

low-order sensory interneurons, all areas of arthropod neuropil are probably comprised entirely of identifiable neurons and clusters.

A nervous system with 10^2 neurons, such as that of a nematode (17), can be constituted entirely of identified neurons and clusters. My data support the notion that a nervous system with 10^5 central neurons, such as that of a locust, could also be so constituted. While studies of identified neurons and clusters in invertebrate nervous systems have progressed from giant interneurons to large interneurons and motoneurons (and now to small interneurons), our knowledge of identified neurons and clusters in vertebrate nervous systems is based solely on a few studies of giant interneurons (3). Although it is not possible to predict where most vertebrate neurons will occur along the spectrum of equivalence, as we investigate the central nervous systems of vertebrates with finer anatomical and physiological techniques, we will probably find less equivalence and a greater tendency toward uniqueness.

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- An *identified neuron* is a unique neuron (a single cell with no other equivalent cells) that has a constant anatomy and physiology in conspecific animals, in that it can be repeatedly recognized from animal to animal and distinguished from all other neurons. An *identified cluster* is a unique cluster (a fixed number of equivalent cells with no other equivalent cells) with a constant anatomy and physiology in conspecific animals; these clusters often contain only a small (numerically fixed) number of equivalent neurons. Two neurons are defined as equivalent when any single cell, considered alone and out of context, cannot be anatomically or physiologically distinguished from the other cell. Theoretically, an identified cluster is numerically invariant (just as an identified neuron is always a single cell). In practice, however, one can occasionally observe a supernumerary cell (anatomical duplicate of normally occurring cell) occurring as an equivalent (or duplicate) cell of an identified neuron (7) or as an additional equivalent cell within an identified cluster (4, 7). An *identified class* comprises equivalent neurons and does not imply that the number of these neurons is constant; these classes often contain a large (numerically variable) number of equivalent neurons.
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- The concept of a spectrum of equivalence, with neurons that are unique having zero-equivalence, comes from T. H. Bullock, in *The Neurosciences; Third Study Program*, F. O. Schmitt and F. G. Worden, Eds. (MIT Press, Cambridge, Mass., 1974), pp. 343-346. In this report I follow that usage of the term "unique."
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Abolition of Direction Selectivity in the Visual Cortex of the Cat

Abstract. *Cats were reared in a stroboscopically illuminated environment, which deprived them of experience with visual movement but allowed them form vision. In these cats, neurons of the visual cortex displayed normal orientation selectivity, but direction selectivity was virtually abolished. The effect remained unaltered by long periods of normal visual exposure.*

The response characteristics of single cells in the cat visual cortex can be profoundly modified by rearing animals in special visual environments (1, 2). Since, in everyday life, visual stimuli are in constant motion on the retinae, interest has been focused on the consequences of restricted experience with visual move-

ment for cortical development. Rearing animals in stroboscopic illumination (strobe rearing), which deprives them of experience with movement but allows them patterned visual input, results in reduced orientation and direction selectivity among cortical neurons (3). The low-frequency stroboscopic environment used in previous experiments (one flash every 2 seconds) can be made progressively more like the normal environment by increasing the frequency of the flashes. As the frequency was increased, we were able to examine the emergence of characteristic cortical properties. We now report that strobe rearing at an intermediate frequency (eight flashes per second) results in a cortex containing neurons with orientation selectivity but rarely with direction selectivity.

Five kittens served as subjects in these experiments. They were raised from birth in a lighttight enclosure in which the only illumination source was a strobe light flashing eight times per second. The 10- μ sec flash duration ensured a series of stationary retinal images. The human subjective experience is that of a series of jerky images, reminiscent of the early motion pictures. After 4 to 6 months, we studied the visual responses of single neurons in the striate cortex according to methods and criteria that have been described elsewhere (4, 5). Responses in strobe-reared kittens were compared with responses of kittens reared in the dark and those of normal cats. We classified units as orientation selective if

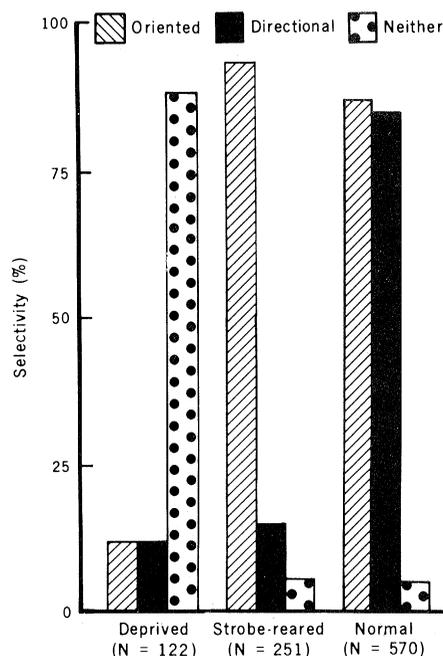


Fig. 1. Percentages of units displaying orientation selectivity, direction selectivity, or neither property in cats reared in the dark, strobe-reared, and reared normally. For each group, N represents the total number of units studied in the various groups of cats. Data for normal and deprived cats were derived from Cynader, Berman, and Hein (5).

they responded well to flashing or moving slits of a given orientation and poorly to other orientations. Orientation-selective neurons were classified as direction selective if thin slits moving in the presumptive preferred direction evoked at least twice as many spikes per presentation as slits moving in the non-preferred direction. In initial experiments, we assessed direction selectivity simply by listening to unit responses over a loudspeaker, but in later experiments an averaging computer was used.

Orientation selectivity was a common feature in both normally reared cats and those reared in the stroboscopic light, although it was rarely found in those reared in the dark (Fig. 1). The breadth of orientation tuning for individual units was comparable in the strobe-reared and normal groups. By contrast, the occurrence of cells with direction selectivity was much rarer in the strobe-reared group than in normal cats and did not differ significantly from the proportion found in cats reared in the dark. The reduction of direction selectivity for the strobe-reared group was observed among both the simple and complex classes of cortical neurons. We also compared responses to visual stimuli moving at different velocities in cortical neurons of strobe-reared and normal cats. No differences either in preferred stimulus velocities or in breadth of velocity tuning were observed; slowly moving visual stimuli were most effective in activating striate cortex neurons in both groups of cats.

We were concerned about the permanence of the changes in cortical organization brought about by the restricted environment. In most situations, alterations caused by early deprivation are largely irreversible, once the "critical period" has passed (2, 6). Because a number of exceptions have been reported (5, 7), however, we assessed the consequences of a recovery period in a normally lit animal colony room. We recorded repeatedly from the same animal at varying intervals after allowing it normal exposure. There was little additional direction selectivity after 6 months in the normal environment (Fig. 2). Thus, the deprivation effects were largely irreversible, although further experiments would be required to establish whether any small residual plasticity remains.

Three main conclusions may be drawn. (i) It seems necessary to expose the retina to motion during postnatal development in order to develop mature direction selectivity among cortical neurons. (ii) The ability to preferentially de-

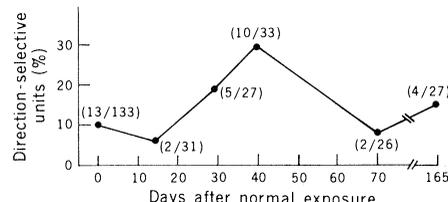


Fig. 2. Percentage of direction-selective units encountered in successive recording sessions from the visual cortex of strobe-reared cats as a function of time after introduction to the normal environment. The numbers in parentheses represent the number of direction-selective units over the total units for that recording session. The $T = 0$ point includes data collected from all five cats. In normal cats, 83 percent of the neurons found are direction-selective.

prive a major facet of cortical selectivity while leaving intact other properties, such as orientation selectivity and velocity specificity, implies that these properties of cortical cells are determined by largely independent mechanisms. (iii) The deprivation effects cannot be reversed by normal visual exposure if the initial deprivation is maintained for the first few months of life. The preparation described above may prove a useful tool

Magnetic Direction Finding: Evidence for Its Use in Migratory Indigo Buntings

Abstract. *The orientational capabilities of caged migratory indigo buntings were studied under differing magnetic field conditions. When tested in a situation allowing minimal exposure to visual cues but in the presence of the normal geomagnetic field, the birds demonstrated a significant orientation in the appropriate migratory direction (to the north). When the horizontal component of the magnetic field was deflected clockwise 120° by activation of Helmholtz coils surrounding the cage, the orientation of the buntings shifted accordingly (clockwise to geographic east-southeast). These results suggest that indigo buntings are not only able to detect the geomagnetic field, but also can use this information in the finalization of their migratory direction.*

In recent years there has emerged a growing body of evidence that birds might detect, and their behavior be altered by, changes in the earth's magnetic field. These range from cases where errors or disruptions of orientation are correlated with magnetic storm activity (1), through experiments where homing abilities of pigeons and gulls are altered when miniature Helmholtz coils or disk or bar magnets are attached to their bodies (2), to cases where nocturnal migratory orientation of caged songbirds shifts predictably when the direction of the surrounding magnetic field is altered (3, 4). Experiments with migratory birds are of especial theoretical importance since, by predictably altering the birds' orientations, they stand practically alone in

for behavioral and structural studies by providing a system in which a specific part of the cortical circuit has been altered.

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demonstrating that magnetic information not only can disrupt normal orientation, but also can be used actively in the finalization of the appropriate direction.

The principal studies of migratory orientation in artificial magnetic fields come from the laboratories of Merkel and Wiltshko at the University of Frankfurt am Main (Germany). They have reported that European robins (*Erithacus rubicula*) and three species of European warbler (genus *Sylvia*) will orient their spontaneous nocturnal migratory activity (zugruhe) in a seasonally appropriate direction when deprived of all meaningful visual cues but in the presence of normal geomagnetic information (3). Further, when the magnetic field is altered by means of Helmholtz coils, the directions