

growth. One way to reverse the effects of Colcemid would be to stimulate de novo synthesis of the microtubule subunit, and thereby decrease the effect of Colcemid on the subunit pool. Another way might be to promote the polymerization of those subunits that are not bound to Colcemid. Consequently, the fact that NGF and dibutyryl cyclic AMP counteract the effects of Colcemid need not imply that both compounds act through the same mechanism.

The evidence presented above indicates that NGF does not alter intracellular cyclic AMP levels, that it does not stimulate adenyl cyclase activity, and that its morphological effects are not enhanced by theophylline. Thus, we infer that cyclic AMP does not mediate the action of NGF.

DANIEL B. HIER

Departments of Biological Chemistry and Medicine, Harvard Medical School, and Massachusetts General Hospital, Boston 02114

BARRY G. W. ARNASON

Department of Neurology, Harvard Medical School, and Massachusetts General Hospital

MICHAEL YOUNG

Departments of Biological Chemistry and Medicine, Harvard Medical School, and Massachusetts General Hospital

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Gamma-Aminobutyric Acid Antagonism in Visual Cortex: Different Effects on Simple, Complex, and Hypercomplex Neurons

Abstract. *Intravenous bicuculline was used to examine how removing gamma-aminobutyric acid-mediated inhibition affects the visual response properties of single cortical neurons. Simple neurons were depressed and complex neurons showed increase in the vigor and range of responses. Hypercomplex cells were no longer inhibited by elongated stimuli. The results are consistent with present evidence concerning the origin and distribution of inhibitory connections within the cortex.*

A number of lines of evidence implicate γ -aminobutyric acid (GABA) as an inhibitory transmitter in the mammalian central nervous system. This evidence is based on the distribution and synthesis of this amino acid in various brain regions (1), its release from nervous tissue in relation to the activity of inhibitory neurons (2), and the observation that microiontophoretically applied GABA hyperpolarizes neurons in the brainstem (3) and cerebral cortex (4) by membrane mechanisms which are indistinguishable from those occurring during synaptic inhibition.

The most recent line of evidence comes from the finding that the plant alkaloid bicuculline, which causes epileptiform convulsions of cortical origin, is a potent and specific antagonist of GABA-induced inhibition (5). Bicuculline has no effect on the strychnine-sensitive inhibition thought to be mediated at other sites, particularly in the spinal cord, by the second putative inhibitory transmitter, glycine (6).

We sought to examine the role played by GABA in the cat's primary visual cortex, where the functional characteristics of single neurons are known in some detail (7, 8) and where inhibitory mechanisms have been proposed to account for some of these characteristics (9). Since intravenously administered bicuculline has been shown to be a potent and reversible antagonist of GABA in the cerebral cortex, we used this method to examine how removal of GABA-induced inhibition affects the highly specific responses of visual cortical neurons to patterned visual stimuli. Bicuculline produced dramatic effects on neurons with complex fields, including marked increases in spontaneous and evoked activity, loss of specificity for the orientation or direction of a moving line, and the appearance of plottable "on" and "off" areas like those of incoming lateral geniculate fibers. Hypercomplex cells, whose response to a line is normally inhibited if the length exceeds some

optimum (8), lost their inhibitory end zones. Simple cells, whose fields can be mapped into "on" or "off" areas with flashing stimuli, showed only mild effects, such as a depression of responsiveness or a slight shift in preferred orientation.

Single neurons were studied in the striate cortex (area 17) of ten normal adult cats weighing between 2 and 3 kg. The preparation was routine (7). Initial surgery was carried out under Fluothane, and anesthesia was maintained during recording with nitrous oxide. Eye movements were prevented by a continuous intravenous infusion of Flaxedil and *d*-tubocurarine (10). Stimuli were held by the arm of an X-Y recorder in the object plane of an overhead projector which focused them on a screen 57 cm from the animal. The X-Y recorder could be controlled by hand for initial receptive field plotting or by a computer that presented a series of sweeps across the receptive field in chosen directions and stored all spike data for later analysis.

Before administering bicuculline to each cell we tried to collect as many data as possible about its functional characteristics. Receptive field plots with flashing spots and lines and averaged responses to various directions of movement, orientation, and line lengths were obtained and usually enabled a cell to be classified according to Hubel and Wiesel's (8) three categories, simple, complex, and hypercomplex. After categorization of the cell, an intravenous dose of bicuculline (0.2 mg/kg) was slowly given and all tests were repeated until the cell's properties had returned to control or until the cell was lost (11).

All cells studied were affected by the drug. Based on our observations of 13 simple, 7 complex, and 2 hypercomplex cells, these effects appear to be consistent within a given class of cell, and reversible (45 minutes to 1 hour). Examples are shown in Fig. 1.

Simple cells were the least affected. Evoked activity was depressed, and in

one case virtually eliminated, but there was no change in the receptive field organization of "on" and "off" areas nor was there any change in the selectivity of the response for the orientation of the line stimulus. Complex cells stood in marked contrast and this was vividly demonstrated in one case where we simultaneously observed a pair of cells, one simple and the other complex, during injection. Hand in hand with the simple cell's decline in responsiveness, the complex cell doubled its spontaneous activity, trebled its

evoked activity, underwent a major change in its receptive field organization with the appearance of an "on" response to a flashing spot, and lost some of its selectivity for the orientation of a moving line. Similar changes were observed in all of the complex cells we have studied. Directional selectivity was often lost as well, and the "on" or "off" area that reversibly appeared to one side of the complex field was similar in many ways to the receptive field of an afferent fiber from the lateral geniculate nucleus. Both hyper-

complex cells reversibly lost their inhibitory flanks and became responsive to lines which were previously too long to be effective. In one case there were also changes comparable to those observed in the complex cells.

It might be thought that bicuculline's cortical effects originate earlier in the visual pathway, particularly since GABA is known to occur in the retina (1). Such an explanation is clearly inadequate for changes in mechanisms underlying direction and orientation selectivity, which do not occur at early stages of the cat visual pathway such as the lateral geniculate nucleus (LGN). Moreover, study of an LGN-sustained (X type) cell, which projects to the simple cell (12), revealed little change in properties after a dose of 0.2 mg of bicuculline per kilogram. We saw only a slight increase in responsiveness and partial loss of the inhibitory surround, both changes in the directions opposite to those needed to explain the depression of simple cells. Therefore, our results strongly support a role for GABA-mediated inhibition in the specific response properties of visual cortical neurons. The hypercomplex cell's properties suggest an inhibitory mechanism which involves GABA release from nearby simple cells with the same preferred orientation but with a flanking receptive field position. In addition, part of the complex cell's specificity appears to be derived from intracortical inhibitory mechanisms, as proposed by other investigators (9). The differential effect of bicuculline on simple and complex cells also appears to be consistent with a number of other observations. Complex cells are usually pyramidal cells (13) that appear to have inhibitory-type terminals densely attached to the cell body, a strategic location for inhibition (14). One might expect the pyramidal cell to be very sensitive to the removal of this inhibition, since it would allow spike initiation to occur after less specific dendritic excitation, such as that produced by the LGN input to complex cells (12). The smaller effect on simple cells may follow from the fact that they are stellate cells (13) which tend to have fewer scattered inhibitory terminals (14) and which themselves probably mediate the GABA-induced inhibition (15).

J. D. PETTIGREW
J. D. DANIELS

*Departments of Physiology-Anatomy
and Electrical Engineering, University
of California, Berkeley 94720*

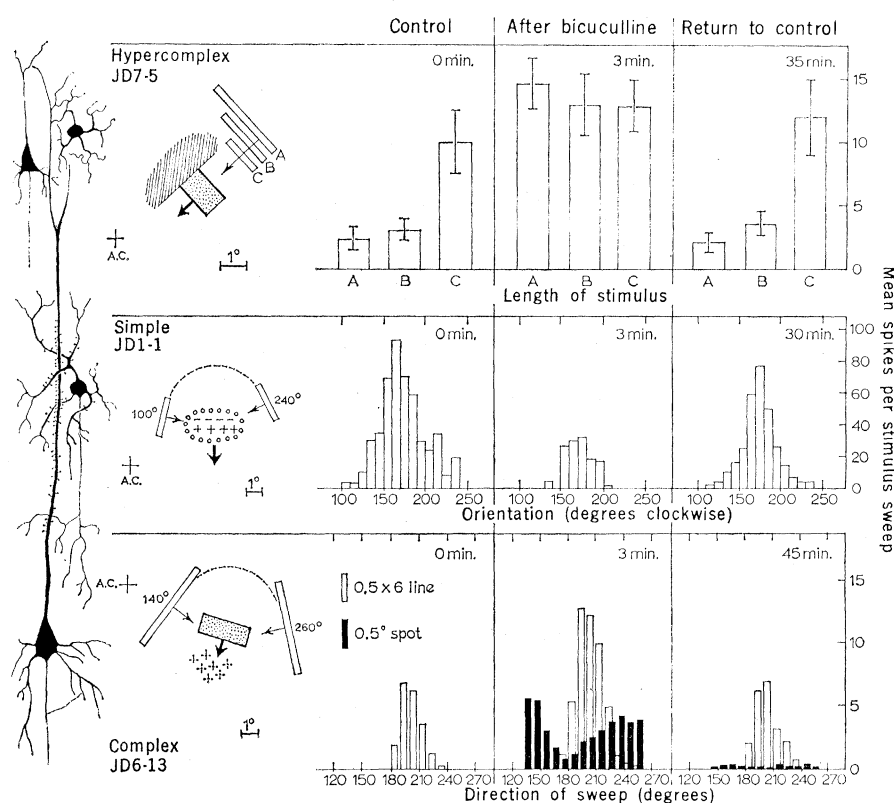


Fig. 1. Effect of bicuculline (0.2 mg/kg, intravenously) on typical visual cortex neurons in the cat. Each bar in the graphs on the right represents the average number of spikes for five sweeps across the receptive field. Each cell was direction and orientation specific; in the diagram at the left the preferred direction of stimulus sweep is shown with a thick arrow. Each cell was studied long enough to obtain a reasonable return to control. (Hypercomplex cell) The receptive field at the left shows the excitatory region with dots and the suppressive end zone with hatched markings. The responses to bars A, B, C moved at 1° per second are shown at the right; note the typical hypercomplex cell decline in response for the longer bars A and B. This decline is reversibly blocked by bicuculline. (The error bars represent the standard error of the mean for five sweeps). (Simple cell) In the diagram at the left, + (plus) represents regions of "on" response, — (minus) represents regions of "off" response, and "○" represents no response. The graphs at the right show the mean response of the cell to a bright bar swept at 2° per second across the receptive field for the orientations shown. Bicuculline reversibly depressed the activity of the cell but did not change its specificity for the stimuli. (Complex cell) The receptive field (shown with dots) for this cell could be mapped only with a moving bar; it had no "on" or "off" responses. After bicuculline, a plottable "on" region appeared, shown by the dotted + signs. The response of this "on" region to a 0.5° spot moved at 2° per second is shown with the black bars in the second and third graphs. The cell also became more responsive to the 0.5° × 6° line, giving more spikes per sweep and responding for a broader range of orientations. Other complex cells studied increased their spontaneous rates and sometimes had their directional preferences changed. The return to control for this cell shows the disappearance of the "on" region. For each cell, fields were plotted and responses recorded for the dominant eye only. On the receptive field diagrams A.C. indicates location of the area centralis.

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3 days a week and in small sections with one of 11 graduate teaching assistants on the other 2 days. The teaching assistants were instructed to answer questions about the lectures and homework and to administer test problems. At the end of the course, all the students took a common final examination and also rated their respective teaching assistants by responding anonymously to a list of questions about the teaching assistants' performance. Rodin and Rodin report a correlation of -0.75 between the average rating on the item "What grade would you assign to his total teaching performance?" and the average course grade of the instructor's students. No data are presented concerning the other questions.

Although Rodin and Rodin purported to investigate their students' ability to identify good teachers, their research assessed the effectiveness of graduate teaching assistants in complementing the teaching style of one of the authors. Note also that they reported ratings on only one ill-defined global item. The correlation might have been quite different if the question had been "How well has the teaching assistant prepared you for the final examination?" They reported the mean final exam score and the mean rating for each instructor but did not report whether the differences among these sample means were reliable, that is, whether the final grades and the student ratings clearly discriminated among the instructors. If one estimates the standard error of each section's average grade from the two sections that were taught by the same teaching assistant, most of the observed differ-

Student Ratings of Teaching: Validity of Several Rating Factors

Abstract. *Students' ratings of their instructors in undergraduate classes in calculus were correlated with class performance on a common final examination. Ratings on several instructional factors were highly related to class performance even though they appeared to be independent of the students' own grades.*

Although research has rather consistently indicated a low positive correlation between students' ratings of instructors and other indices of teaching performance (1), the validity of student rating data remains a subject of controversy. Kossoff has questioned whether good teaching can be measured at all and has suggested that many criteria employed for students' ratings (such as friendliness, helpfulness, appearance, interest in students) may provide little information about the teacher's ability to stimulate learning (2). More recently, Rodin and Rodin con-

cluded from a study of their own that "students rate most highly instructors from whom they learn least" (3). Because of the practical import of this issue on my own campus and because of reservations about the technical soundness of the Rodins' study, I replicated their basic research design with several modifications.

To explain my methodological concerns, a brief summary of their study will be helpful. Students enrolled in an undergraduate calculus course taught by Burton Rodin met with him in a large (293 students) lecture section

Table 1. Class performance on final examination and student ratings of instructor. Ratings are on a 7-point scale, 7 being the highest.

Instructor	Mean final exam grade		Students (No.)		Instructional factor (mean rating)					
	Observed	Regressed	Taking exam	Making ratings	Work load	Student accomplishment	Organization-planning	Grading	Teacher's presentation	Teacher accessibility
<i>Introductory Calculus</i>										
A	87.1	88.1	54*	38	5.52	5.02	5.64	5.42	5.10	5.10
B	84.9	84.5	38	32	5.35	4.86	4.72	5.37	4.53	4.59
C	89.2	83.9	28	23	4.20	4.96	5.28	5.48	5.16	5.74
D	85.6	83.8	34	25	4.79	5.17	4.85	5.55	5.04	6.01
E	83.4	83.3	34	27	4.27	4.75	5.22	4.97	5.35	6.33
F	77.0	79.8	24	16	5.10	4.98	4.39	5.44	4.08	5.17
H	75.6	76.9	37	26	4.63	4.63	4.46	5.33	3.56	5.63
J	70.5	72.1	46*	33	4.56	3.82	4.13	4.68	3.00	4.97
<i>Multidimensional Calculus</i>										
K	77.8	76.0	19	13	4.74	4.87	5.31	5.54	4.74	6.05
M	74.0	74.1	35	27	4.21	4.75	4.91	5.02	4.37	5.52
P	71.5	72.7	48	39	3.21	4.68	5.17	5.33	5.55	5.81
S	71.2	71.4	40	32	4.22	4.41	4.63	4.58	3.81	4.72
T	62.9	62.3	37	23	3.62	4.26	4.93	4.59	3.67	5.23

* Taught in two separate sections.