deprivation for the cells preferring obliques, and the other similar to that of monocular deprivation for the cells preferring horizontal or vertical, together account for the results obtained. There is no need to postulate some unknown new

\* Also, personal communication.

mechanism by which the preferred orientation of a cortical cell can be modified by experience.

Other recent results are also consistent with the theory that the role of early visual experience is only to maintain the responsiveness and selectivity of cells already selective for an innately preferred orientation. When kittens are reared wearing striped goggles that show the same orientation to both eyes, the theory would predict that a larger fraction of the cells should effectively be binocularly deprived, and hence become unresponsive or nonselective, than was the case when the goggles showed different orientations to the two eyes. This prediction has recently been confirmed.\* Blasdel, Mitchell, Muir, and Pettigrew (1977) raised kittens that were allowed their only visual experience while their heads were fixed in place within a striped drum so as to restrict visual experience in a manner intermediate in severity and effectiveness between having the kittens wear striped goggles and allowing them to walk around in the striped drum. Almost a third of the cells studied were not selective for orientation, and among the remaining selective cells there was a bias toward the orientation to which the animal had been exposed. These results are completely consistent with those above, if the nonselective cells are assumed to be those whose original innately preferred orientations were different from the orientation prominent in the animals' early visual experience.

Other theories proposing more elaborate roles for early visual experience than mere maintenance of innate selectivity, i.e., that some cells may be innately specified while others are not or that some may be modifiable even if originally selective while others remain rigid, may also be made consistent with the experimental findings. However, current results do not seem to force us to concede a role for visual experience in guiding the normal development of orientation selectivity in the cat. A role for visual experience in only the maintenance of selectivity is all that is required to explain the results in the cat and is consistent with the findings in the monkey.

Teleological considerations do make a more extensive role for visual experience in the development of the visual cortex extremely attractive. For example, it is difficult to imagine an innate mechanism for binocular cells by which the receptive fields of the two eyes are made to match as closely as they do in the normal adult animal. A mechanism

\*M. Stryker, H. Sherk, H.V.B. Hirsch, and A.G. Leventhal, Orientation Selectivity in Cat's Visual Cortex Following Restricted Early Visual Experience Using Goggles: A Quantitative Study, manuscript in press.

by which connections from the two eyes to such a cell are modified by visual experience, strengthened when the activity of the cell and its inputs are correlated and weakened by passive decay or uncorrelated activity, can easily account for the similarity of the receptive fields of the two eyes (Hebb, 1949; Marlsberg, 1973; Blakemore and van Sluyters, 1974; Nass and Cooper, 1975). But some cells in Siamese cats with "mirror fields" (such a cell has two separate receptive fields in different retinal locations of the same eye) are equally striking in the similarity of the properties of their two receptive fields (Hubel and Wiesel, 1971). It seems that this similarity must be determined by an innate mechanism, however difficult it may be to imagine, since the activity from the two receptive fields would not be correlated by visual experience. If such an innate mechanism is available to the Siamese cat, then presumably it would also be available to the normal cat, eliminating the need for an experience-dependent mechanism. This example illustrates that teleological considerations, however seductive, can only suggest a role for early experience in the development of the visual cortex. The demonstration of such a role will require more extensive experimental evidence than we have at present.

Stryker proposed that orientation selectivity, one of the organizing features of the visual cortex, develops innately in the cat as it does in the monkey. Ocular dominance, another organizing feature of the cortex, develops innately also, but it is easily modifiable in both cat and monkey by abnormal early visual experience (Hubel et al., 1976, 1977a; and see Wiesel, above). Present evidence suggests that orientation selectivity may not be modified by visual experience in any way except destructively, by the cells' becoming less selective.