playing the PDS or the interneurons of the recurrent pathways. This model based on bursting behavior is purely speculative at this time, since information concerning the latent ability of neocortical cells to acquire bursting properties is not available. However, the finding that the convulsant and anticonvulsant agents affect the NRC and bursting properties in this invertebrate model are highly suggestive that a similar mechanism may occur in mammalian neurons.

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- We thank W. A. Spencer for critical reading of the manuscript. Supported by grants from the Minnesota Medical Foundation and the Graduate School, University of Minnesota, to D.J., and by NIH grant NS09784 and a grant from the American Epilepsy Foundation to G.F.A. 16

Loss of X-Cells in Lateral Geniculate Nucleus with Monocular Paralysis: Neural Plasticity in the Adult Cat

Abstract. Chronic immobilization of one eye by cranial nerve resection in adult cats led to selective but substantial loss of X-cells in the binocular segment of the dorsal lateral geniculate nucleus.

No plasticity is usually seen in the visual systems of adult animals subjected to aberrations of visual input (1, 2). In contrast, the neural plasticity displayed by kittens reared under conditions of abnormal interocular interaction is well documented (1, 3).

Recently, however, Buchtel et al. (4) have observed behavioral as well as physiological changes following chronic monocular paralysis in adult cats. In a more detailed analysis of the physiological effects of monocular paralysis, Fiorentini and Maffei (5) found a loss of binocularity in simple cells of visual cortex, while the binocularity of complex cells was apparently unaffected. After chronic paralysis, fewer than 15 percent of simple cells could be driven binocularly, whereas 95 percent were binocular during the first week of immobilization. Furthermore, this loss of binocularity in simple cells occurred rather abruptly about the seventh or eighth day of monocular paralysis and remained unaltered over several months regardless of any recovery of oculomotricity.

We have investigated the possibility that monocular paralysis in adult cats produces 19 SEPTEMBER 1975

changes in the lateral geniculate nucleus (LGNd) in addition to the effects described in cortex. Certain specific changes in the LGNd, following chronic monocular paralysis, may be expected from the parallel



Fig. 1. Comparison of acute and chronic monocular paralysis with respect to the percentage of X- and Y-cells in the binocular segment of the LGNd. With monocular paralysis lasting 3 days or less (acute condition), X- and Y-units were encountered with roughly equal frequency. After more than 14 days of monocular paralysis (chronic condition) the percentage of X-units had declined to less than 10 percent, while that of Y-cells had risen to more than 90 percent. Numbers in parentheses refer to absolute number of units represented by these percentages.

processing model of connectivity within the geniculostriate system (6). This model states that visual information is conveyed from retina to LGNd and finally to visual cortex by two parallel pathways, one containing X-cells and the other Y-cells. The axons of X-type retinal ganglion cells contact X-cells in the LGNd which then contact primarily simple cells in the visual cortex. The Y-cells in the lateral geniculate receive input from Y-cells in the retina and contact complex cells directly. Since Fiorentini and Maffei found that monocular paralysis has its principal effect on simple cells, we anticipated that we would see a selective disruption of the X-cells in the LGNd. Therefore, we investigated the effects of chronic eve immobilization on the relative proportions of X- and Y-cells in the cat's lateral geniculate nucleus.

Under sodium pentobarbital anesthesia, one eye in each of six cats was surgically immobilized by transection of cranial nerves III, IV, and VI at the common point of their entry into the orbit. During the same surgical procedure, the animal was prepared for semichronic microelectrode recording.

During recording sessions the animal was sedated, but not anesthetized, with a mixture of acepromazine maleate and sodium pentobarbital. The head was fixed in the stereotaxic plane by means of chronically implanted bolts attached to a metal mount (7). Complete muscular paralysis was unnecessary since cells under investigation were driven by the surgically immobilized eye. The eyes were protected by plano contact lenses, and refractive errors were corrected with spectacle lenses, so that sharp focus was obtained on a tangent screen 1 m from the cat's eye. The projections of the optic disc and the area centralis of each paralyzed eye were estimated on the tangent screen after the method of Fernald and Chase (8), and receptive fields were located and mapped with respect to these retinal landmarks. Each recording session lasted from 7 to 8 hours, and cats were allowed to recover completely before further recording.

Action potentials from units responsive to illumination of the immobilized eye were recorded with stainless steel microelectrodes, amplified on a WPI DAM 5 preamplifier and a Grass a-c amplifier, and stored on magnetic tape for subsequent analysis. Units were classified as X or Y on the basis of visual tests such as those described by Enroth-Cugell and Robson (9), Cleland, Dubin, and Levick (10), Fukada (11), Fukada and Saito (12), Cleland, Levick, and Sanderson (13), and Stone and Hoffmann (14). Ambiguous cases were decided by the radial grating method described by Dubin (15).

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Because the results reported by Fiorentini and Maffei were limited to cells whose receptive fields fell within 5° of the area centralis, we were initially concerned primarily with units whose receptive fields were in the central area of visual space. Although cells with more peripheral receptive fields were sampled, only those within the binocular segment were included in this report. Recordings were made at either 1 to 3 days after surgery (acute monocular paralysis) or at periods of more than 14 days (chronic monocular paralysis). These intervals were chosen to place our observations clearly on either side of the period reported previously to be critical for changes in simple cortical cells (5).

Of the 124 LGNd units which received visual information from the paralyzed eye, 119 could be classified with confidence as X or Y. The few units which could not be classified occurred with roughly equal frequency in both chronic and acute conditions and were excluded from the analysis. Figure 1 summarizes the data obtained from both conditions. As in other reports (16), in acutely paralyzed animals, X-units represent approximately 51 percent of the cells, while Y-cells constitute the remaining 49 percent. When recordings were made at more than 14 days after paralysis, these percentages were drastically altered. Only 7 percent of the units encountered were X-cells, while the remaining 93 percent were Y-cells.

In Fig. 2, the fraction of recorded units which were X-cells is displayed as a function of eccentricity. Although the X-cell loss appears to be present in all areas of the binocular segment, the small sample size in the most peripheral areas limits confidence with respect to our estimate of the loss in this region. Our estimate of the magnitude of the overall loss of X-cells is probably conservative because, in the chronically paralyzed cats, we sampled proportionately more from those regions of the LGNd which normally have a higher concentration of X-cells (16).

These results indicate that the number of functional X-cells in the LGNd was reduced by chronic monocular paralysis. The attrition of the X-cell population provides a new demonstration of neural plasticity in the adult visual system. The data are in large part consistent with the parallel processing model for connectivity within the visual system (6). Monocular paralysis simultaneously disrupts binocularity among simple cells in the visual cortex and produces loss of X-cells in the LGNd, while at the same time apparently leaving unaffected complex cells in the visual cortex and Y-cells in LGNd.

At the same time, however, the results raise a possibility which has not been con-



Fig. 2. Same data as in Fig. 1, expressed as a function of eccentricity of receptive field location Eccentricities run from the vertical meridian (0°) to the beginning of the monocular segment (M). The frequency of X-units is expressed as a function of the total population (frequency of X fields plus frequency of Y fields) at each location. The numbers in parentheses refer to the total number of fields from which the percentage of X fields was calculated at each point. Following chronic monocular paralysis, X-cells in the LGNd were encountered with markedly diminished frequency at all retinal eccentricities in the binocular segment.

sidered in the parallel processing model (6). According to Fiorentini and Maffei (5), a certain proportion of simple cells continue to be driven by the paralyzed eye after chronic monocular paralysis. It seems unlikely that these cells receive their input from LGNd X-cells, since so few Xcells remain responsive to stimulation via the paralyzed eye. This suggests that after

Surface Albedo and Desertification

Otterman (1) has proposed that desertification in regions of marginal rainfall may be due to an increase in surface albedo caused by the removal of vegetation by overgrazing. He hypothesizes that, when high-albedo soils are denuded, the resultant increase in surface albedo causes lower surface temperatures, which in turn reduce the heat input to the lower atmosphere, decrease its temperature lapse rate, and hence somewhat reduce convective activity leading to rainfall. Over a period of several years we have measured albedos and surface temperatures of soils and plants in the Sonoran Desert climate of the southwestern United States, and, from the results of our investigations, we would predict that the denuded surface would be warmer than the vegetated one. Since the importance of correctly identifying the climatological mechanisms of desertification cannot be overemphasized in light of the devastation and human suffering caused by these processes in the Sahel (2), we believe that further analysis is warranted.

The primary data to be used in this context were obtained in May-June 1974 at

monocular paralysis, many simple cells in the visual cortex may be driven by Y-cells of the LGNd.

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Phoenix, Arizona. For about a week, we kept four different soils in 25-m² plots very wet by spraying them with water every morning, noon, and night. During this time, air temperature (T_A) , surface soil temperatures (T_s) , and albedos were measured every 20 minutes with fine-wire copper-constantan thermocouples and upright and inverted solarimeters. The soils were then allowed to dry. When the volumetric water contents of their upper 2 cm were between 2 and 4 percent, similar data were obtained for another week. Details of this work and closely allied experiments have been reported elsewhere (3).

Figure 1 shows the average difference between T_s and T_A for the four different soils when wet and when dry at 1400 local time as a function of their mean albedo at that time. When the soils are wet, T_s is nearly equal to T_A and is insensitive to albedo variations. When the soils are dry, however, T_s rises far above T_A and is very sensitive to albedo. Indeed, the predicted drop in T_s relative to T_A in traversing the postulated albedo range 0.25 to 0.37, suggested by Otterman (1) as representative of