

Cats Reared in Stroboscopic Illumination: Effects on Receptive Fields in Visual Cortex

(developmental physiology/deprivation effects/vision)

M. CYNADER*, N. BERMAN†, AND A. HEIN‡

Department of Psychology, Massachusetts Institute of Technology, Cambridge, Mass. 02139

Communicated by Eliot Stellar, March 2, 1973

ABSTRACT Cats were reared in a light-tight box in which the only source of illumination was a 9- μ sec strobe flash every 2 sec. This allowed them to experience visual form but they did not experience visual movement. Receptive-field properties of single units in area 17 of the visual cortex of cats reared in stroboscopic illumination (strobe-reared) were compared with properties of units in area 17 of normally reared cats. In strobe-reared cats both direction selectivity and orientation selectivity were greatly reduced relative to normally reared cats, and some units in the strobe-reared cats responded only to strobe flashes.

A fundamental property of visual stimuli is their constant motion across the retina. The importance of stimulus motion for perception, which has been demonstrated by experiments with stabilized images (1), suggested that motion deprivation should have a substantial effect on the development of the visual system. To examine this suggestion, two kittens were reared from birth for 6 months in an enclosure in which the only source of illumination was a strobe light (strobe-reared). A 9- μ sec flash and a 2-sec interflash interval provided virtually stopped images on the retinae. The receptive-field organization of single cells in the striate cortex was studied when the kittens were removed from the enclosure at 6 months of age.

We recorded from cats under conditions of reversible intubation (2-4). The responses of 98 units in two cats studied during a total of five recording sessions were compared with those of 248 units in the visual cortex of nine normally reared cats. Three aspects of receptive-field organization in striate cortex cells were examined: (i) direction selectivity, (ii) orientation selectivity, and (iii) responses to diffuse strobe flashes. Columnar organization was not studied systematically. Preferential firing to certain directions of movement was the criterion for direction selectivity. A direction selective unit was judged to be orientation-selective if (a) it responded well to moving slits, bars, or edges and poorly to moving spots, or (b) it responded differentially to flashed slits of various orientations confined entirely within the activating region of the receptive field, or (c) its direction tuning for movement was narrower for long slits or edges than for spots. A nondirectional unit was judged to be orientation-selective if it responded differentially to moving slits of certain orientations.

* Present address: Max-Planck Institut für psychiatrie, Munich, Germany.

† Present Address: Department of Anatomy, University of Pennsylvania, Philadelphia, Pa. 19104

‡ Address reprint requests to this author.

Table 1 compares the responses of units in the strobe-reared cats and normally reared cats with regard to these parameters. In the normal cat, virtually all units exhibited orientation selectivity and most were direction-selective as well. Few units responded to diffuse strobe flashes. In contrast, the fraction of units exhibiting orientation or direction selectivity was severely reduced in strobe-reared cats, while more than half of all units tested responded to diffuse strobe flashes. Some units in strobe-reared cats could only be activated by the strobe flashes. Almost all units in normal cats could be classified in one of two groups: simple or complex (5, 6). Units in the strobe-reared cats could not easily be identified as simple or complex; however, they could be classified as direction-selective or nondirectional. The responses of a representative unit from each group are illustrated in Fig. 1.

The nondirectional group comprised 62% of the units in strobe-reared cats. These units did not reveal orientation, direction selectivity, or preference for slits or edges over spots. Presentation of flashing spots elicited only "on" responses throughout the activating region, and annuli revealed a weak "off" region surrounding the strong "on" center. These units, distinguished from lateral geniculate nucleus afferents in that they have cell-type spikes, were sometimes activated binocularly and often lacked spontaneous activity. They resemble the simple cells in the striate cortex of the normal cat in that both have receptive fields, which can be mapped into discrete "on" and "off" zones with flashing stimuli. In addition to these units, we encountered four cells that were orientation-selective and had strong "on" regions with weak "off" flanks. It is possible that the concentrically organized units in strobe-

TABLE 1. Comparison of receptive-field properties in strobe-reared and normally reared cats

	Normally-reared	Strobe reared
Direction selective	187 (83%)	32 (38%)
Nondirectional	43 (17%)	52 (62%)
Total tested	230	84
Orientation selective	241 (97%)	12 (15%)
Nonoriented	7 (3%)	73 (85%)
Total tested	248	85
Response only to strobe	0	13
Total strobe responsive	12 (10%)	32 (53%)
Strobe unresponsive	109 (90%)	28 (47%)
Total tested	121	60

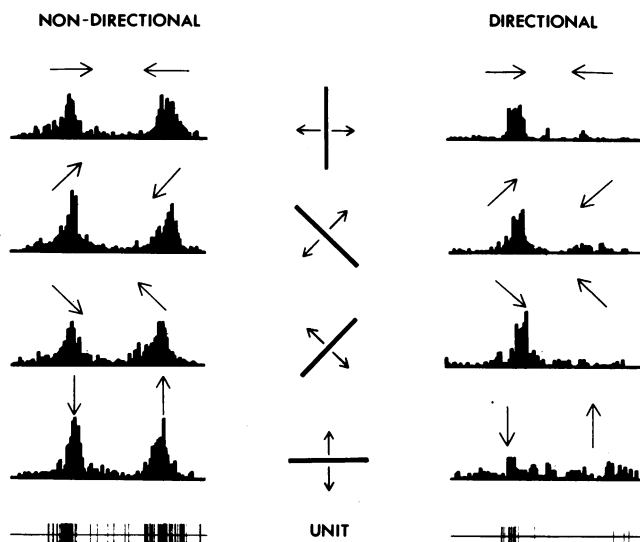


FIG. 1. Histograms illustrating the sum of 16 sweeps and a sample unit record showing the responses on one sweep of two units in strobe-reared cats to slits moved in various directions across their receptive fields. The unit illustrated (*left*) displays neither orientation nor direction-selectivity, responding well to slits moving in any of the eight directions illustrated. Receptive-field size: 3° ; stimulus velocity: $4^\circ/\text{sec.}$; slit size: $\frac{1}{2}^\circ \times 10^\circ$; stimulus cycle: 4 sec. The unit illustrated (*right*) displays a broadly tuned direction selectivity, responding vigorously to the three or eight directions of movement shown. Receptive field side: 5° ; stimulus velocity: $7^\circ/\text{sec.}$; slit size: $\frac{1}{2}^\circ \times 10^\circ$; stimulus cycle: 4 sec.

reared cats are simple cells that have either failed to develop orientation selectivity (7) or have lost an innate orientation selectivity (8).

A second group of cells comprise 32% of the units encountered in strobe-reared cats. They showed broadly tuned direction selectivity when tested with spots and responded well to moving slits over a wide range of orientations (Fig. 1, *right*). These units typically did not meet the first two criteria for orientation selectivity described above. About 25% of them met the third criterion by exhibiting a somewhat narrower direction tuning when tested with moving slits than with moving spots. Tests with flashing stimuli revealed similarities be-

tween direction-selective cells of strobe-reared animals and complex cells in the normal cat. Most units in both groups gave "on" and "off" responses intermingled throughout the receptive field, although in direction-selective units in the strobe-reared cats the "on" responses were typically stronger. In some units of the strobe-reared cats, "off" responses were absent. Tests with moving spots and slits indicated further similarities with the normal cat. Many complex cells in the normal cat gave surprisingly strong responses to small moving spots, as also shown recently by Palmer, Rosenquist, and Sprague (9). The complex cells in normal cats, and those units in strobe-reared cats which show direction-selectivity, display comparable breadth of tuning for direction-selectivity. These features suggest a resemblance between direction-selective cells in the strobe-reared cats and complex cells in the normal cat. Although most of these direction-selective units in the strobe-reared cats showed substantially broadened tuning for orientation, a few were indistinguishable from complex cells in the normal striate cortex.

The data presented here show that strobe rearing augments responses of striate cortex units to strobe flashes and alters the normal balance between "on" and "off" responses to flashed stimuli. The percentage of units having direction and orientation selectivity is considerably reduced. Raising kittens in an environment where a strobe light provides the only source of illumination can substantially alter the basic characteristics of the visual cortex.

This research was supported by the National Institutes of Health and the Sloan Foundation.

1. Ditchburn, R. W. & Ginsborg, B. L. (1952) *Nature* **170**, 36-37.
2. Cynader, M. & Berman, N. (1972) *J. Neurophysiol.* **35**, 187-201.
3. Berman, N. & Cynader, M. (1972) *J. Physiol.* **224**, 363-389.
4. Wickelgren, B. G. (1971) *Science* **173**, 69-72.
5. Hubel, D. H. & Wiesel, T. N. (1962) *J. Physiol.* **100**, 106-154.
6. Pettigrew, J. D., Nikara, T. & Bishop, P. O. (1968) *Exp. Brain Res.* **6**, 373-390.
7. Barlow, H. B. & Pettigrew, J. D. (1971) *J. Physiol.* **218**, 98P-100P.
8. Hubel, D. H. & Wiesel, T. N. (1963) *J. Neurophysiol.* **26**, 994-1002.
9. Palmer, L., Rosenquist, A. C. & Sprague, J. M. (1973) *Corticothalamic projections and sensorimotor activities*, eds. Frigges, T. L., Rinvik E. & Yahr, M. D. (Raven Press, New York), in press.