

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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16. Data which appear to be consistent with the

present results have been obtained by R. D. Freeman and J. D. Pettigrew [*Nature (Lond.)* **246**, 359 (1973)].

17. It is conceivable, if unlikely, that rotations of the animals' eyes while they were wearing the masks might help explain why there are units responding to horizontal or to vertical stimuli in animals exposed only to diagonal stripes. Such an explanation would require that eye rotations in cats exposed to diagonal lines are approximately 45° greater than in animals exposed to horizontal and vertical ones. Such abnormal eye movements, in any event, would have to be elicited specifically by diagonal lines since cells preferring diagonal edges are not found in cats exposed only to horizontal and vertical lines.
18. We thank P. Carruccio, C. Edwards, L. Festinger, R. Gordon, R. Priest, M. Salzman, S. B. Tieman, and J. West. Support for this work was provided by grant RO1EY-01268 from the Public Health Service.

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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 organiza-

tion: 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 $\pm .301$, 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

ty of a sample of cells in the visual cortex using techniques designed to overcome the difficulties described above.

Kittens were kept in a totally dark room (12) from a few days after birth until time of recording, except for a period of restricted visual experience (13). During exposure the kitten wore a black ruff (14) and sat on a clear glass plate mounted halfway between the top and bottom of one of two cylinders 48 cm in diameter and 2 m tall. The inside walls of the cylinders were covered with parallel black and white stripes of several different widths; the stripes were horizontal in one cylinder and vertical in the other (15). Each kitten saw only the inside of one striped cylinder and had no other visual experience before the recording experiment was carried out (Table 1).

To prevent the experimenters from knowing whether the cat had been exposed to horizontal or to vertical stripes, the identifying collar was removed by an assistant (16). Surgery was then carried out under Fluothane supplemented by thiopental anesthesia; tracheal and venous cannulas were inserted, a recording chamber was fixed to the skull, and a dural flap over the lateral gyrus was reflected to expose cortical area 17. Platinum-iridium microelectrodes were positioned to traverse the medial bank of the lateral gyrus or to travel parasagittally at a shallow angle to the cortical surface. Surgical anesthesia was discontinued, and the cat was paralyzed with Flaxedil and artificially respired with a mixture of 75 percent N_2O and 25 percent O_2 at a rate which maintained alveolar CO_2 at 3.8 to 4.0 percent. The eyes were focused with contact lenses onto a tangent screen, on which retinal landmarks were then plotted.

As the microelectrode was advanced through the cortex, we tried to sample the

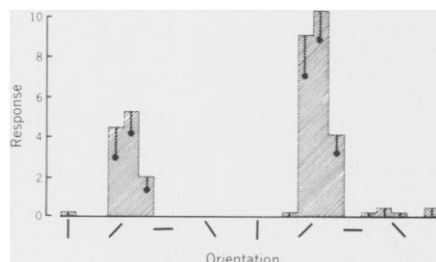


Fig. 1. An example of an orientation-tuning histogram like that obtained for each site studied. Abscissa gives orientation of the stimulus bar which swept the receptive field; because for one stimulus orientation two directions of movement are possible, every orientation is represented twice. Ordinate shows mean response (in spikes per sweep) and mean minus standard deviation of the response (heavy dots when > 0). The cell illustrated responds to both directions of movement of a stimulus oriented obliquely 60° from vertical.

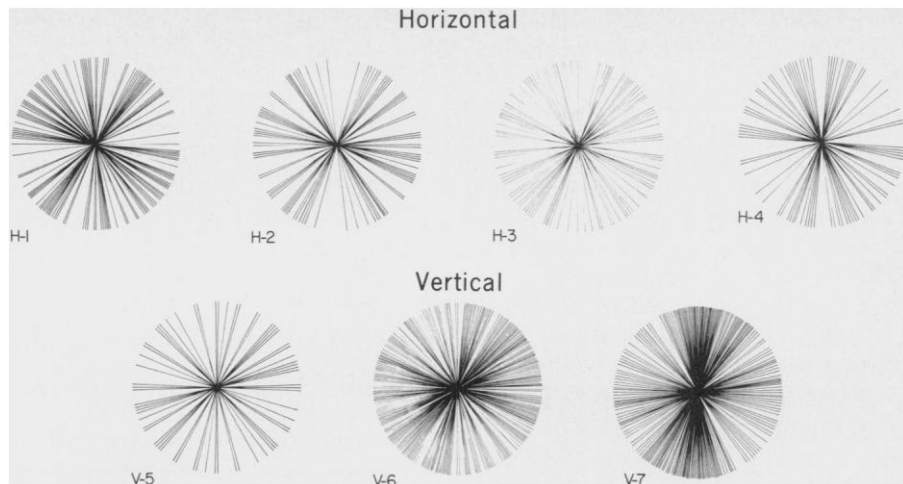


Fig. 2. Polar plots of data from seven kittens. Each line is drawn at the preferred orientation of the unit or multiple units at one site.

preferred orientation of one unit in each $100 \mu m$ of electrode travel. When it was not possible to isolate a single unit in this interval, the multiple-unit or unresolved visual background response was plotted. This procedure was designed to give a picture of the distribution of preferred orientation across a large region of cortical surface.

The preferred orientation and width of tuning of each unit was determined using a computer-driven optical display, which swept a light bar across the receptive field center at 24 different orientations (15° apart) in a random order, with each orientation appearing a total of three times. The computer recorded the mean and standard deviation of the response to each orientation (17). For each site we obtained an orientation-tuning histogram such as that illustrated in Fig. 1. Recordings were obtained from 456 sites in 17 penetrations (Fig. 2). At 378 of these recording sites, preferred orientation was determined for well-isolated single units; at the remaining 78 sites multiple-unit activity was used (18). All conclusions remain the same whether the data are analyzed in terms of units or of sites. Recordings were also obtained from 359 units studied by similar techniques in 12 penetrations in the visual cortices of five normal cats.

No experimental animal showed a bias in the distribution of preferred orientations outside the range found in normal cats. These biases toward the exposed orientation in H-2, H-3, and V-7 were matched by equally strong biases against the exposed orientation in H-4, V-5, and V-6 (Table 1). Furthermore, the orientation-tuning histograms showed no tendency for units near the exposed orientation to be more highly selective than other units (19). Finally, most penetrations disclosed a high degree

of order in the representation of orientation across the cortical surface, with nearby units representing similar orientations (Fig. 3).

In these kittens the restriction of visual experience to the insides of horizontally or vertically striped cylinders resulted in distributions of orientation selectivity like those found in normal cats. These results are in sharp contrast to those of Blake-more and others (2-5). Our recording techniques differed from theirs in that we used (i) regularly spaced sampling over an extensive area of cortex, (ii) quantitative measurement of each unit's orientation-tuning curve, and (iii) a blind procedure in which, at the time of recording, the experimenter did not know the kitten's previous visual experience. Whether any of these factors or some other unrecognized factor is responsible for our different results remains unclear.

Note added in proof: Using similar recording techniques to those reported here and working in collaboration with H.V.B. Hirsch and A. G. Leventhal, we have recently studied a group of cats whose early visual experience was restricted. We fitted them with goggles within which one eye viewed horizontal lines and the other eye viewed vertical lines. Our results,

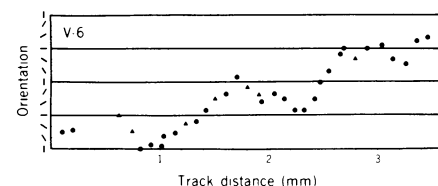


Fig. 3. A reconstructed penetration from cat V-6. Abscissa shows the location of each site along the electrode track. Ordinate shows the preferred orientation at each site. Dots represent isolated single units, and triangles represent multiple unit activity.

though more variable, largely confirm two of the findings of Hirsch and Spinelli (4): (i) About half of the 350 cells studied were either unresponsive, poorly and erratically responsive, or nonselective in their responses to visual stimuli. (ii) The majority of the remaining selective units were monocularly driven and preferred orientations near the one to which the effective eye had been exposed. These results will be reported in full elsewhere.

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9. An exception to this is the study by Hirsch and Spinelli (4), who mapped elongated receptive fields by computer for 32 cells in nine cats. Because they inferred best orientation from receptive field shape and plotted receptive fields using horizontally or vertically moving spot stimuli, their results are not directly comparable to conventional plots.
10. The only published report of an experiment using a blind procedure is a study of one animal by Pettigrew *et al.* (5).
11. C. Blakemore, personal communication.
12. A light lock was used so that the room was always dark, and the system was tested with occasional 24-hour exposures of Tri-X film.
13. An exception to this procedure was H-4, whose eyes were sutured shut before opening and remained so until he was placed in the dark room at 47 days of age.
14. A ruff was a section of a 130° cone which prevented the kitten from seeing its own body.
15. Stripes ranged between 0.6 cm and 10 cm in width, and the kitten was free to move around the glass plate. The floor of the cylinder was black matte. A 32-watt Cool White fluorescent tube and several layers of diffusers provided uniform illumination across the ceiling of the cylinder. Halfway up the cylinder the white stripes were 153 cd/m² and the black stripes were 9.4 cd/m².
16. Subject H-4, which had no littermate, was the only one whose orientation exposure was known during the recording experiment.
17. The bar was of optimal length and width and was swept at optimal velocity as determined from stimuli moved by hand.
18. We think that analysis in terms of regularly spaced sites provides more information about the preferred orientations represented in a region of cortex than an analysis limited to well-isolated unit responses. Isolation of a single cell's activity at a given site depends to a great extent on electrode characteristics, and failure to isolate a single cell probably does not reflect an absence of responsive cells near that site. Probably because neighboring

cells have similar preferred orientation (8), simultaneously recorded responses from several cells usually show a well-defined orientation preference.

19. Orientation selectivity (the width of the orientation-tuning function) was considered only for response histograms compiled from well-isolated unit responses. In addition, there was no tendency for units whose preferred orientations were near the exposed orientation to be more frequently encountered earlier in the recording experiment than later.

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Perceived Visual Motion as Effective Stimulus to Pursuit Eye Movement System

Abstract. Human eye tracking of a foveal afterimage during angular head oscillation in the dark produced smooth eye movements exceeding those for normal vestibular nystagmus, and a reduction in the frequency of the fast phase component of the nystagmus eye movements. These results may support a closed loop extension of the corollary discharge theory, with oculomotor commands based on perceived object velocity.

The relative stability of the visual world during voluntary eye movements is a classical problem in psychophysics (1). The debate has centered around inflow (proprioceptive feedback) versus outflow (efferent copy, Helmholtz's effort of will, corollary discharge) explanations to account for compensation of the influence of eye movements upon retinal image motion. Psychophysical evidence involving active or passive eye movements tends to support the outflow theory (2). The control of eye tracking movement has more recently been studied from the servomechanical point of view, where the emphasis of experiments and cybernetic models has been on the

causal relationships between the target motion or retinal motion and the resulting saccadic and pursuit eye movements (3). The need to relate the new (objective) and old (subjective) studies has been recognized (4). Might not the perceived target motion (rather than the actual target motion) be utilized for generating eye movement commands? This possibility, raised independently by Heywood (5) and by Rashbass (6) and Robinson (7) in interpreting the eye tracking model of Young *et al.* (8), is examined here through an experiment involving afterimage tracking during vestibular stimulation.

The experiment is intended to test the

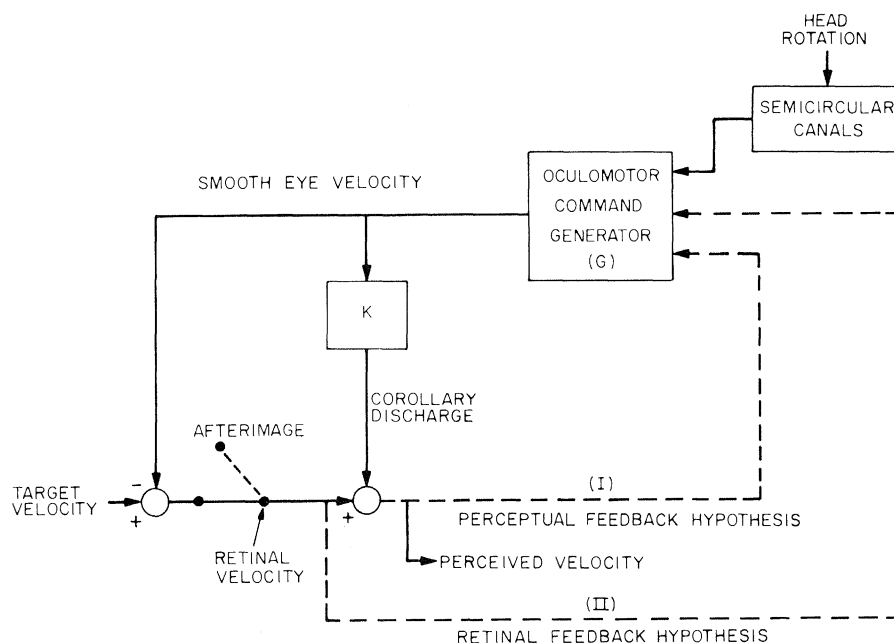


Fig. 1. Compensation by corollary discharge for the eye movement effect on the retinal image motion. In this experiment the input is from head rotation. Tracking a foveal afterimage rather than an external target opens the retinal feedback loop and activates only the internal positive feedback loop that results from connecting the corollary discharge with the postulated perceptual feedback path; *G*, open loop gain of vestibulo-ocular reflex arc; *K*, gain of corollary discharge path.