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9. Detection of spherical refractive error by retinoscopy is made difficult by uncontrolled variations in the accommodative state of the infant's eye. However, since spherical error would equally effect the response to targets of all orientations, such defects cannot account for relative orientational differences. We thank Dr. S. Wittenberg and Dr. I. Mohindra, Massachusetts College of Optometry, for performing the retinoscopy.
10. Contrast was calculated from the following formula: $(L_1 - L_2)/(L_1 + L_2)$, where L_1 is the luminance of the light area and L_2 the luminance of the dark area.
11. In accordance with previously determined differences in acuity as a function of age (*7, 8*), the youngest group was tested with gratings of 0.75, 1.5, 3.0, and 6.0 cycle/degree, while 1.5, 3.0, 6.0, and 12.0 cycle/degree gratings were used for the older age groups.
12. Two experimental sessions were run on most subjects. Approximately 64 trials were obtained on each subject in the youngest age group (6 to 13 weeks), and approximately 109 trials for each subject in the three older groups (14 to 22 weeks, 23 to 36 weeks, and 37 to 50 weeks). For infants in the youngest group, we often obtained fewer than 48 trials per session because of lack of subject cooperation.
13. There were no appreciable differences between results obtained with the parents facing toward or away from the stimulus targets; this makes it unlikely that the parents were biasing the infant's looking behavior. Furthermore, the possibility that the few parents who had any knowledge of the oblique effect could have predicted its interaction with spatial frequency is slight.
14. By 2 months of age, the infant's accommodative capacity is sufficiently developed to allow sharp focusing of targets at this distance [H. Haynes, B. L. White, R. Held, *Science* **148**, 528 (1965)].
15. Subjects showed an elevated fixation percentage for vertical and horizontal patterns at more than one spatial frequency. This dispersion in the data can be explained either if the actual threshold for subjects in a given age group lies between two of the spatial frequencies tested or if subjects in a given group have slightly different thresholds, or both.
16. The possibility exists that instead of measuring the infant's limit of resolution (his threshold), the preferential looking technique is a measure of the spatial frequency beyond which the infant no longer attends to visual stimuli. But, even if this were the case, our finding of differential responses to vertical and horizontal versus oblique gratings would imply an underlying disparity in orientational visibility.
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Cortical Effect of Early Selective Exposure to Diagonal Lines

Abstract. *Neurons in the visual cortex that respond preferentially to diagonal contours are present only in cats exposed to diagonal lines early in life. In contrast, cells that prefer horizontal or vertical contours are found following exposure to horizontal, to vertical, and to diagonal lines. Such cells do not require a specific visual input for maintenance or for development; neurons responding preferentially to diagonal lines do.*

Most neurons in the visual cortex of the cat and the monkey respond maximally to line-shaped stimuli presented at a given orientation and position on the retina (*1*). The particular stimulus orientation that elicits a maximum response varies from cell to cell. If an animal's early postnatal visual experience is restricted, the distribution of the preferred stimulus orientations of these neurons, and to some extent the animal's behavioral capabilities, are modified (*2, 3*). The precise conditions necessary for the development of orientation specificity, however, remain unclear (*4, 5*).

In a wide range of animals, including man, behavioral and physiological evidence indicates that the visual system responds preferentially to horizontal and vertical patterns (*6*). To determine whether this bias is a consequence of an animal's early visual experience, we compared the effects of early selective exposure to diagonal lines and to horizontal and vertical lines. In cats exposed only to horizontal and vertical patterns, nearly all orientation-sensitive cells studied responded most strongly to lines oriented either horizontally or vertically (*2*). In contrast, in cats exposed to diagonal patterns alone, we found more cortical cells responding preferentially to horizontal or to vertical lines than to diagonal patterns. Since, with our techniques, the cat's visual system cannot be made to respond preferentially to diagonal lines, we suggest that the preferential response of the visual system to horizontal and to vertical lines reflects its inherent organization and is not simply the response to an early visual environment dominated by horizontal and vertical contours.

Eight cats born in a laboratory colony served as experimental subjects. They were housed with their mother in total darkness from birth. Beginning at 4 weeks of age the animals were exposed daily to a controlled visual environment; they were fitted with masks within which each eye could view a circular field, 40° to 50° in diameter, containing three parallel black lines on a white background (*2*). The lines were 1° wide, their centers separated by 6°, and their ends blurred and distorted by the lenses. At the end of an 8-hour exposure period the animals were returned to their mother. Since the masks were put on and taken off in the darkroom, the animals' only visual experiences were provided by the masks.

Three cats viewed vertical stripes with one eye and, simultaneously, horizontal stripes with the other eye. Five other animals viewed a similar pattern, but the stripes were oriented at 45° for one eye and at 135° for the other.

Selective exposure was continued daily until the animals had been exposed to the patterns for approximately 100 hours. Subsequently, all of the animals remained in the darkroom until they were at least 16 weeks of age (*7*). Four cats were then exposed for 6 months to a normally illuminated environment before single unit recordings were made. Two cats had both eyes sutured shut immediately after they were removed from the darkroom, and two were left in the darkroom until the recordings were carried out. These four animals thus received no patterned visual stimulation subsequent to the selective exposure provided during the rearing. Three cats raised from birth in a normally illuminated laboratory colony served as control animals.

The response properties of single units in the visual cortex were determined with conventional procedures (*1, 5, 8*). Animals were anesthetized with either Fluothane or Sodium Pentothal during preparation for recording. The skin, bone, and dura over the striate cortex were removed, and a chamber was positioned over this craniotomy. The animals were paralyzed with intravenously infused *d*-tubocurarine and gallamine triethiodide (Flaxedil) and artificially ventilated with a mixture of nitrous oxide, oxygen, and carbon dioxide. Incisions and pressure points were infiltrated with a long-acting local anesthetic, and general anesthesia was discontinued. Standard procedures were used to protect the eyes, correct the optics, and minimize eye movements. The projections of the optic disc were plotted and the position of the area centralis inferred (*9*). Recording began after the animal had recovered from general anesthesia.

An Insl-x-coated tungsten microelectrode was lowered hydraulically through the medial bank of the primary visual cortex (*5, 10, 11*), and responses of single units were amplified and isolated. Once a unit had been isolated, ocular dominance was determined (*1*). Line-shaped stimuli were presented with a hand-held projector in order to test the cell's response properties. Minimum response fields were obtained for each unit (*8*), and directional selectivity was assessed (*12*). For units showing orientation-sensitivity, the preferred orientation and the range of orientations that activate the cell were determined (*11*).

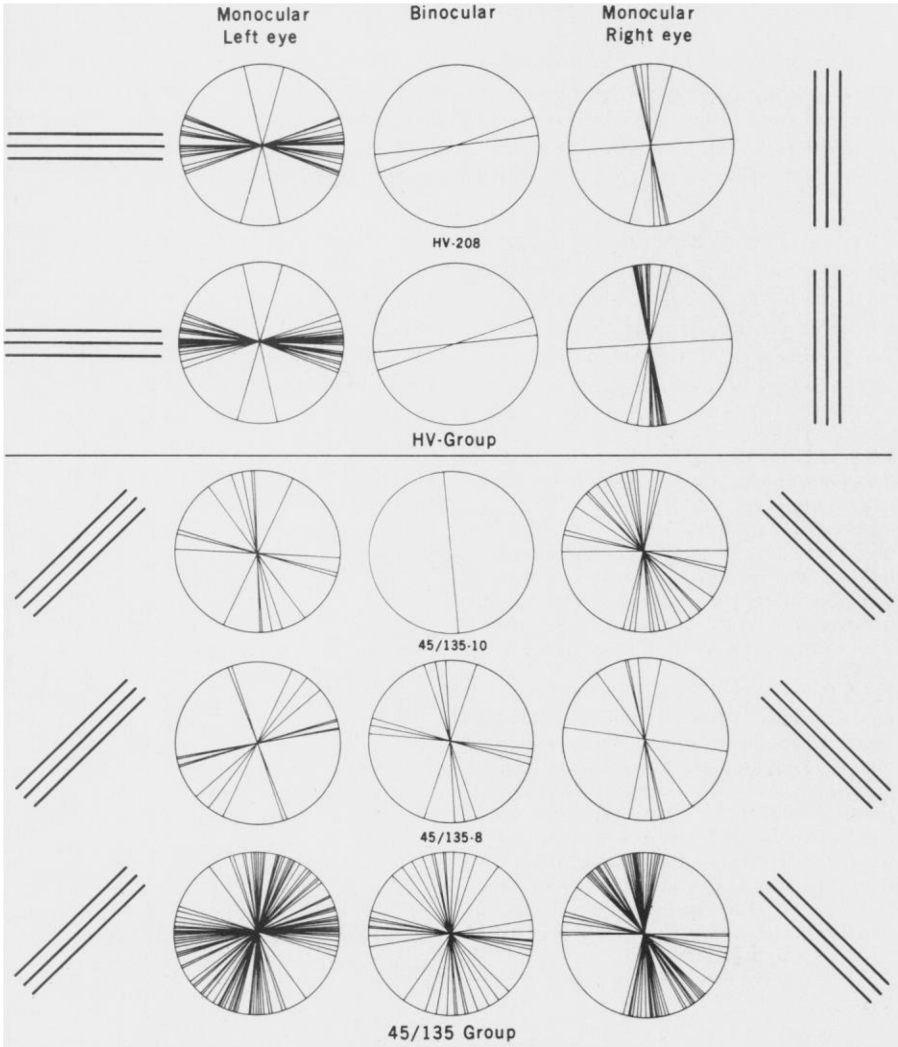
Data were collected from 210 units in experimental animals and from 50 units in normal cats. The receptive fields of most cells were within 15° of the estimated projection of the area centralis. In normal animals, units were activated binocularly (92 percent) and displayed a full range of orientation preferences as reported by others (*1, 8, 13*).

The distribution of the preferred orientations of units examined in the three animals exposed to vertical stripes with the right eye and to horizontal stripes with the left eye agrees with earlier results (*2*) (Figs. 1 and 2). In these animals the units sensitive to orientation respond to stimulation of only one eye and fall into two major classes, (i) units responding most strongly to lines near the vertical axis (± 22.5°) and (ii) those responding most strongly to lines near the horizontal axis (± 22.5°). As expected, 11 of the 12 units that preferred vertical lines were activated exclusively by the eye exposed to vertical stripes during rearing, and 20 of the 22 that preferred horizontal stimuli were activated only by the eye that viewed horizontal stripes. The exceptional units had preferred orientations at right angles to the patterns presented during rearing (*12*).

Early selective exposure to diagonal lines had a very different cortical effect. Again, the majority of units responded to stimulation of only one eye. However, 71 percent of the orientation-sensitive units responded preferentially to either horizontal or to vertical lines and not to diagonal lines. The distribution of orientation preferences of the remaining 29 percent of the orientation-sensitive units did reflect the visual environment to which the animals had been exposed; all but one of these units responded most strongly to stimuli which had the same orientation as the stripes presented during rearing. Thus, for each eye of these animals, there was an absence of cells activated monocularly that prefer lines oriented at right angles to the pattern presented to that eye during rearing (Figs. 1 and 2).

In animals that did not receive any normal visual experience subsequent to the rearing, 15 percent of the units were activated binocularly after exposure to diagonal lines, while none were activated binocularly after exposure to horizontal and to vertical lines. Units activated binocularly found in cats exposed to diagonal lines usually had preferred orientations within 22.5° of the horizontal or of the vertical axis (Fig. 1).

To determine whether unrestricted visual experience modifies the effects of early selective exposure, half of the animals were kept in a normal environment for several months prior to recording. In no case was the distribution of preferred orientations resulting from the early restricted visual exposure modified by subsequent normal



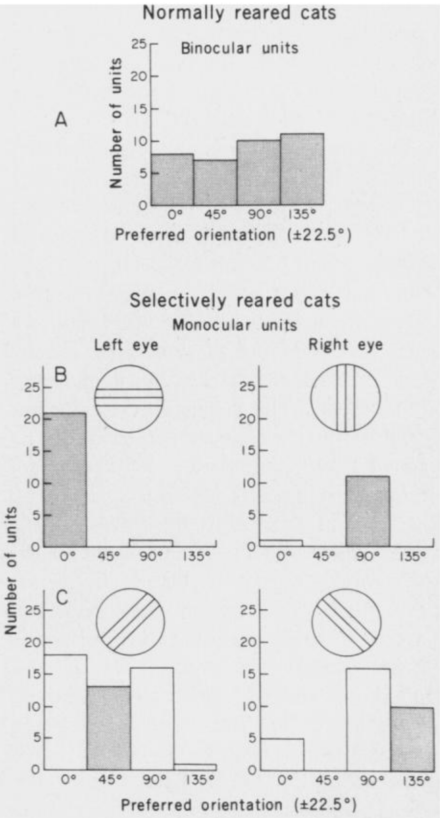


Fig. 1 (left) Cortical effects of early exposure to horizontal or to vertical lines and to diagonal lines. Each line represents the preferred orientation of one cortical neuron. The patterns presented to each eye during rearing are illustrated in the right and left margins. Data in the left column represent neurons activated exclusively by the left eye; those in the right column represent cells activated exclusively by the right eye; those in the center column represent cells activated by both eyes. The top row represents cells recorded from an animal exposed to horizontal and vertical lines. Data for all cats reared under this condition are presented in the second row (36 orientation-sensitive cells). The third and fourth rows present data for animals exposed to diagonal lines. Data for all five cats reared under these conditions are summarized in the bottom row (97 orientation-sensitive cells). Cat 45/135-8 and HV-208 received 6 months of normal exposure subsequent to the selective exposure; cat 45/135-10 received no patterned visual stimulation subsequent to the selective exposure. Fig. 2 (right). Number of neurons with preferred orientation within each of four ranges. The shaded areas in each histogram indicate the orientation of the lines (± 22.5°) to which the animals were exposed during their first 4 months of life. The lines inscribed in each circle illustrate the patterns presented during rearing. (A) A full range of orientation preferences was found in animals raised in a normal visual environment. (B) In animals that viewed only horizontal and vertical lines, most orientation-sensitive neurons responded preferentially to horizontal or to vertical stimuli. (C) In animals that viewed only diagonal lines, most orientation-sensitive neurons responded preferentially to horizontal or to vertical lines. The rest were activated most strongly by lines with an orientation matching that of the patterns presented during rearing.

visual experience (Fig. 1). As was found in other experiments, normal visual experience following early selective exposure increases the proportion of binocular units (*14*). Similarly, there were increases in the proportion of units responsive visually and of those that demonstrated well-defined orientation preferences. These results are to be presented in detail elsewhere (*15*).

In summary, exposing a young cat to only vertical and horizontal lines produces a dramatic modification in the distribution of the orientation preferences of its cortical neurons (*2*). This distribution seems to match the animal's early experience. Exposing animals to only diagonal lines, however, does not result in a corresponding modification of the distribution of the orientation preferences of its cortical units. On the contrary, the majority of cells respond best to horizontal or to vertical lines; the remaining units respond preferentially to diagonal lines and are activated through only the eye which was exposed to the corresponding diagonals (*16*).

The presence of units exhibiting preferences for horizontal or for vertical lines in cats exposed to only diagonal patterns demonstrates that such units maintain or develop their intrinsic specificity even when horizontal and vertical lines are excluded from the animal's visual environment (*17*). Whether these neurons require some form of stimulation during ontogeny is unknown. Cells displaying a preference for diagonal lines, however, may be recruited from a population of neurons uncommitted initially, whose orientation specificity is affected by the animal's early visual experience. These cells might receive the neuronal inputs necessary for proper development or function from cells that have an intrinsic preference for horizontal or for vertical lines (*18*). If so, the distinction between 45° lines and 135° lines requires use of another response property, such as directional selectivity in addition to orientation (*15*). This remains to be determined.

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Modification of Cortical Orientation Selectivity in the Cat by Restricted Visual Experience: A Reexamination

Abstract. *Recent reports have stated that the orientation selectivity of cells in the cat's visual cortex can be biased by limiting the early visual environment to stripes of one orientation. Data obtained from seven kittens using systematic and quantitative sampling of preferred orientation, together with a blind procedure, do not show a bias toward the orientation presented in one type of restricted rearing environment.*

The role of early experience in the development of the brain has been probed since the early 1960's through a number of experiments on the cat's visual system (*1*). Recent investigations have focused on a major feature of visual cortical organization: orientation selectivity. Experiments by Hirsch, Blakemore, and others have suggested that when a kitten's early visual experience is limited to contours of a single orientation, a later sample of units from the visual cortex is biased toward the orientation to which the animal has been exposed (*2–5*). Furthermore, it has been reported that units preferring orientations near the one to which the cat was exposed are much more highly selective than units preferring different orientations (*3, 6, 7*).

Three aspects of the recording techniques used in such studies have made the results difficult to interpret. (i) Units were not sampled at regular intervals across the cortical surface. Instead, orientation for every unit encountered has generally been reported. Since orientation in the normal cat is represented in an orderly fashion across the cortical surface with nearby units representing similar orientations (*8*), a sample taken from a small region can be heavily biased toward one orientation. (ii) Preferred orientation and the degree of orientation selectivity were estimated with the use of stimuli moved by hand; quantitative measurements were not made (*9*). (iii) The experimenters knew during the recording session the orientation to which the cat had been exposed, possibly introducing an error attributable to personal bias (*10*). We attempted to replicate a rearing procedure reported by Blakemore and Mitchell (*6, 11*) to powerfully bias the distribution of preferred orientations of cells in the cat's visual cortex. We then recorded the activi-

Table 1. The letter (H or V) preceding each kitten's number indicates the orientation of stripes in its exposure cylinder. Exposure occurred for 3 hours per day starting on the date shown in column 2 and continuing on successive days until the total number of hours shown in column 3 had accumulated. Kittens were then kept in darkness until the day of age shown in column 4. The orientation bias shown in column 5 is log (E/C), calculated from the number of sites (E) which responded best to orientations within 30° of the exposed orientation and the number of sites (C) whose preferred orientations were more than 60° away from the exposed orientation. A positive value indicates a bias toward the exposure condition; a negative value indicates a bias toward the orthogonal orientation. This log scale is symmetrical about zero. Thus when there is no bias ($E/C = 1$) this value is 0, and a 2 to 1 bias would be represented by ± .301, the sign depending on whether it favors the exposed or orthogonal orientation.

Subject	Exposure conditions		Age (days)	Orientation (log bias)
	Day begun	Total hours		
H-1	22	39	73	0.0
H-2	24	39	57	+.230
H-3	24	39	82	+.113
H-4	48	36	60	–.229
V-5	24	30	60	–.211
V-6	22	39	69	–.156
V-7	21	168	85	+.281