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11. We thank I. Kupfermann for beneficial discussions; I. Kupfermann, A. O. D. Willows, and M. V. S. Siegler for criticisms of the manuscript; K. Hayes and E. Wildenradt for technical assistance; B. McLaughlin for advice with the statistical analysis; D. Kennedy for the loan of electrophysiological equipment; and A. Donaldson for assistance in photography. Supported by a Helen Hay Whitney postdoctoral fellowship (to G.J.M.) and by NIH research grants NS-09050 (to W.J.D.) and NB-02944 (to D. Kennedy).

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Selective Visual Experience Fails to Modify Receptive Field Properties of Rabbit Striate Cortex Neurons

Abstract. *During development, rabbits were exposed only to vertical or horizontal lines to determine if the receptive field characteristics of visual cortex cells would be altered as they are in the cat. Motion and directional selectivity were preserved, and orientation specificity remained unaffected by the restricted experience, which suggests that the rabbit may lack the neural plasticity seen in some other mammals.*

It is well known that modifications of the visual environment can produce dramatic alterations in the brain. Enrichment of visual experience as well as visual deprivation have been shown to cause corresponding changes in the anatomy, physiology, and behavior of some mammalian species (*1–3*). Recently, it has been demonstrated in the cat that the type of visual experience to which that mammal has been exposed during development may actually determine the receptive field properties of single neurons in its visual system (*4, 5*). Most single cells in the cat's visual cortex are responsive only to straight line stimuli such as edges or bars, and these must be of a specific orientation. In the normal animal, the optimal orientation of such stimuli varies from cell to cell, so that all axes of orientation are represented (*6*). When the visual experience of kittens is restricted to vertical or horizontal stripes, the neurons in the visual cortex of these animals will respond only to bars whose orientation is similar to that experienced during infancy (*4, 5*). These experiments suggest that the visual environment can influence the functional neural connections of at least one species.

The mechanisms which permit these neural modifications in the cat have not yet been specified, although phylogenetic status or type of visual system organization may in part determine the extent to which a given species is capable of such alterations. These considerations would seem to be of particular relevance in the light of evidence that the formation of neural connections in some lower vertebrates cannot be appreciably modified by visual experience (*7*). Thus, the degree of encephalization of visual function, the extent to which the retinal projection is crossed, the amount of binocular interaction present, or the complexity of visual processing which occurs at the level of the retina may all relate to the degree of neural plasticity possible in the visual system of different animals.

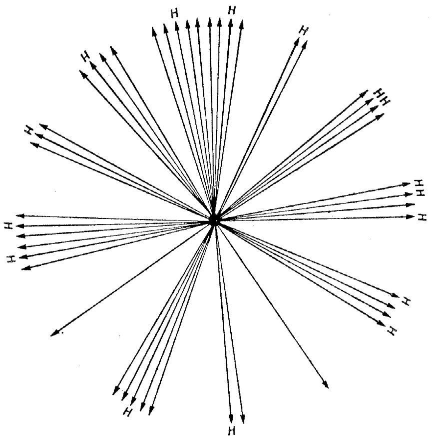

Fig. 1. Preferred directions of 45 directionally selective single cells recorded from the striate cortex of nine rabbits. Directional preference is indicated by the arrow and is related to the animal's visual field. Cells recorded from rabbits exposed to horizontal stripes are designated by an *H* at the arrowheads. All others were recorded from vertically experienced animals. Directional preference was always classified in 30° axial steps. Arrows have been equally distributed around the 30° axes for clarity only. Top, superior; bottom, inferior; left, anterior; right, posterior.

The rabbit visual system provides an excellent opportunity to explore the relation of these factors to plasticity in the nervous system, since the organization of this visual system combines properties seen in both lower vertebrates and higher mammals. As with the visual systems of higher mammals, a high degree of encephalization of visual function is present in the rabbit. On the other hand, the visual system of the rabbit parallels that of certain lower vertebrates to the extent that complex analysis of specific stimulus features occurs at the level of the retina.

We have found that receptive field properties of single neurons in the primary visual cortex of the rabbit are not modified by selective visual experience. Restriction of visual experience to stripes of a particular orientation fails to produce changes in the orientation preferences of orientation-sensitive cortical cells, and neither motion nor directionally selective cells, also found in the visual cortex of the rabbit, are altered by the selective environment. Our findings suggest that the capacity for visual system reorganization imposed by selective visual environments may vary dramatically among various mammalian species.

We reared Dutch belted rabbits in the dark from shortly after birth, and at about 10 days of age, when their eyes normally open, we began placing them in "visual experience" tubes which replicated as precisely as possible those previously used in kitten studies (*5*). Each tube was constructed of molded plexiglass 92 cm high and 46 cm in diameter with black and white stripes of different widths placed all around the perimeter of the tube. Some of the tubes had horizontal stripes, some vertical. Each tube was illuminated by a photoflood lamp whose light was evenly diffused through a translucent plexiglass lid which covered the top of the tube.

On each test day, the rabbits were placed on a clear plastic disk in the middle of the tubes so that the stripes were visible both to the superior and inferior portions of their visual field. The visual world of each animal was further limited by placing an opaque black collar around its neck to prevent sight of its own body. The rabbits were given almost daily experience in the tubes, averaging 6 hours per day, and were kept in total darkness at all other times.

When the animals were 60 to 100 days of age, they were removed from the dark room long enough to prepare them for electrophysiological recording, using techniques previously described (*8*). Single unit recordings were initiated several days later. Each animal was anesthetized with halothane and nitrous oxide, a tracheotomy was performed, and the animal was placed in a stereotaxic instrument by means of a previously attached bolt. The dura was removed and agar gel was placed over the visual cortex. A long-lasting anesthetic (Zyljectin) was applied to all incised areas and the gaseous anesthetic was discontinued. The animal was paralyzed with an injection of galamine triethiodide (Flaxedil) and artificially respirated.

During the experiment, the animal faced a tangent screen placed 57 cm in front of his eye, which was fitted with a +1 diopter contact lens. Spectacle lenses were used to focus the eye on the screen. Stimuli were various hand-held light and dark objects projected on the screen. Most were projected from a hand-held ophthalmoscope.

Single neuron activity was recorded extracellularly with tungsten microelectrodes, conventionally amplified, displayed on an oscilloscope, and recorded on magnetic tape. At the end of a penetration, the electrode tract was marked with an electrolytic lesion for subsequent verification of the recording site.

We have now studied the receptive field properties of 160 striate cortex neurons from 12 stripe-experienced rabbits. The full complement of receptive field types found in the normal rabbit striate cortex (*9*) were also identified in our experimental animals, as shown in Table 1. The percentages of each type of receptive field agree well with those found in the normal animal. Thus, selective visual experience failed to prevent the development of any type of receptive field observed in the striate cortex of the normal rabbit.

The response properties of motion and directionally selective units were examined in particular detail, since the tube environment of our experimental rabbits eliminated all experience with objects moving in the visual field. Although eye and body movement assured that the animals experienced self-induced motion with respect to a stationary environment, the animals experienced virtually no movement of the environment with respect to themselves. Despite this absence of external movement, we found a normal percentage of motion and directional cells. In addition, neither vertical nor horizontal stripe experience influenced the directional preferences of directionally selective cells. As in the normal rabbit striate cortex (*9, 10*), no directional axis within the visual field was favored to the exclusion of other directions (Fig. 1).

The selective stripe experience also failed to modify the distribution of orientation preferences of elongate receptive fields in our experimental animals. In the rabbit, three classes of

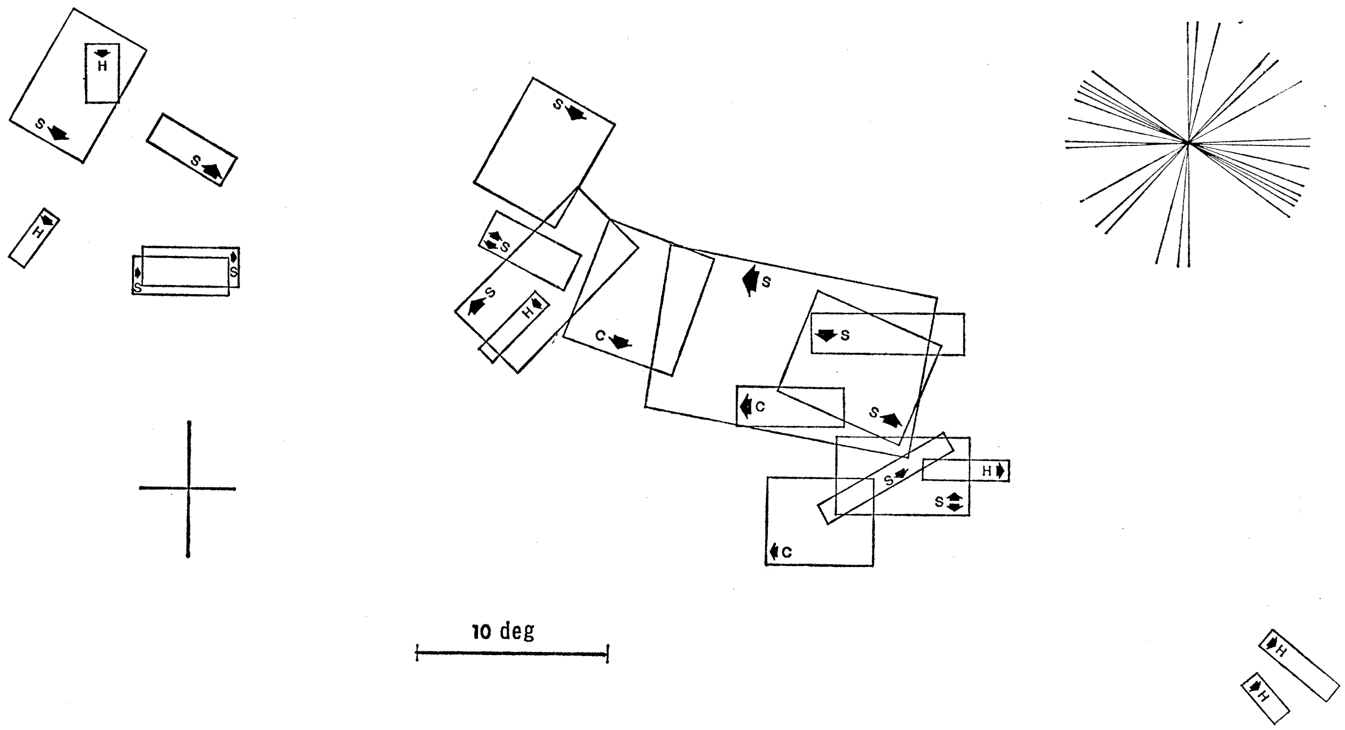

Fig. 2. The receptive fields of simple, complex, and hypercomplex cells recorded from seven rabbits reared in vertically striped tubes. The position and size of each field has been preserved. The type of each cell is indicated by a letter within the receptive field boundary: S = simple cell; C = complex cell; H = hypercomplex cell. Arrows indicate the direction of movement which produced the optimal response. For simple and complex cells, the preferred stimuli were bars or edges oriented parallel to the trailing edge of each arrow. For hypercomplex cells, the optimal stimulus was a bar or "tongue" whose orientation was parallel to the long axis of the receptive field and moved in the direction indicated by the arrow. The inset at the upper right graphically represents the preferred stimulus orientations of all 13 simple cells recorded from vertically experienced animals. The receptive fields of one simple and one hypercomplex cell are not shown because of their location in the far anterior field. The + designates the position of the optic nerve head.

Table 1. Classes of receptive fields identified in rabbit primary visual cortex. Data from Chow *et al.* (*9*) from the normal rabbit have been included for comparison with data following selective visual experience.

Study	Type of receptive field								
	Concentric	Uniform	Motion	Direction	Simple	Complex	Hypercomplex	Indefinite	No response
Chow *et al.* (1971)									
No. of units	25	6	31	40	37	18	8	29	18
Percent total	12	3	15	19	17	8	4	13	8
Mize-Murphy									
No. of units	19	9	36	45	19	4	8	16	4
Percent total	12	6	22	29	12	3	5	10	3

elongate fields have been identified—simple, complex, and hypercomplex cells (*9*). In most respects, they are identical to the same type of unit described in the cat (*6*). Although the three elongate receptive field classes in the rabbit vary in the specificity of their response to some stimulus parameters, they share the common characteristic of responding selectively to bars or edges of a specific orientation. In the normal rabbit, most receptive fields of simple cells are oriented along an axis which parallels the visual streak—a specialized region of the rabbit retina with a high ganglion cell concentration extending across most of the horizontal axis of the retina (*9*). Consequently, if the selected environment had affected the orientation preferences of our sample of simple cells, the effect should have been most pronounced in animals which were reared in tubes with vertical stripes.

Figure 2 shows the receptive field plots of 21 elongate cells which we recorded from seven vertically experienced animals. It is clear that the preferred orientations of bars or edges which produced the optimal response in these cells vary widely. Of the neurons with simple receptive fields recorded from vertically experienced animals, 62 percent have orientation preferences within 35° of the horizontal axis. The majority of these simple fields lie along the axis which nearly parallels the visual streak, as is the case with the normal rabbit. The three neurons which preferred nearly vertical orientations also probably lie within the limits of the normative data, since simple cells with vertical orientation preferences are occasionally seen in normal rabbit visual cortex (*9, 10*). In our much smaller sample of complex and hypercomplex cells, there was also no bias toward the vertical orientation.

We recorded from only four horizontally experienced rabbits, since we did not anticipate that the effects of this type of environmental modification would be revealed in an animal whose simple cells normally prefer horizontally oriented elongate stimuli. Of the six simple cells recorded from animals with horizontal experience, four preferred orientations within 45° of the horizontal axis. One unit was found which had a preferred orientation 30° from the vertical axis, so it seems apparent that the horizontal stripe experience also failed to produce changes in the orientation selectivity of single cells in rabbit visual cortex.

In conclusion, we have found no evidence that restricted visual experience in infancy can modify the functional organization of single neurons in the visual cortex of the rabbit (*11*). This result contrasts markedly with the rather dramatic modifications found in the visual system of the cat following selective visual experience. However, our findings receive support from studies (*12, 13*) showing that in the rabbit visual system deprivation during development does not result in any of the dramatic behavioral or physiological anomalies reported for the cat reared under these conditions (*2, 3*).

Why environmental influences should affect the cortical physiology of the cat but not the rabbit remains uncertain. The degree of encephalization of visual function in the two species is unlikely to account for the differences, since the striate cortex is prominently involved in pattern and form vision in both the rabbit and the cat (*14*). The extent to which the functional organization of the visual cortex of the two species can be modified by visual experience may be related to the amount of binocular interaction present at this level of the visual system. However, even in the small region of rabbit visual cortex where binocular interaction is present, visual deprivation has little effect on neural response properties (*13*).

It remains possible that the degree of visual system plasticity seen in various mammalian species is related to the complexity of functional organization at the level of the retina. In this respect, there are conspicuous differences between the cat and rabbit. The retinal ganglion cells of the cat have concentrically organized receptive fields which are not specialized for the detection of complex spatial forms (*15*). Detailed analysis of specific stimulus features is postponed until the level of the primary visual cortex, where almost all receptive fields are selectively responsive to orientation information. In the rabbit, on the other hand, complex spatial analysis of specific stimulus features is already occurring at the retina, where both local edge detection and orientation selectivity are observed in the ganglion cells of this species (*16*). Distinctions between the retinal organization of the two species are further supported by anatomical evidence demonstrating a much more complex synaptic arrangement in the retina of the rabbit than is seen in the cat (*17*).

Thus, the apparent lack of plasticity in the visual cortex of the rabbit may be the result of a complex retinal organization determined by rigid genetic specification. By contrast, the functional reorganization found in the cat following selective visual experience may depend upon the delay in complex feature analysis until the level of the visual cortex, where neural organization may be more susceptible to functional modification. Although corroborative data from other species are needed to decide this point, our data do emphasize the extent to which neural plasticity in development can vary in different mammals and suggest that the effects of developmental manipulations in cats and primates are much more likely to be applicable to human studies.

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Preserve Guatemalan Teosinte, a Relict Link in Corn's Evolution

Wilkes (1) describes how Mexican maize depends upon a limited gene flow from its closest relative, teosinte, for variability, heterotic vigor, and yield. Because of increased grazing and other land uses in the teosinte habitats around Mexican maize fields, as well as the replacement of the native races of maize with uniform commercial varieties, this sympatric relation between the crop plant and its wild relative is threatened. Wilkes suggests that the genetic wealth represented by these sympatric partners from Mexico be preserved.

Apparently the Mexican teosintes and their maize partners have undergone a coevolution that permits a constant gene flow between them while maintaining their distinct female spikes through block inheritance of the controlling genes. This response of the Mexican teosintes to gene flow from maize, imposes two limitations upon their usefulness for maize breeding, limitations not shared by their more primitive counterpart isolated from maize in Jutiapa, Guatemala: (i) the introgression from cultivated maize in Mexico would cause some loss of teosinte's original ability to endure the rigors of a truly wild plant and (ii) some of the germplasm of Mexican teosinte has become locked up in blocks and is, thereby, less available for maize improvement. This block inheritance in crop plants is assumed to be a product of disruptive selection between man, on the one hand, and nature, on the other (2). The presence of four or five of these inherited blocks in segregating progenies from hybrids of maize and Mexican teosinte has been demonstrated repeatedly (3).

In contrast, the more primitive teosinte from Jutiapa, as shown by Rogers (4, p. 555), "differs from maize by genes distributed upon most of the chromosomes, while other teosintes [Mexican] represent types which differ from maize by genes of a more localized nature on a few chromosomes." Furthermore, while the hybrid of maize with the Guatemalan teosinte called "Florida" has the same amount of crossing over in the sugary glossy-3 ($SuGl_3$) region as does maize itself, the maize–Nobogamé teosinte (Mexican) hybrid has suppressed crossing over in this same region on the long arm of the definitive fourth chromosome (5). Thus, the Guatemalan teosintes appear to have the primitive kind of genetic architecture that would be expected in a remote common ancestor before an assemblage of block inheritance under the domestication of *Zea* spp. (maize or teosinte or both) in Mexico. In Mexico, where maize and teosinte became genetically symbiotic during domestication, the two species were able to maintain their distinct female spikes by assembling blocks of the controlling genes.

That the Guatemalan teosintes are primitive rather than just derived in isolation from the Mexican teosintes is suggested by a number of traits that are more similar to those of *Tripsacum*, a more distant and primitive relative of maize, than they are to those of Mexican teosinte and maize. Like most species of *Tripsacum*, rather than its Mexican counterparts, the Guatemalan race, the teosinte found in the region of Jutiapa, has terminal knobs on its chromosomes (6), elongate trapezoidal fruit cases, and large flattened staminate glumes. In addition, it tends to be a perennial (as is the tetraploid teosinte of Jalisco, Mexico), and has adapted to moist, medium elevations rather than dry, high elevations (7). Unlike both *Tripsacum* and Mexican teosinte, the Guatemalan teosinte has large pollen that compares favorably in size with that of present-day maize and that of the oldest known archeological remains of maize (5). Thus, the Guatemalan type of teosinte appears to be a primeval source of variation from which both maize and Mexican teosinte could have emerged under domestication.

The Guatemalan teosintes, as well as the Mexican teosintes, should be preserved as a reservoir of variability for maize improvement.

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