fell to chance when the pattern was removed by the insertion of pieces of diffusing material in the paths from the projectors to the screens. We also ascertained that the cats did not tilt their heads during either discrimination task.

Figure 1 shows the results for the three deprived cats together with similar data obtained from two normally reared control animals. In each graph, the mean percentage of correct responses over the days of asymptotic performance are plotted as a function of grating spatial frequency. The two normally reared cats (Fig. 1, A and B) exhibited no systematic differences in their performance for vertical and horizontal gratings. However, the performance of the deprived animals (Fig. 1, C to E) for test gratings exceeding 0.46 cycle/deg was clearly superior for the orientation that they experienced in early life (*10*). In fact, for spatial frequencies higher than 1.5 cycle/deg, there was virtually no overlap of the daily scores for the two grating orientations.

It is possible to obtain an estimate of the cutoff spatial frequency from these data on the assumption that this is the frequency at which the cat's performance is at chance (50 percent). The estimates for the two normal cats, 3.0 and 3.1 cycle/deg, are only slightly smaller than values obtained earlier (*11*) by behavioral means and estimates obtained from evoked cortical potentials (*12*), but fall well short of the cutoff spatial frequency for the optics of the cat eye (*13*). The values obtained from the deprived animals for gratings of the experienced orientation—3.4, 3.0, and 3.3 cycle/deg for V_1, H_1, and V_2, respectively—are comparable to the estimates obtained from the normally reared cats. By contrast, the cutoff spatial frequencies for gratings of the corresponding orthogonal orientations were only 2.6, 2.45, and 2.0 cycle/deg, respectively. This suggests that the early selective visual experience of these cats resulted in consistent disparities of between 18 and 40 percent in the cutoff spatial frequencies for gratings of the experienced and its orthogonal orientation. The largest difference (40 percent) was observed in V_2, which had been reared in the stripes for the shortest period. Interestingly, the physiological effects of deprivation also appear to be more pronounced with shorter exposures. Recent studies (*4, 14*) suggest that the distribution of preferred orientations of cortical neurons is more tightly clustered about the experienced orientation in animals whose exposure to stripes lasted only a few weeks rather than several months as in the original studies (*3, 4*).

The long-term behavioral deficits observed in our cats are considerably smaller than might have been expected from the dramatic temporary defects described by Blakemore and Cooper (*3*) when the cats are first exposed to a normal lighted environment. A similar conclusion was reached by Hirsch (*15*) from quite different behavioral tests. Our results show that the long-standing consequence of early selective visual deprivation is not a blindness for contours of the orientation orthogonal to those present in the early visual environment, but only a slight reduction in acuity, a result consistent with the deficits observed in many optically corrected human astigmats (*6*). There is good evidence that the acuity deficits we found are long-lasting. Although most of our cats have been in normal lighted environments for nearly a year, current repetitions of the curves of Fig. 1 have revealed no improvement in performance. This result is thus concordant with the recent finding (*16*) that, apart from changes in ocular dominance, the most dramatic physiological effects of deprivation remain largely unchanged even after nearly 2 years of normal visual exposure.

The results of our experiments indicate that the ability of the cat to resolve contours is influenced by its early visual experience. This finding provides strong support for the suggestion (*6*) that the meridional differences in acuity observed in optically corrected human astigmats as well as the lesser ones (for oblique orientations) observed in normal eyes result from certain asymmetries in the early visual input.

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7. At first the kittens all showed the gross behavioral deficits described by Blakemore and Cooper (*3*) but most of these disappeared within between 12 and 16 hours of exposure to a lighted environment. However, the ability to strike or visually follow sticks held orthogonal to the experienced orientation remained poor in two cats for several weeks. While these cats learned within 16 hours to successfully strike at the stick when it was held at the rearing orientation, they either stopped responding to it or struck at it in a hesitant fashion when the stick was held orthogonal to this orientation.
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9. Blank-field slides had an average luminance of 75 cd/m^2 and a range of ± 15 cd/m^2. At this luminance level the pupil diameter was about 6 mm.
10. Statistical analysis by the Wilcoxon matched-pairs signed-ranks test [S. Siegal, *Nonparametric Statistics* (McGraw-Hill, New York, 1956), p. 75] revealed that the curves obtained with vertical and horizontal gratings for each control cat (Fig. 1, A and B) were very similar (smallest value obtained was $P = .29$), whereas the two curves for each experimental cat (V_1, V_2, and H_1) were markedly different (largest value obtained was $P = .00006$).
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Disinhibition of Tectal Neurons by Pretectal Lesions in the Frog

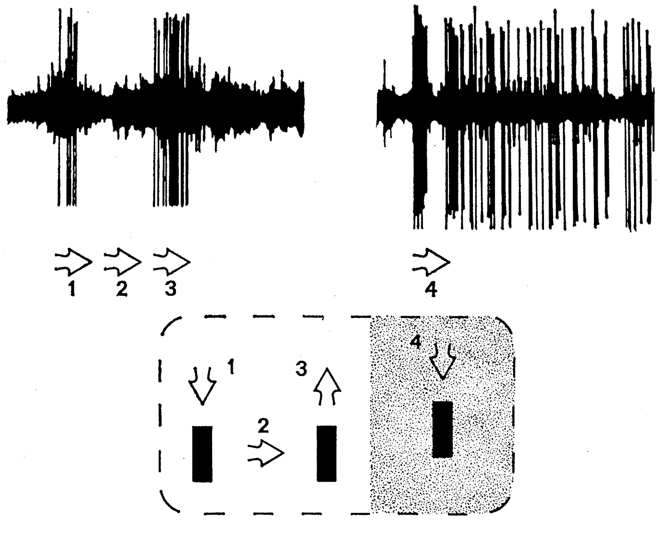
Abstract. *The rapid habituation of many neurons in the frog optic tectum to moving spots is presumed to underlie the behavioral habituation of the frog to repeated movement of prey objects. The "disinhibited" feeding of frogs after pretectal lesions is paralleled by the consistent failure of tectal neurons to ignore moving buglike stimuli.*

In the frog, the optic tectum provides a major interface between vision and action, receiving retinofugal fibers from the opposite eye (*1*) and discharging directly into brainstem and spinal motor centers (*2*). Furthermore, the tectum appears to play a critical role in the initiation of prey-catching movements since these sequences can be elicited by electrical stimulation of the tectum in the free-moving toad (*3*). At all levels of vertebrate phylogeny, the optic tectum seems to participate in directing body, head, or eyes toward objects of interest (*4*). In the frog, as in some mammals, tectal neurons may rapidly habituate to any but novel objects moving through their receptive fields (*5*). The tectum, therefore, acts as an active filter between the continuous discharge of retinal ganglion cells and the initiation of prey-catching responses. I am concerned here with this mechanism of visual selectivity within the tectum, which closely parallels the selective behavior of the whole organism toward prey objects (*6*).

In the mammal, prominent corticotectal pathways appear to play an important role in the response characteristics of tectal cells (*7*). But in the frog descending pathways from the telencephalon do not seem to enter the optic tectum (*8*) so that a level of control strictly homologous to the corticotectal system must be ruled out. However, recent studies by Ewert (*9*) implicate the caudal thalamus as a modulator of prey-catching activity in the toad. Appropriate lesions invading the pretectal region produce a dramatic "disinhibition" syndrome, such that toads persistently approach any moving stimulus including very large objects that they would normally avoid. In these toads with lesions, orienting or snapping responses do not habituate on repeated stimulation as with the normal toad. Therefore, Ewert has suggested that neurons in the anuran caudal thalamus normally exert an inhibitory influence on the optic tectum, which preserves realistic behavior toward visual objects. My study directly examines the assumption that the response characteristics of tectal cells in the frog can be altered by those lesions in caudal thalamus that produce the disinhibition syndrome.

Frogs were disinhibited by either of two methods: (i) a vertical knife cut through the dorsomedial tectum and pretectal region as described by Ewert (*9*) or (ii) suction ablation of the pretectal region from behind, after transection of the intertectal commissures. Seven frogs were selected from the lesioned group on the basis of their compulsive pursuit of large objects, such as the experimenter's hand. After film records of this behavior had been taken, frogs were curarized and the dorsal surface of thalamus and midbrain were exposed for recording. Tungsten microelectrodes, sharpened to 3-μm tips and coated with Insul-X, were used to monitor spikes from retinofugal axon terminals and from tectal cells. These unit responses were displayed on a Tektronix 564 memory scope where Polaroid photographs could be taken of repeatable phenomena. Quantitative data were obtained by stimulating tectal units with a black 4° square (that is, the length of the side subtends an arc of 4°), moved by means of a Hewlett-Packard X-Y recorder behind the window of a white frontal screen, 20 cm from the snout of the frog. Visually elicited spikes were converted into pulses by means of the internal trigger mechanism of the oscilloscope, and these pulses were fed into a Fabritek 1062 instrument computer.

In this study, I have examined some response characteristics of "newness neurons" as recorded in the rostral-lateral optic tectum of the frog. Within a sample of more than 100 isolated units of this class, most cells had receptive fields of 15° to 20° and nearly all showed marked habituation of response to motion of a black 4° square through the receptive field. These cells were always encountered about 100 nm below the upper boundary of class 3 (changing contrast detector) optic fiber terminals, which would place them within the uppermost layer of cells seen in histological sections. Studies of degenerating optic fiber terminals (*1*) do indeed show overlap of the second band



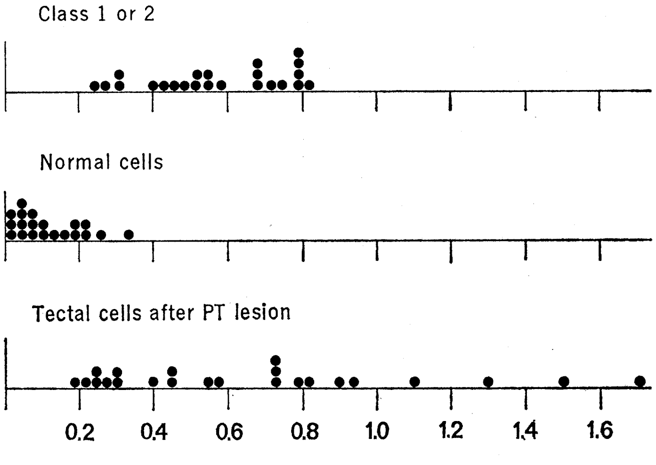


Fig. 1 (left). A single tectal neuron, of a "disinhibited" frog, showing division of the receptive field into normal and hyperexcitable regions. Lengthwise movement of a black rectangle (1° by 4°) within the left side of the field produced only brief discharge, as with tectal neurons of the normal intact frog. However, a stimulus entering and stopping within the excitable (stippled) zone always elicited a prolonged response in this neuron. For some disinhibited neurons the entire field was hyperexcitable, and for others the threshold for the less excited zone was variable, such that these neurons appeared to spontaneously change their excitory receptive field size. Oscilloscope records depict the unit response to four successive movements of the rectangular stimulus. Each trace was 10 seconds long and the receptive field was 25° wide. Fig. 2 (right). Each black circle represents the data of a particular tectal multiple-cell group (that is, three to five units), where eight responses to spot motion were recorded. The sum of four responses after 10-second recovery intervals was divided by the sum of four intervening responses obtained after 60-second recovery intervals to give the "habituation ratio" (that is, the number of spikes at 10-second intervals per 60 seconds) for each unit population. While afferent input from the eye (class 1 or 2 fibers) show significant adaptation after a 10-second recovery, the normal postsynaptic cells show a much greater decrement (habituation). The second process does not appear after appropriate pretectal lesions and, therefore, is not intrinsic to the tectum.

of degeneration taken to be class 3 axon terminals, with the most dorsal cells (layer 8 of Cajal). Since I report data from cells that overlap the class 3 fibers in depth, further localization of these "newness neurons" was deemed unnecessary.

The responses of these cells could be distinguished from that of class 3 fibers by each of three criteria. (i) Class 3 unit spikes, of which two or three could be discriminated at any given locus, had tightly overlapping receptive fields of 10° to 15° each, and these were invariably grouped within a 20°-wide region that remained fixed through a given penetration. In order to avoid contamination of my sample by class 3 fiber spikes, I studied only cells whose receptive fields lay at least 10° beyond the receptive field region of fiber terminals. (ii) The class 3 units could be easily identified by their brief and nonhabituating response to sudden covering of the receptive field with a large black card or switching the room lights off. At this level, cells did not respond to such changes in illumination. (iii) Newness cells in the normal frog could be identified by their habituation after one or two movements of a small dark stimulus within the receptive field, while class 3 fibers continued indefinitely to give transient responses to such incursions. Although cells of the "disinhibited" tectum did not so clearly habituate, they gave a prolonged discharge that was entirely foreign to class 3 units.

The behavior of cells at this level within the tectum of frogs with lesions can without reservation be termed "disinhibited." Although it proved difficult to isolate units because of the much greater spike density encountered at the class 3 level, the behavior of some 35 isolated cells was qualitatively identical to that of a larger number of multiple-spike groups. Nearly all units now gave prolonged discharges after a 4° spot moved into the field and stopped (Fig. 1), although a 2- or 3-second latency was often observed prior to maximum discharge frequency. Such units typically discharged from 5 to 10 seconds, and further movements could sometimes escalate the response to a seizure-like intensity. These "pathological" types of cell discharge were observed in four of the seven frogs, and they probably correspond to instances of seizure-like forced movements sometimes seen in freely moving animals with lesions, in response to repeated stimulation with dummy prey objects. Although details of receptive field organization of some disinhibited cells are complex and will be reported in a later presentation, it should be noted that these receptive fields were distinctly larger than those of normal cells, typically 30° or more in diameter. In 12 isolated units, spontaneous increments in receptive field from 15° to 30° were seen, very much as reported for some tectal neurons in cat (*10*) and monkey (*11*). These observations fit well with behavioral data, since frogs and toads disinhibited by pretectal lesions pursue larger prey objects than do normal animals (*9*).

In order to document the extent of these enhanced cell responses produced by the thalamic lesions, I made a quantitative assessment of the habituation rates of these cells. A so-called "habituation ratio" was calculated for each of numerous multiple unit groups by the following procedure. The X-Y recorder swept the stimulus spot through the receptive field at about 10° per second for a series of eight repetitions, separated by intervals that alternated between 10 and 60 seconds in length. All spikes above a critical amplitude (a signal to noise ratio of about 4 : 1) were converted into 0.05-msec pulses and fed into the Fabritek during a given stimulus sweep (see Fig. 2).

Those spikes activated after the 60-second interval were stored in one memory channel, while those activated after the intervening 10-second intervals were stored and summed within a second channel. After four repetitions at each interval, the cumulative spike count for each channel was displayed and measured. The habituation ratio was obtained by dividing the spike count after a 10-second recovery interval with the baseline rate obtained after 60 seconds. Thus a ratio of 1.0 would indicate 100 percent recovery or no habituation for that experiment. In each frog, two to four such experiments were performed, each on a different set of multiple-unit groups.

Figure 2 summarizes the distribution of habituation experiments performed on normal frogs and frogs with pretectal lesions, with each circle indicating the value of a particular eight-trial experiment. First of all, it is evident that some adaptation occurs at the level of the retina, since the class 1 or 2 axon terminals showed habituation ratios ranging between 25 and 80 percent. Normal tectal cells showed further habituation; in fact, 19 of 20 experiments yielded habituation ratios of less than 25 percent, and most were less than 10 percent. However, the third line of Fig. 1 shows that tectal cells in the group with lesions do not habituate normally. Their distribution of ratios is nearly the same as that of class 1 and 2 fibers, which presumably supply the chief input to these cells. In addition, five experiments were carried out with class 2 fibers in the frogs with lesions, and their ratios were entirely normal.

I conclude that tectal cells in frogs with lesions cannot ignore their retinal input, so that successive stimuli continue to drive the prey-catching system. Although the thalamotectal modulation process is here abnormally reduced so that the frog resembles an automaton, it seems likely that thalamus plays a more subtle role in the moment-to-moment shifts of motivation in the normal life of the animal. For example, Ewert (*6*) notes that excitement by the odor of the prey reduces habituation rate and induces toads to pursue larger objects than usual. Thus the optic tectum, whether in a frog or a monkey, may prove to be a convenient place to monitor the effects of various brain processes that restrain or direct the attention of the organism to selected features of its world.

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