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FINAL TECHNICAL REPORT

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"NEURONAL ANALYSIS OF VISUAL PERCEPTION"

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During the past years this grant supported two general areas of research conducted in our laboratories. This first group includes studies on the receptive fields of single cells in the visual system of cat and squirrel monkey, on the vestibular input affecting these cells, and on the cell's responses during visual discrimination learning process. The second group includes extensive studies on the receptive field characteristics of the .abbit visual system, its normal development, its abnormal development following \isual deprivation, and on the structural and functional re-organization of the visual system following prenatal and prenatal surgery.

I. Studies on the Visual System of the Cat and Squirrel Monkey

A. Effect of body-tilt on the orientation specificity of striate cortical cells--: Receptive fields of single units in the visual cortex of the cat were studies in an attempt to find manifestations of sensory interaction between visual and vestibular systems. The preferred direction of cortical units was mapped in paralyzed unanesthetized animals with the cat horizontal and again when the cat was tilted. Results did not support the idea of any specific receptive field compensatory mechanism, but the existence of nonspecific vestibular effects on visual cortex cells was not ruled out.

B. Effect of vestibular stimulation on the cell responses in the striate cortex and superior colliculus: 1) The effect of labyrinthine polarization on single cells in the cat visual system was studied in 106 visual cortex and 137 superior colliculus neurons. The principal influence observed in cortex was an increase in unit firing rate above spontaneous activity and a facilitation of the unit's response to light; the dominant effect in colliculus was a decrease in spontaneous firing rate and/or a depression of the unit's response to light.

2) Suppressive effects in colliculus were not mediated by visual cortex, since such suppressive effects were present in cats with visual cortex lesions.

3: Round window stimulation effects were compared to the effects of stimulation calculated to induce general arousal; similar effects were sometimes observed, but different responses were often elicited from the same unit by round window and forepaw or reticular formation stimulation.

4) In cats in which the VIIth-VIIIth nerve complex had been sectioned, round window polarization still had a definite influence on visual neurons.

5) The use of labyrinthine polarization as a method for activating specific vestibular pathways was discussed; experimental evidence suggested that multiple pathways, including non-specific ones, may be activated by round window stimulation.

C. Lateral geniculate neurons--: Thirty-nine neurons were recorded through implanted microelectrode from the lateral geniculate body of three normal, behaving cats. They were obtained when the cats were performing two different visual discriminations. Using go-no-go method, they were trained to discriminate: 1) different rates oflight flashes and 2) light flashes against light flashes against light flashes plus tone. There is little evidence for task-related changes in neuronal discharge patterns as seen in post-stimulus time histograms. Instead transient and unsystematic trial-to-trial variations are greater than any correlated with the cat's performance.

D. Response characteristics of pulvinar cells in the squirrel monkey: Visual and somatosensory responses were studied in 329 neurons in the pulvinar of the squirrel monkey. Almost all somatosensory neurons (total = 46) were in pulvinar lateralis (PL); most had continuous peripheral fields, though a few were bilaterally activated. Visual neurons (total = 179) were found in PL, pulvinar inferior (PI) and pulvinar medialis (PM). Of these, 29 responded only to diffuse illumination, while 150 had definable receptive fields. Approximately twice as many neurons in PI were responsive to light than neurons in PL or PM. The majority of visual units was responsive to some form of moving stimulus, and for some neurons there were additional specificities for directionality and orientation. Most visual neurons were monocularly driven (75%); nearly all visual units which could be mapped had receptive fields within 25° of the fovea. The majority of fields was in the visual hemifield contralateral to the recording electrode. Most visual neurons had receptive fields of at least 100 sq. degrees in area. A third group of 104 neurons was found unresponsive to visual and somatosensory stimuli.

II. Studies on the Rabbit Visual System

Our studies on the rabbit visual system were concerned with the following six general areas: 1) We have completed a series of studies on the development of receptive field characteristics of neurons in the lateral geniculate nucleus (LGN), the superior colliculus (SC), and the striate cortex (CTX) in the neonatal rabbits. 2) We have completed another series of studies on the effects of visual deprivation (monocular eyelid-suturing) on the receptive field development, especially on the effects of the length of the deprivation period. 3) Several anatomical studies on the prenatal and neonatal development were initiated; including the corpus callosum and the retinotectal projection. 4) Analytic studies on the physiological organization of the visual system included a study on the classification of the LGN and striate cortical cells into X or Y types, and another on the functional organization of the spatial columns in the striate cortex. 5) Anatomical studies on the temporal visual area, on the distribution of the corticogeniculate and the corticotectal cells, and on the lack of cytoplasmic laminated bodies in the LGN were completed. 6) We had initiated studies on the possibility of structural and functional reorganization in the rabbit visual system following neonatal or prenatal surgery.

A. Normal development of receptive field characteristics

In a series of 4 papers we have studied the receptive field characteristics of neurons in the rabbit visual system and determined our relative proportions of each receptive field type in each structure (Stewart, et al, 71; Masland, et al, 71; Chow, et al, 71; Mathers and Mascetti, 76). We found that neurons in the rabbit visual system, like those in other animals, respond differentially to specific stimulus features, and can thus be classified into several receptive-field types. We have consistently employed the following classificatory scheme for receptive field types. The receptive field types in the dorsal nucleus of lateral geniculate body (LGN) are: the familiar concentric type, the uniform type, the motion-sensitive type; and the directionally-selective type. The former three types are further grouped as cells with non-oriented fields. There are very few cells unresponsive to light stimulation in the LGN. Besides the four types of cells listed above, three additional types can be distinguished in the striate cortex: simple cells; complex cells; and oriented-directional cells. These three types are collectively termed cells with oriented receptive fields. In addition, some cortical cells respond either to strong whole eye illumination, or respond erratically to stimuli in a local area; these are classified as cells with indefinite fields. The cells in supeior colliculus (SC) compromise the three non-oriented cell types, and the directionally-selective, oriented-directional and indefinite cells.

In a series of four papers (Mathers et al., '74; Rapisardi et al., '75; Spear et al., '72; F[illegible] et al., '78) we have completed a survey of the development of receptive fie[illegible] characterisitics of neurons in the LGN, SC, and CTX in rabbit pups. The findings showed that cells with adult-like receptive field properties existed prior to the time when the rabbit's eyes opened (at about 10 days of age). But their numbers were small. Most of these cells were unresponsive to higher stimulation. We, therefore, used a population approach to study the maturation process. We reasoned that a structure may not be considered matured until all neurons or neuronal groups not only reach their final stages of morphological and physiological development, but also the same proportions found in the adult. When viewed this way, the visual pathways of rabbit appeared to develop continuously long after the animals' eyes first open.

Fig. 1 shows the development of the proportions of all light-excitable cells in the LGN, SC, and CTX. As early as 5-6 days after birth, there were about 30 percent of geniculate cells, and about 10 percent of striate corticla cells, could be excited by light stimulation. The proportions of cells responsive to any sort of light stimulation grew to about 80 percent at the time of eye-opening, and continued to increase for another 10-30 days before reaching adult levels. The displacement of the LGN curve to the left indicated that geniculate cells developed earlier than collicular and cortical cells by about two days.

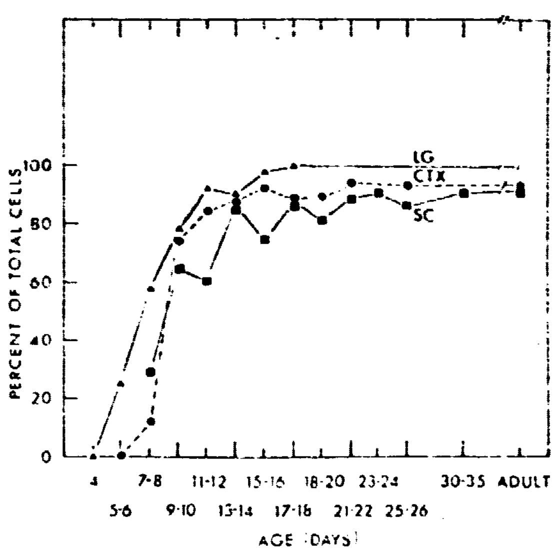

Fig. 1. Postnatal development of responsive cells in the rabbit's lateral geniculate nucleus (LG), superior colliculus (SC), and striate cortex (CTX). Percentages of cells responsive to any light stimulation are plotted as a function of age. In this, and the following two figures, the shaded column indicates the time when the eyes normally open.

The development of the individual receptive field types in these structures is plotted separately in Fig. 2. The developmental curves of the three types of non-oriented cells were comparable. They were combined in the collicular and cortical graphs. Similarly, the three oriented cell types in the cortex were combined. (The directionally selective cells were not included.) These graphs clearly showed that the development of specific feature extraction was a continuous process, starting well before the animal's eyes open for cells disolaying non-oriented fields, and after eye-opening for cells with oriented fields. Both these types increased in relative numbers over the subsequent weeks. The indefinite cells were an exception. These cells have a complex growth pattern: their relative numbers first increased to a peak at, or slightly after, eye-opening, and progressively decreased to the adult proportion. The declining phase of their growth curve appeared to be the reciprocal of the inclining phase of the oriented cells' curve in the striate cortex.

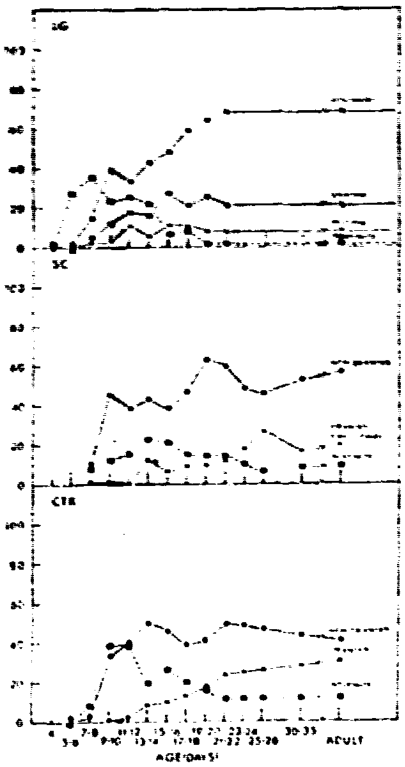

Fig. 2. Time course of receptive field development in the rabbit's LG, SC, and CTX. The percentages of cells exhibiting various receptive field characteristics are plotted as a function of age. The concentric, uniform and motion-sensitive receptive fields are grouped under non-oriented cells. The simple, complex, and oriented-directional receptive fields are grouped under oriented cells.

B. Effects of Visual Deprivation

In another series of publications (Fox et al., '78; Baumbach & Chow, '79; Grobstein et al., '75). We have studies one aspect of the visual development seldom addressed by other investigators; how the length of monocular deprivation affected the development of the different types of receptive fields.

In the LGN, the relative proportions of different cell classes reached the adult status at about 20-25 days of age. When the animal was monocularly-deprived during this period, the distribution of receptive fields in the deprived LGN was significantly different from that obtained in the control LGN ($P < 0.001$, χ^2 test). There were significantly more unresponsive and indefinite cells in the deprived LGN, i.e., 24% in corresponding lack of uniform cells in the deprived LGNd. When deprivation was continued to the young adult age (82-116 days), such abnormal distributions persisted, but were less severe than those obtained by shorter deprivation periods. There was still a higher proportion of unresponsive and indefinite cells than were seen in the undeprived structure, and this difference was significant ($P < 0.001$). But the proportion (16%) of such cells was considerably lower than the proportion (24%) obtained from the 20-25 day deprivation group.

The results of a more detailed study on the SC cells are shown in Fig. 3. The top two graphs show that the increase in percentages of all light-responsive neurons and the non-oriented cells in the deprived colliculus did not differ from that in the control colliculus. However, the oriented-directional cells showed an initial growth rate which was identical in the deprived and normal colliculus for about 3 weeks; but starting at day 21-22, a precipitous decrease in the percentage of oriented-directional cells occurred in the deprived colliculus. These cells reached a high of 12% at day 19-20, but fell to a low of 4% at day 25-25, and maintained that level to the end of the fifth week. The curves for the indefinite cells also show that there were complex changes in the development of these cells, changes which were highly correlated with those which were seen in the development of the oriented-directional cells. These two groups of cells in the deprived SC appear to grow normally after eye-opening, but then abruptly departed from the normal course; i.e., showing a decrease of oriented cells accompanied with an increase of indefinite cells.

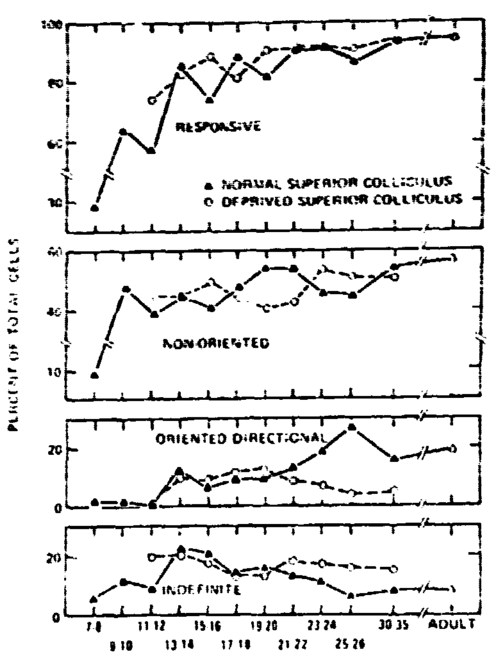

Fig. 3. Comparison of the postnatal development of responsive cells in the rabbit's SC receiving either normal light stimulation or inputs from a sutured eye. The solid lines are the normal data and the interrupted lines the data from the deprived colliculus. The top panel depicts the percentages of cells responsive to any light stimulation. Note the differences between the two sets of curves evident in the lower two panels which represent the oriented-directional cells and the iddefinite cell.

The effect of visual deprivation on striate cortical cells was less extensively studied. Only four groups of neonatal rabbits were used. The lengths of deprivation ranged from 20-25 days to 3-14 months. Fig. 4 illustrates the results. The open bars are the percentages of cortical cell types in normal 9-10 day old rabbits and adults. The filled bars represent the percentages found in the deprived animals. The deprived group at 25 days old showed a significantly lower number of cells responsive to any light stimulation, a significantly higher number of indefinite cells, and practically no oriented cells. With longer deprivation, the relative frequency of the receptive fields progressively changed toward the normal adult level. By 3-14 months, the distribution of cell types in the deprived cortex looks very much like that in the normal adult, except there were still more non-oriented cells, and fewer indéfinite cells.

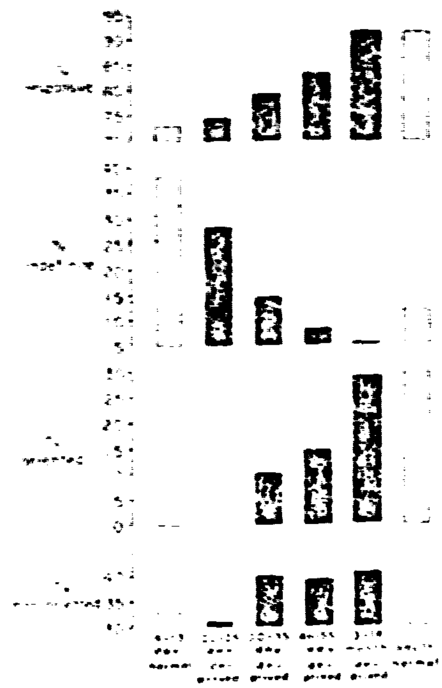

Fig. 4. Postnatal development of cortical cells responsive to any light stimulation, and of those exhibiting specific receptive field characteristics in rabbits monocularly deprived for various lengths of time. The four sets of solid bars are the cortical data from four groups of rabbits deprived for 20-25 days, 30-35 days, 46-55 days, and 3-14 months. The open bars are the data collected from normal 9-10 day olds, and normal adult rabbits.

Three general conclusions can be drawn from these data. First, visual deprivation significantly alters the relative proportions of receptive fields; second, this alteration takes the form of a sharp increase of unresponsive and indefinite cells at the expense of some other specific field types; third, the longer the visual deprivation, the less anomalous the distribution becomes.

C. Studies on Structural Development

We have studied the distribution of the callosal projection from the striate cortex in neonatal rabbits using the techniques of orthograde transport of tritiated leucine and retrograde transport of horseradish peroxidase. The results showed not only the existence of adult like commissural fibers in the lateral striate cortex bordering the occipital area in the 4-8 day old rabbits, but also an abberant projection from the medial striate cortex, an area not known to have any commissural fibers in the adult. The HRP labelled cells in the medial striate cortex are located in the lower half of layer II + III with a few cells scattered into layers IV and V, similar to that in the lateral striate cortex. The radioactively labelled terminals spread from the lower tier of layer II + III to the upper tier of layer VI showing some variation in terminal densities among the layers. A report of this study is in preparation.

Proline autoradiograph was used to examine the development of uncrossed retinotectal projection in neonatal rabbit. Preliminary results showed a much wider retinal projection to the colliculus in the one-day old rabbit than that in the adult.

D. Studies on Physiological Organization

We have used the criterion of linearity of spatial summation within a receptive field to classifying LGN and CTX cells into X or Y cells. Our stimuli were sine wave grating patterns, of varying spatial frequencies, generated for display on an oscilloscope by an electronic visual stimulata. During the test, the phase angle of the grating relative to the field center was systematically shifted in an effort to locate a "null position". The existence of such a position indicated a linear summation of excitatory and inhibitory influences within the receptive field, and such cells were named X cells. Cells that did not have a "null position" were named Y cells.

In the LGN, about half of the cells with concentric field were X cells, and the other half, were Y cells. All the cells with uniform fields behaved like Y cells. An abstract has been published (Glanzman and Miller, '78).

In the striate cortex, the cells with concentric fields were again divided into X or Y cells. Some cells with simple receptive fields appeared to received primarily linear excitatory input and behaved like X cells, but others behaved like Y cells. A report of these results was submitted for publication (Glanzman and Chow, submitted).

A third study concerned with the functional organization of the striate cortex. Microelectrode recordings of units or unit clusters were made tangentially to the rabbit cortical surface. The penetrations were placed at the large, monocular area; therefore no ocular dominance columns were found. There also were no clear-cut orientation columns. However, in each electrode penetration there were periodic discontinuities of shifts in receptive field locations. These shifts were separated by a distance of about 0.5 mm. Between the shifts the field positions were extensively overlapped, and the cells within showed both oriented and non-oriented fields. It was concluded that the rabbit visual cortex was organized into spatial columns, each representing a subdivision of the visual field. A report of this study is in preparation.

E. Anatomical Studies

Two papers on the organization of the temporal visual area were published (Mathers et al., '77; Chow et al., '77). The first one used evoked potential and unit-cluster methods to map this area. It is roughly over-shaped, 3 mm x 2 mm in size and at about the level posterior to the apex region of auditory area 1. It is located ventral to and continuous with visual area 11, at about the caudal half of M. Rose's temporal cortices 1 and 2 (T1 and T2). Only about two-thirds of 96 units studied responded to some sort of moving light stimulation. These motion-sensitive cells were divided into four groups. Cells in the first group (22) responded best to a large light spot or shadow sweeping quickly across the field. Cells in the second group (29) responded to slow moving, jerking spot. Nine cells responded to a narrow, dark bar thrusting into a lighted field. Four cells are "direction-selective", responding to light stimulus moving in one direction and showing either no response or decreased background discharges in the opposite direction. In addition, 3 cells required unusual stimulus features. Of the 38 cells tested, nine of them were found tobe binocularly driven. The second is a histological study using Fink-Heimer, autoradiographic and horseradish peroxidase techniques to examine the connections of the temporal visual cortical region of the rabbit. The temporal visual area covered portions of areas T_1 and T_2, and is reciprocally connected with the dorsal medialgeniculate and suprageniculate nuclei of the thalamus. It was also shown that the temporal visual area projects to a similar region in the opposite hemisphere and to intermediate laminae of the superior colliculus.

Horseradish peroxidase was injected into either the lateral geniculate or the superior colliculus, and the cell bodies displaying the HRP reaction products were examined. The corticotectal cells were found to occupy the upper tier of the 5th layer and the corticogeniculate cells, at the upper tier of the 6th layer of the striate cortex. Data collected from the retina showed no clear-cut difference between the sizes of ganglion cells projected to the LGN or the SC. A report of this study is in preparation.

In another study, using both light and electronmicroscopic materials, we have tried but failed to detect any cytoplasmic laminated bodies in the rabbit LGN neurons. This inclusion body has been shown to exist in most of the X cells in the cat LGN, which may serve as a morphological marker for X cells. Since there were about 30% of X cells in the rabbit LGN (see Section 4), they were unlikely to be missed. These negative results suggested that such a structural correlate of X cells may not be universally applicable (Glanzman et al., '79).

F. Re-organization in the Visual System

The following four studies are attempts to detect any structural and functional re-organization in adult, neonatal, or prenatal rabbits following either striate cortical ablation or unilateral enucleation.

(1) Synaptic reorganization in the lateral geniculate body. An investigation of synaptic plasticity in the lateral geniculate nucleus has been carried out in rabbits surviving one day to one year following ipsilateral visual cortex removal. There is extensive retrograde degeneration of LGN neurons, and the altered nucleus thus provides a model for examining reorganization of optic tract axons which have been deprived of their normal postsynaptic membrane.

The distribution of synaptic contacts in normal LGN was quantitatively determined. In the animals surviving 1-14 days after cortex ablation, there was extensive cell death and loss of the axodendritic synapses of cortical origin, which constitute the most numerous synaptic type in normal LGN.

In animals surviving 4-12 months, there were few remaining neurons and dendrites. The fine structure of the nucleus was characterized by a shift from axodendritic synaptic contacts, as in the normal, to a ten-fold increase in axoaxonal synapses, which became the dominant population. The contribution of optic axons to this synaptic population was determined by contralateral retinal removal. It was found that the synaptic axoaxonal organization in the altered LGN follows the rules of normal organization, in that optic afferents are invariably the presynaptic component in round to flat vesicle axoaxonal synapses.

The LGN's undergoing chronic retrograde degeneration shrank to about two-thirds the size of the normal nucleus. There was no evidence of reduction in the length of optic tract axons within the nucleus (Ralston and Chow, 73).

The evidence indicates that there are new synaptic contacts formed between surviving axons in the degenerating LGN, as a consequence of the loss of postsynaptic dendtitic membrane. The new synapse formation is guided by the normal rules of axoaxonal organization, indicating a maintenance of recognition of appropriate membrane for synaptic contact in the reordered LGN. It cannot be stated whether sprouting of axons accompanies the formation of new synapses or whether the new synaptic contacts are exclusively between preexisting synaptic knobs in LGN.

(2) Spreading of uncrossed retinal fibers to superior colliculus. Dutch-belted rabbits were enucleated shortly after birth and allowed to survive 14-26 weeks. In some animals, the second eye was then removed and the distribution of retinal axons studied. It was found that while there was no evidence of axonal sprouting in the lateral geniculate body, uncrossed retinofugal axons had spread throughout the lateral half of the superior colliculus in areas normally innervated only by the contralateral eye (Chow, Mathers, and Spear), '73).

Other animals were prepared for electrophysiological recording, to see if neurons in the area of new axonal growth could be activated by light or electric shock to the optic nerve. Only four of 70 neurons tested could be driven by light, and only two of 26 tested could be driven by shock. All responsive neurons were judged to be located within the limits of the normal ipsilateral projection. It is concluded that while anatomical evidence of spreading of the uncrossed retinal input has been shown, the functional significance of this new growth is yet to be demonstrated.

(3) In order to test whether the negative finding reported in the above study may not due to the more matured status of rabbit brain at birth, we have performed unilateral enucleation of rabbit fetus. It is hoped that this early lesion may lead to a greater degree of morphological and functional re-organization of the retinotectal system.

Rabbit fetuses were unilaterally enucleated at day 20 or 25 of gestation. Birth is at day 31. After three months, the degree of re-organization of the uncrossed retinotectal fibers was assessed using (a) autoradiographic demonstration of the retinal projection, (b) electrophysiological recording of SC unit activity, (c) a combination of these methods. The results showed that there was a greater expansion of the uncrossed fibers in the fetally enucleated rabbit than those enucleated at birth. But again practically all the SC cells showed no responses to either light stimulation to the eye or electric shock to the optic nerve. Only a few cells encountered in the lateral border area receiving the normal uncrossed projection could be driven by light stimulation (Chow et a ., in preparation).

(4) We have studied the effects of bilateral striate cortical ablation on visual discrimination learning in adult rabbits and in newborn rabbits. The animals in both the lesion groups took longer time to learn pattern discrimination than normal adults. They failed to discriminate striations differing by 22°, or a cross vs. circle discrimination. Although they learned a brightness discrimination within the normal time. This result was unexpected. For in the cat striate corical ablation in newborn kittens caused much less detrimental effects on visual learning than such lesion performed on adults. (Murphy and Chow, '74; Murphy and Stewart, '74).

PUBLICATIONS:

Stewart, D. L., Chow, K. L., and Masland, R. H. Receptive-field characteristics of lateral geniculate neurons in the rabbit. J. Neurophysiol., 1971, 34:139-147

Masland, R. H., Chow, K. L., and Stewart, D. L. Receptive-field characteristics of superior colliculus neurons in the rabbit. J. Neurophysiol., 1971, 34:148-156

Chow, K.L., Masland, R. H. and Stewart, D. L. Receptive field characteristics of striate cortical neurons in the rabbit. Brain Res., 1971, 33:337-352.

Galeano, C. and Chow, K. L. Response of caudal photogreceptor of crayfish to continuous and intermittent photic stimulation. Can. J. Physiol. Pharmacol., 1971, 49: 699-706

Chow, K. L. and Stewart, D. L. Reversal of structural and functional effects of long-term visual deprivation in cats. Exp. Neurol., 1972, 34:409-433

Chow, K. L. and Leiman, A. L. The photo-sensitive organs of crayfish and brightness learning. Behav. Biol., 1972, 7:25-35.

Cohen, E. N., Chow, K. L. and Mathers, L. Autoradiographic distribution of volatile anesthetics within the brain. Anesthesiology, 1972, 37:324-331.

Spear, P. D., Chow, K. L., Masland, R. H. and Murphy, E. H. Ontogenesis of receptive field characteristics of superior colliculus neurons in the rabbit. Brain Res., 1972, 45:67-86.

Grobstein, P. and Chow, K. L. Receptive field organization in the mammalian visual cortex: the role of individual experience in development. Studies on the Development of Behavior and the Nervous System, Volume 3, pp. 155-193, 1976.

Chow, K. L., Douville, A., Mascetti, G. and Grobstein, P. Receptive field characteristics of neurons in a visual area of the rabbit temporal cortex. J. Comp. Neurol. 171:135-146, 1977.

Mathers, L. H., Douville, A. and Chow, K. L. Anatomical studies of a temporal visual area in the rabbit. J. Comp. Neurol, 171:147-156, 1977.

Chow, K. L., Baumbach, H. D. and Glanzman, D. L. Abnormal development of lateral geniculate neurons in rabbit subjected to either eyelid closure or corticofugal paroxysmal discharges. Brain Res., 146:151-158, 1978.

Baumbach, H. D. and Chow, K. L. Receptive field development in the dorsal lateral geniculate nucleus in rabbits subjected to monocular eyelid suture. Brain Res., 159:69-83, 1978.

Fox, P. C., Chow, K. L. and Kelly, A.S. Effects of monocular lid closure on development of receptive-field characteristivs of neurons in rabbit superior colliculus. J. Neurophysiol., 41:1359-1372, 1978.

Mathers, L. H. and Mascetti, G. Electrophysiological and morphological properties of neurons in the ventral lateral geniculate nucleus of the rabbit. Exp. Neurol., 1975, 46:506-520.

Schwartzkroin, P. A. The effect of body tilt on the directionality of units in cat visual cortex. Exp. Neurol., 1972, 36:498-506.

Schwartzkroin, P. A. Effects of round window stimulation on unit discharges in the visual cortex and superior colliculus. Exp. Brain Res., 1973, 17:527-538.

Mathers, L. H. and Rapisardi, S. C. Visual and somotosensory receptive fields of neurons in the squirrel monkey pulvinar. Brain Res., 1973, 64:65-83.

Murphy, E. H. and Stewart, D. L. Effect of neonatal and adult striate lesions of visual discrimination in the rabbit. Exp. Neurol., 1974: 42:89-96.

Masland, R. H., Schwartzkroin, P. A., and Chow, K. L. Responses of single lateral geniculate cells during performance of a visually guided discrimination. Brain Res., 1973, 45:271-277.

Ralston, III, H. J. and Chow, K. L. Synaptic reorganization in the reorganization in the degenerating lateral geniculate nucleus of the rabbit. J. Comp. Neurol., 147:321-350, 1973.

Grobstein, P., Chow, K. L., Spear, P. D. and Mathers, L. H. Development of rabbit visual cortex: late appearance of a class of receptive fields. Science 180: 1185-1187, 1973.

Chow, K. L., Mathers, L. H. and Spear, P. D. Spreading of uncrossed retinal projection in superior colliculus of neonatally enucleated rabbits. J. Comp. Neurol., 151:307-322, 1973.

Chow, K. L. Neuronal changes in the visual system following visual deprivation in the handbook of sensory physiology, R. Jung (ed.), Springer-Vertag, Berlin, 1973, pp. 599-626.

Murphy, E. H. and Chow, K. L. Effects of striate and occipital cortical lesions on visual discrimination in the rabbit. Exp. Neurol., 42:78-88, 1974.

Chow, K. L. and Spear, P. D. Morphological and functional effects of visual deprivation on the rabbit visual system. Exp. Neurol. 42:429-447, 1974.

Mathers, L. H., Chow, K. L., Spear, P. D. and Grobstein, P. Ontogenesis of receptive fields in the rabbit striate cortex. Exp. Brain Res., 19:20-35, 1974.

Rapisardi, S. C., Chow, K. L., and Mathers, L. H. Ontogenesis of receptive field characteristics in the dorsal lateral geniculate nucleus of the rabbit. Exp. Brain Res., 22:295-305, 1975.

Grobstein, P., Chow, K. L., and Fox, P. C., Development of receptive fields in rabbit visual cortex: changes in time course due to delayed eye-opening. Proc. Nat. Acad. Sci. USA, 72:1543-1545, 1975.

Grobstein, P., and Chow, K. L. Receptive field development and individual experience. Science, 190:352-358, 1975.

Grobstein, P. and Chow, K.L. Receptive field organization in the mammalian visual cortex: the role of individual experience in development. Studies on the Development of Behavior and the Nervous System, Volume 3, pp. 155-193, 1976

Chow, K.L., Douville, A., Mascetti, G. and Grobstein, P. Receptive field characteristics of neurons in a visual area of the rabbit temporal cortex. J. Comp. Neurol 171: 135-146, 1977.

Mathers, L.H., Douville, A. and Chow, K.L. Anatomical studies of a temporal visual area in the rabbit. J. Comp. Neurol., 171: 147-156, 1977.

Chow, K.L., Baumbach, H.D. and Glanzman, D.L. Abnormal development of lateral geniculate neurons in rabbit subjected to either eyelid closure or corticofugal paroxysmal discharges. Brain Res., 146: 151-158, 1978

Baumbach, H.D. and Chow, K.L. Receptive field development in the dorsal lateral geniculate nucleus in rabbits subjected to monocular eyelid suture. Brain Res., 159: 69-83, 1978.

Fox, P.C., Chow, K.L. and Kelly, A.S. Effects of monocular lid closure on development of receptive-field characteristics of neurons in rabbit superior colliculus. J. Neuophysiol., 41: 1359-1372, 1978.