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Intracerebral Influences on the Microstructure of Receptive Fields of Cat Visual Cortex*

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Summary. Effects of electrical stimulation of the basal ganglia (caudate nucleus and putamen) and cortex (gyrus proreus and compositus) on the receptive fields and response properties of units in the visual cortex of cats were assessed using single lines, double lines and multiple lines (gratings). In the single line experiment caudate stimulation significantly increased the spontaneous activity, optimal firing rate and receptive field size of visual cortex neurons whereas putamen stimulation decreased these parameters. Stimulation of gyrus proreus enhanced, while that of gyrus compositus diminished optimal firing rate without affecting spontaneous activity; in addition, stimulation of ipsilateral proreus and compositus increased the receptive field size whereas their contralateral homologues decreased it. In the double line experiment, proreus and caudate stimulation increased the magnitude of the facilitatory effect of progressive separation of the lines over certain ranges whereas compositus and putamen stimulation increased the inhibitory influences. Orientation selectivity and spatial frequency tuning characteristics were unaffected by the electrical stimulations of any of the four sites. Thus three categories of network properties were delineated: those characterized by remaining invariant to any cerebral stimulation; those characterized by overall activation as by basal ganglia stimulation; and those characterized as interactive which were responsive especially to cortical stimulation.

Key words: Visual properties – Visual cortex – Receptive fields – Spatial frequency – Interactive properties

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Hughlings Jackson (1932) first proposed that cerebral functions constituted an equilibrium which becomes disrupted by brain lesions. Jackson's proposal has been tested behaviorally and received support with regard to the difference in effect of lesions of the frontal and posterior intrinsic (association) cortex (Pribram 1966; Brody et al. 1977). The question was raised, therefore, as to what mechanism might be involved in maintaining the Jacksonian equilibrium.

In order to explore this question a series of electrophysiological experiments was undertaken, of which the current report is a part. The initial studies showed opposing effects of electrical stimulations of frontal and posterior intrinsic (association) cortex on recovery cycles in the visual system (Spinelli and Pribram 1966) and on the apparent size of visual receptive fields (Spinelli and Pribram 1967). These studies left in doubt, however, whether the changes in apparent receptive field size were due to differences produced in the level of background activity or due to alterations in the configuration of the receptive field itself.

A further question is raised by these experimental findings: by what pathway is the electrophysiological result effected? Behavioral data have implicated the head of the caudate nucleus as the locus most intimately related to the functions of the frontal intrinsic (association) cortex (Rosvold et al. 1958) and anatomical studies have demonstrated heavy projections from the frontal cortex to this basal ganglion (Kemp and Powell 1970; Goldman et al. 1971; Yeterian and Van Hoesen 1978).

Similarly, the posterior intrinsic cortex projects to the putamen (Reitz and Pribram 1969) and behavioral data intimately relate this portion of the striatum to posterior cortical function (Buerger et al. 1974). Though the pathways from the basal ganglia to the visual system are as yet uncharted, Kadobayashi (Kadobayashi et al. 1972; Kadobayashi and Ukida

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1971) has shown that electrical stimulations of the basal ganglia will influence gross and unit potentials evoked by flashes of light in both the lateral geniculate nucleus and the primary visual cortex.

Thus the experiments reported here were undertaken to investigate the influence of electrical stimulation of the frontal and posterior intrinsic cortex (gyrus proreus and gyrus compositus of the cat), and of the caudate nucleus and putamen, on the properties of receptive fields of neurons in the visual cortex. As noted in the preceding paper, it was essential to this enterprise to attempt first to understand these properties by classifying them with the aim that such classification would clarify the nature of the transfer functions involved. The results of the electrical stimulation experiments reported here are analyzed within the frame of the classifications arrived at in the preceding paper. The findings are reported in two sections. The first reports results where the properties of the receptive field did not vary with electrical stimulation. The second section reports the results where receptive field properties were influenced by such stimulations. These effects were sufficiently differential to allow specification of the transfer functions involved, and to suggest mechanisms by which the effects might operate.

Methods

A. Chronic Implantation

Fourteen adult cats were bilaterally implanted under deep general anesthesia (Nembutal, 18 mg/kg) with bipolar stimulating electrodes made out of nicrome wire, 2 mm diameter, dimit insulated. Their exposed tip was 0.5 mm. The sites of implantation were gyrus proreus (frontal cortex) and gyrus compositus which is thought to correspond to the inferotemporal cortex in the cat on the basis of behavioral studies performed by Blake (1965). The electrodes were placed by hand through small burr holes in the skull (1 cm posterior to the interaural line for gyrus compositus and 3 cm anterior to the interaural line for gyrus proreus). In other cats electrodes were bilaterally implanted stereotaxically into the putamen (HC: A16, L8, H0) and the caudate nucleus (HC: A18.5, H3.5). These coordinates were derived from the Atlas of Jasper and Ajmone-Marsan (1960) and corresponded for the caudate, to the anatomical projection from gyrus proreus, for the putamen, to the center of the structure. A plug (socket, DIP 8 pins) was connected to the electrodes, the contact being made by crimping the ends of soft brass tubing, one end on the electrode, the other on the plug's prongs. Dental cement was then poured around the plug. Finally, a recording chamber (Pitto et al. 1976) was implanted. This system permitted painless and stable immobilization of the head without the use of earbars, avoiding surgical preparation during the actual recording sessions.

B. Recording Preparation

Twenty-four hours prior to the recording session the animal was food deprived to prevent subsequent vomiting. Thirty minutes before the experiment the cat was subcutaneously injected with atropine sulfate (0.25 mg) in order to block laryngeal secretions that could be caused by intubation and received an intramuscular injection of Ketamine. At the onset of the experiment anesthesia was induced with thiopental (Pentothal, Abbot, 18 mg/kg), and the saphenous vein was cannulated with a catheter (angiocath 22 gauge, 1 in., Deseret, 29621).

A local anesthetic was then sprayed on the glottis (Cetacaine) and the animal intubated with an endotracheal tube covered with Xylocaine. The tracheal tube and venous catheter were secured to prevent uncomfortable movements of these canulae. Body temperature was monitored through a rectal thermometer and normal temperature was maintained by a circulating water heating pad. The animal's head was then secured in the holder fixed to screws previously embedded in the skull with cement, obviating the necessity of using earbars. After the cornea was anesthetized with topical application of Dorsocaine, and mydriasis and cycloplegia were induced with phenylephrine (Neosynephrine) and atropine, contact lenses were applied to the eyes. The eyes were refracted by streak retinoscopy and lenses were installed in front of the animal's eyes in order to bring them to focus on a projecting screen. An initial dose of gallamine triethiodid (Flaxedil, 20 mg) was given intravenously, and respiration was maintained artificially. The respirator was set to distribute a stroke-volume per body weight according to the chart of Kleinman and Radford, Jr., and physiological parameters (heart rate and rectal temperature) were monitored. A mixture of 3 mg Tubocurarine chloride and 14 mg Flaxedil was administered by a motor-driven syringe by continual automatic infusion at a rate of 2 cc/h. The duration of an average recording session was 24 h. The animal was then revived. The normal behavior displayed by the cats in the same surroundings on subsequent days suggested that no psychological trauma had occurred during the previous recording sessions. Each cat was used for either two or three recording sessions.

C. Apparatus

Cells were first hand-mapped with the use of a retinoscope. They were further investigated by a computer controlled system (PDP 8) which allowed the presentation of stimuli (one line, two lines and gratings) and recorded the cell's responses to those stimuli. In addition, electrical stimulations were administered to the cerebral structures through a square wave pulse generator. Prior to the brain recording session various electrical stimulations to brain structures were given first to the unanesthetized and unparalyzed subject to determine the intensity and frequency of the stimulating current to be used during electrophysiological recordings. The intensity and frequency used were those which were just under threshold for eliciting a behavioral response (pupil dilation, attempt to escape . . .) from the fully awake animal. For the basal ganglia these stimulations had the following parameters: I = 0.2–0.4 mA; D = 0.2 ms; F = 2 Hz. In the cortex experiments parameters found to be optimal were: I = 2.5 mA; D = 1.0 ms; F = 2 Hz. Electrical stimulation continued throughout the presentation of visual stimuli. Comparisons entailing electrical stimulation were therefore with a baseline produced with electrical stimulation in the absence of visual stimulation.

D. Experimental Protocol

The following steps constituted the experiment:

1. A baseline reading was taken with electrical but no visual stimulation.

2. An initial control presentation of visual stimulation without electrical stimulation consisted of: (a) one line moving in each of 36 directions in 10° increments; or (b) five repetitions of

separate scans of two parallel lines moving in the preferred orientation and direction and at the preferred velocity with various separations (0–2°) or ten sine wave gratings (spatial frequency = 0.2–2.0 cycles/degree of visual angle) drifted in the preferred orientation and direction at the preferred velocity.

3. The same procedure was then repeated while administering electrical stimulation to one of the four implanted electrode sites.

4. Control and stimulation series were alternated until the four sites (ipsilateral and contralateral frontal or inferotemporal cortex; or ipsilateral and contralateral putamen or caudate) had each been stimulated. The order of sites of electrical stimulations was randomized. A final control series was then run (1) without visual, and (2) without electrical or visual stimulation.

E. Histological Procedure

At the completion of the final recording session, cats were given an overdose of sodium pentobarbital and perfused through the left ventricle, first with normal saline and then with 10% Formalin. Part of the cranium was removed and the head placed in Formalin for three days, after which it was mounted in a stereotaxic instrument and blocked in coronal planes. The brain was then removed and placed for seven days in sucrose Formalin (10% Formalin, 30% sucrose). The block containing the lesion was then embedded in an albumin-gelatin solution (18 gm. of gelatin, 800 cc of distilled water at 50° C, 180 gm of albumin) and cut into 50-μ sections on a freezing microtome. Every fifth section was mounted and stained with cresyl violet.

The placements of the stimulating electrodes could be identified unequivocally, and most of the electrode tips were in the intended loci. In the case of gyrus proreus and compositus, the electrodes were all in the desired loci. The electrodes intended for caudate nucleus were on target except four, as shown in Fig. 1. One was located in the right capsula interna, and one in the left capsula interna. Two were located in the anterior ecto-sylvian gyrus, one in the left one, one in the right. For the putamen (Fig. 2) also four of the electrode tips did not reach the intended target: three were located in the Claustrum (two in the right, one in the left) and one in the stria medullaris of the thalamus.

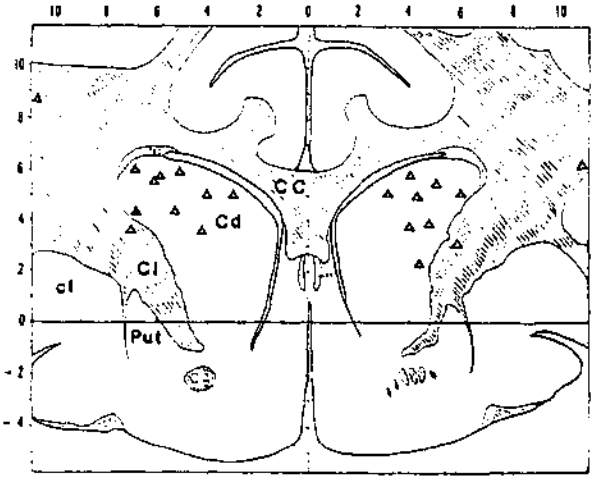

Fig. 1. Loci of stimulating electrodes in caudate nucleus. CC: corpus callosum; Cd: caudate nucleus; Cl: capsula interna; cl: claustrum; Put: putamen

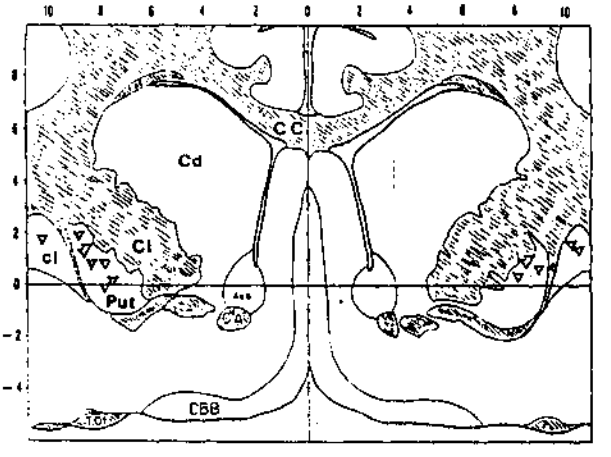

Fig. 2. Loci of stimulating electrodes in putamen. CC: corpus callosum; Cd: caudate nucleus; Cl: capsula interna; cl: claustrum; Put: putamen

Results

The results are divided into two parts. In the first part, we shall report the effects of electrical stimulation of the basal ganglia and of gyrus proreus and compositus on those properties (orientation selectivity and spatial frequency tuning characteristics) of striate cortex neurons that did not vary as a result of the electrical stimulations. In the second part, those properties (spontaneous activity, optimal firing rate, receptive field size and double line interactions) of visual cortex neurons which varied as a result of the electrical stimulation will be reported.

1. Invariant Properties

A. Orientation Selectivity

1. Putamen and Caudate Stimulation. The average change in the preferred orientation of 106 units was computed (analysis of variance – ANOVA) and showed that the effects of electrical stimulation of putamen and caudate on orientation selectivity of visual cortex neurons were not significant ($F_{(3,42)} = 0.42$, $p > 0.5$). Moreover, in order to see if there was any difference between the simple and the complex receptive field properties with respect to any change in their orientation selectivity, a chi-square analysis was performed on the two subgroups. Neither of these properties showed any significant change and the probability of change was the same for the two groups ($X^2_{(12)} = 10.41$, $p < 0.25$ for the simple, $X^2_{(12)} = 15.85$, $p < 0.20$ for the complex property).

2. Cortical Stimulation. Twenty cells were studied with regard to the possibility that their selectivity to

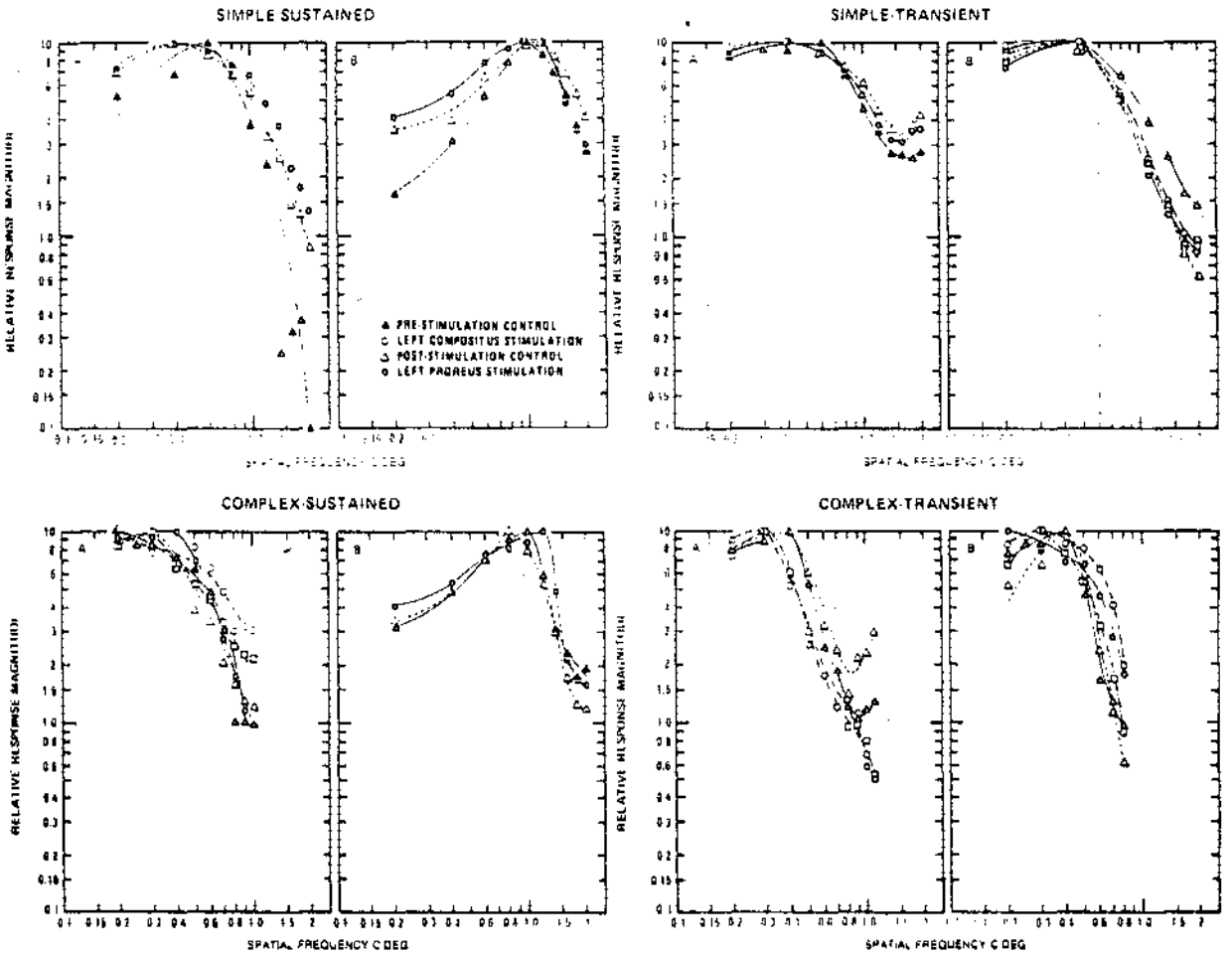

Fig. 3a–d. Examples of the spatial frequency response patterns of individual units during electrical stimulation of gyrus proreus and compositus. Response of a cell with (a) simple-sustained properties; (b) simple-transient properties; (c) complex-sustained properties; (d) complex-transient properties. Abscissa: spatial frequency in C deg; Ordinate: relative response magnitude

Table 1

	Classification							
Experiment	Simple	Complex	Sustained	Transient	Simple Sustained	Simple Transient	Complex Sustained	Complex Transient
Spatial Frequency Peak Shifts with Cortical Stimulation	$X^2 = 6.64$ $p < 0.5$	$X^2 = 4.57$ $p < 0.5$	$X^2 = 4.55$ $p < 0.05$	$X^2 = 3.83$ $p < 0.05$	$X^2 = 6.7$ $p < 0.25$	$X^2 = 6.11$ $p < 0.25$	$X^2 = 2.93$ $p < 0.75$	$X^2 = 8.53$ $p < 0.1$
Spatial Frequency Width of Tuning Curves with Cortical Stimulation	$X^2 = 5.68$ $p < 0.25$	$X^2 = 5.19$ $p < 0.5$	$X^2 = 7.11$ $p < 0.25$	$X^2 = 9.02$ $p < 0.10$	$X^2 = 4.96$ $p < 0.5$	$X^2 = 5.25$ $p < 0.5$	$X^2 = 4.94$ $p < 0.5$	$X^2 = 7.5$ $p < 0.1$
Spontaneous Activity with Cortical Stimulation	$X^2 = 0.38$ $p < 0.75$	$X^2 = 3.16$ $p < 0.50$	$X^2 = 4.37$ $p < 0.25$	$X^2 = 1.35$ $p < 0.50$	$X^2 = 2.1$ $p < 0.25$	$X^2 = 4.85$ $p < 0.10$	$X^2 = 1.7$ $p < 0.50$	$X^2 = 0$ $p < 0.9$

orientation could be changed by electrical stimulation of gyrus proreus or compositus. No significant effects (ANOVA) were obtained from electrical stimulation of these structures ($F_{(3,40)} = 2.85$, $p > 0.10$). Nor were differences found between simple and complex receptive fields with regard to change in orientation.

B. Spatial Frequency

1. Peak Shifts. As illustrated by the tuning curves of individual receptive fields shown in Fig. 3, stimulation of proreus and compositus did not significantly shift the spatial frequency of the peaks of such suprathreshold curves ($F_{(3,112)} = 0.59$, $p < 0.5$).

The changes in peak frequency occurring during cortical stimulation were also tabulated according to receptive field properties. No significant differences (see Table 1) in shifts of peak frequency were found for any property or combination of properties.

2. Width of Spatial Frequency Tuning Curves. The widths of those tuning curves shown in Fig. 3 were also not significantly (ANOVA) affected by proreus and compositus stimulations. ($F_{(3,72)} = 1.18$, $p < 0.25$).

Nor did analysis performed on the different receptive field properties or combination of properties show any significant changes (see Table 1) in curve widths following proreus and compositus stimulations.

II. Varying Properties

A. Spontaneous Activity

In order to determine the spontaneous activity, post-stimulus time histograms (PSTH) were derived while the unit was firing in the absence of electrical or specific visual stimulation. Then, electrical pulses were delivered to the basal ganglia or the cortical sites, and additional controls without visual stimulation were taken as indicated in the Methods section.

1. Putamen and Caudate Stimulation. As shown in Fig. 4, the electrical stimulation of putamen induces (on the average) a decrease in the spontaneous activity while electrical stimulation of caudate induces an increase.

An analysis of variance performed on a total sample of 82 units showed that the increase and the decrease in spontaneous activity during caudate and putamen stimulation respectively were significant ($F_{(3,78)} = 7.31$, $p < 0.01$). These results are reported in Table 2. This effect was observed irrespective of which receptive field properties characterized the unit.

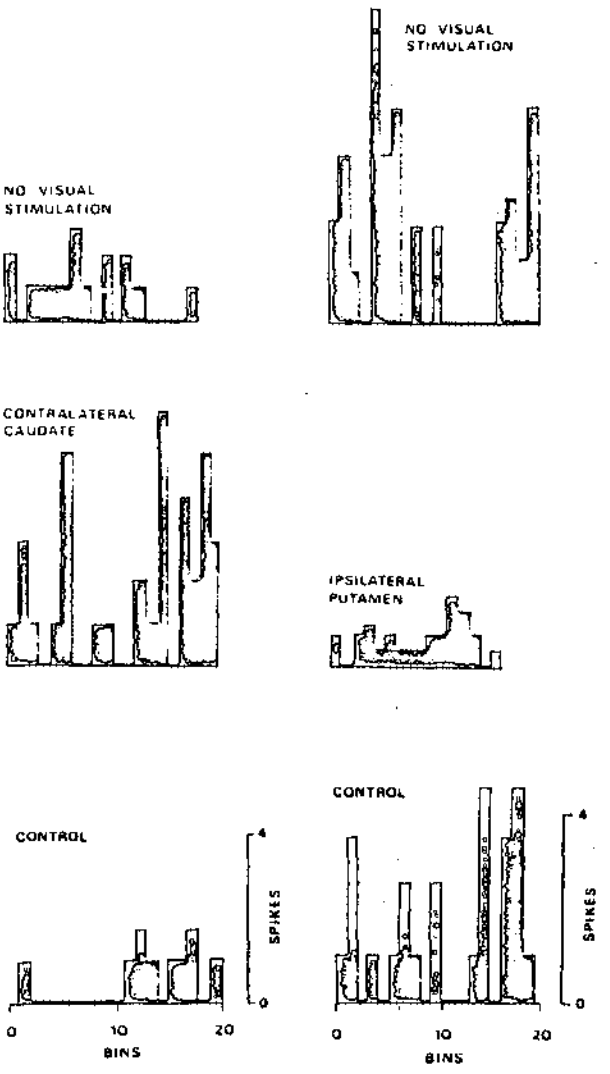

Fig. 4. Effects of electrical stimulation of putamen and Caudate nucleus on a cell's spontaneous activity. All histograms were derived over the time that would be taken by a single line presented in one orientation (but the line was not presented during this run) while the cell was firing in the absence of specific visual stimulation. The second histogram on the right shows a decrease in the cell's response during electrical stimulation of the ipsilateral putamen and the second histogram on the left shows an increase during electrical stimulation of the ipsilateral caudate. The first and last histograms (left and right) were obtained without any electrical stimulation. The same effects were observed when the time was extended to cover the duration that would have been taken by presentations in 36 orientations. Abscissa: time (bin width: 200 ms); Ordinate: cell's response in spikes/s calculated by dividing the total number of spikes by the number of bins × bin width

2. Cortical Stimulation. No significant differences were found with either proreus or compositus stimulation with respect to change in spontaneous activity ($F_{(3,178)} = 0.29$, $p < 0.50$). Nor were there any

Table 2. Mean change in spontaneous activity during basal ganglia stimulation

	Ipsilateral Putamen	Contralateral Putamen	Total Putamen	Ipsilateral Caudate	Contralateral Caudate	Total Caudate
Number of cells	14 (17%)	36 (43%)	50 (60%)	16 (20%)	16 (20%)	32 (40%)
Mean change spikes/s	−5.91	−18.18	−15.36	+12.06	+14.57	+13.31
Standard deviation	8.67	22.45	19.53	12.38	20.52	18.03

The number in parenthesis indicates the percentage of the *total* sample of cells which responded in this fashion

changes in spontaneous firing rate (see Table 1) when tabulated according to receptive field properties and combinations of properties.

B. Optimal Firing Rate

PSTH were taken in the following sequence: (1) Electrical stimulation of basal ganglia and cortex only; (2) No electrical stimulation while the cell was visually driven with an optimal stimulus; (3) Electrical stimulation of basal ganglia and cortex during continued visual stimulus presentation; (4) Optimal visual stimulation only.

1. Putamen and Caudate Stimulation. Figure 5 shows an example of the effect of electrical stimulation of putamen and caudate on the response of two units. On the left, the first histogram is a subhistogram of the total of 36 such subhistograms obtained in determining the orientation selectivity of the receptive field. This subhistogram is chosen a posteriori because it showed that the best response is obtained when the bar of light has an orientation of 220° and is moved in the preferred direction at a preferred velocity. During electrical stimulation of the putamen, the firing level of the unit drops drastically. In the last histogram, the cell returns to its pre-electrical stimulation level. The histograms on the right show that during electrical stimulation of the caudate nucleus, a unit whose optimal orientation is 190° increases its firing level and shows a return to the pre-electrical stimulation level during the control run (Fig. 5).

These caudate and putamen effects were found in most of the 79 units studied and are summarized in Table 3. The increase and decrease in optimal firing rate were statistically (ANOVA) significant ($F_{(3,75)} = 6.5$, $p < 0.01$).

In order to see if units showing simple and complex properties were equally affected by electrical stimulation of putamen and caudate, a chi-square

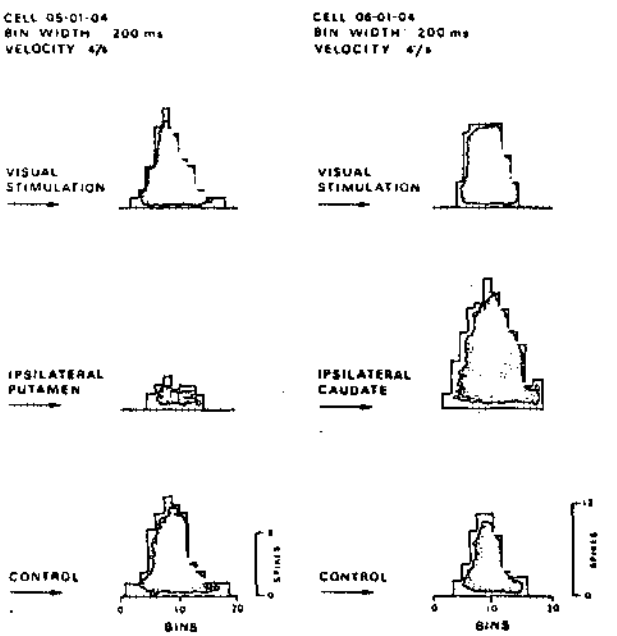

Fig. 5. Effects of electrical stimulation of putamen and caudate nucleus on the optimal firing rate and receptive field size (RF) of two complex cells. For all histograms the abscissa represents the position of the stimulus as it moves once across the field (bin width = 200 ms) and the ordinate, the unit's discharge (spikes/s). *The arrow to the left of each histogram represents the level of spontaneous activity*. Note that this level remains unchanged throughout the experiment. In the left column, the first histogram represents the optimal firing rate of the unit 05-01-04 chosen a posteriori from presentation in 36 orientations because it showed the preferred orientation and direction. The upper histogram was made under the control condition of visual stimulation only. This is followed in the middle histogram by electrical stimulation of ipsilateral putamen. Note that the unit's discharge dropped drastically and its RF size shrank (the number of bins on the abscissa diminished). Finally, the control condition of visual stimulation only shows a return to pre-electrical stimulation level. In the right column, the first histogram represents the control condition optimal firing rate of another unit (06-01-04). During electrical stimulation of ipsilateral caudate, there is a drastic increase in the RF size as well as its discharge. Control: return to pre-electrical stimulation level

Table 3. Mean change in optimal firing rate during putamen and caudate stimulation

	Ipsilateral Putamen	Contralateral Putamen	Total Putamen	Ipsilateral Caudate	Contralateral Caudate	Total Caudate
Number of cells	12 (15%)	21 (27%)	33 (42%)	23 (29%)	23 (29%)	46 (58%)
Mean change (spikes/s)	−3.62	−8.31	−6.61	+6.69	+1.89	+4.29
Standard deviation	10.08	15.04	13.48	16.61	13.49	15.16

The number in parenthesis indicates the percentage of the *total* number of cells which responded in this fashion

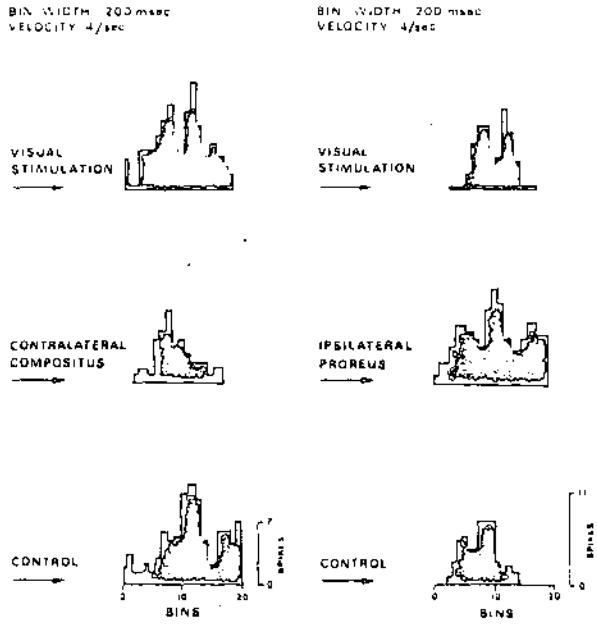

Fig. 6. Effects of electrical stimulation of gyrus proreus or gyrus compositus on two units in the visual cortex. The arrow indicates spontaneous activity which again remains unchanged with cortical stimulation. In the left column the first histogram represents the optimal firing rate of the unit according to preferred orientation and direction chosen a posteriori from presentation in 36 orientations. The second histogram was taken during electrical stimulation of the contralateral gyrus compositus. Note that the unit's optimal firing rate and receptive field size are decreased. The third histogram shows that the unit's discharge returns to the pre-electrical stimulation level during the final control run. In the right column the first histogram represents the optimal firing rate of another unit under the same condition as the first control. The second histogram shows that during electrical stimulation of the ipsilateral gyrus proreus there is an increase in the cell's firing rate and receptive field size. The third histogram shows the return to the pre-electrical stimulation level during the final control run. For all histograms the abscissa represents the time (bin width = 200 ms) and the ordinate, the unit's discharge in spikes/s. The arrow to the left of each histogram represents the level of spontaneous activity

test was performed for each of the subgroups. For cells with complex properties, the directional effect was significant ($X^2_{(6)} = 14.28$, $p < 0.05$) but those with simple properties seem on the whole to be equally affected ($X^2_{(6)} = 1.85$, $p > 0.10$) even though on the average, they show a decrease after putamen stimulation and an increase after caudate stimulation.

2. Cortical Stimulation. The optimal firing rate of 113 cells was measured before and during electrical stimulation of proreus and compositus in the same manner as described under putamen and caudate stimulation. A significant (ANOVA) effect ($F_{(3,109} = 2.69$, $p < 0.05$) was obtained. Both ipsilateral and contralateral proreus stimulations increase the optimal firing rate of cortical units whereas ipsilateral and contralateral compositus stimulations decrease it. Figure 6 shows an example of the effect of electrical stimulation of proreus and compositus on the response of two units. On the left are PSTH obtained from a unit whose optimal orientation is 120° while stimulated by a line moving in the preferred direction and velocity. It can be seen that the cell's optimal firing level decreases drastically during compositus stimulation. On the right are PSTH for a unit whose optimal orientation is 100° and whose optimal firing rate is increased by electrical stimulation of proreus. Notice also that in both cases the unit's firing rate returns to its pre-stimulation level in the last histograms.

Further, the effects of stimulation of gyrus proreus and compositus were studied with regard to the simple vs complex properties of the units. A chi-square analysis performed on the data revealed no significant effects for the simple property ($X^2_{(5)} = 5.16$, $p < 0.20$) and none for the complex property ($X^2_{(5)} = 1.51$, $p < 0.5$). However, a trend is manifest in that 63% of the cells with simple properties and 61% with complex properties showed an increase in optimal firing rate after proreus stimulation and 86%

Table 4. Mean change in receptive field size during putamen and caudate stimulation

	Ipsilateral Putamen	Contralateral Putamen	Total Putamen	Ipsilateral Caudate	Contralateral Caudate	Total Caudate
Number of cells	22 (19%)	26 (23%)	48 (42%)	34 (30%)	32 (28%)	66 (58%)
Mean change (degrees of visual angle)	−0.81	−1.09	−0.92	+0.81	+0.72	+0.77
Standard deviation	3.19	2.39	2.88	2.71	2.71	2.71

The number in parenthesis indicates the percentage of the *total* sample of cells which responded in this fashion

of cells with simple properties and 63% with complex properties showed a decrease after compositus stimulation.

C. Receptive Field Size

1. Putamen and Caudate Stimulation. Figure 5 also shows an example of a unit whose receptive field was modified during electrical stimulation of the putamen. The size of the receptive field was derived from the receptive field profile using the formula F = V × T, where V = velocity of the line moving across the field and T = number of bins (abscissa) × bin width. During putamen stimulation the receptive field became smaller, that is, the number of bins on the abscissa diminished. During the control run the receptive field came back to the pre-electrical stimulation level. Conversely, caudate stimulation increased the size of the receptive field after which the receptive field returned to the pre-electrical stimulation level during the control run. The increase and decrease in receptive field size following caudate and putamen stimulation were found in most of the units studied ($N = 114$; $F_{(3,110)} = 3.82$, $p < 0.01$). These data are summarized in Table 4. The effects of putamen and caudate stimulation on the receptive field size were compared for the simple and complex properties of the receptive field. A chi-square analysis on the data showed that the effects were highly significant for both subgroups ($X^2_{(1)} = 7.5$, $p < 0.01$ for the simple property; $X^2_{(1)} = 7.45$, $p < 0.01$ for the complex property). 70% of cells with simple properties showed a decrease in their receptive field size during putamen stimulation and 90% showed an increase during caudate stimulation. As to cells with complex properties, 70% showed a decrease in their receptive field size during putamen stimulation and 74% showed an increase during caudate stimulation.

2. Cortical Stimulation. 115 cells were investigated to study the effects of proreus and compositus stimulation on receptive field size. The data show that *ipsilateral* proreus and compositus stimulations *increase* the size of the cell's receptive field whereas *contralateral* cortical stimulations *decrease* it. These effects are significant at the 0.05 level ($F_{(3,112)} = 2.77$, $p < 0.05$). Examples of units whose receptive field was modified during electrical stimulation of proreus and compositus are shown in Fig. 6.

No differential effect was found with regard to the simple-complex distinction. A chi-square analysis showed the effects of stimulation do not differentiate at the 0.05 level of significance.

D. Double Line Interaction

In order to test whether basal ganglia and cortex stimulation affects the inhibitory and facilitatory interactions within the receptive field, the response of the cells to each separation of the two lines (0.1°–1.8°) was compared during and before electrical stimulation. Inhibitation (and facilitation) were defined as a one standard deviation decrease (increase) in the firing rate produced by the presentation of a double bar over that produced by the presentation of a single bar at preferred orientation, direction and velocity. Inhibition (and facilitation) were computed for each degree of separation.

Fig. 7a–c. Graph of the number of cells in which facilitation and inhibition is produced for all receptive field properties and combinations of properties by the interaction of two lines moving at the preferred orientation, direction and velocity. a During visual stimulation only; number of cells studied = 40. b During caudate nucleus electrical stimulation; number of cells studied = 56. c During putamen electrical stimulation; number of cells studied = 23. Abscissa: stimulus separation in degrees; Ordinate: number of units

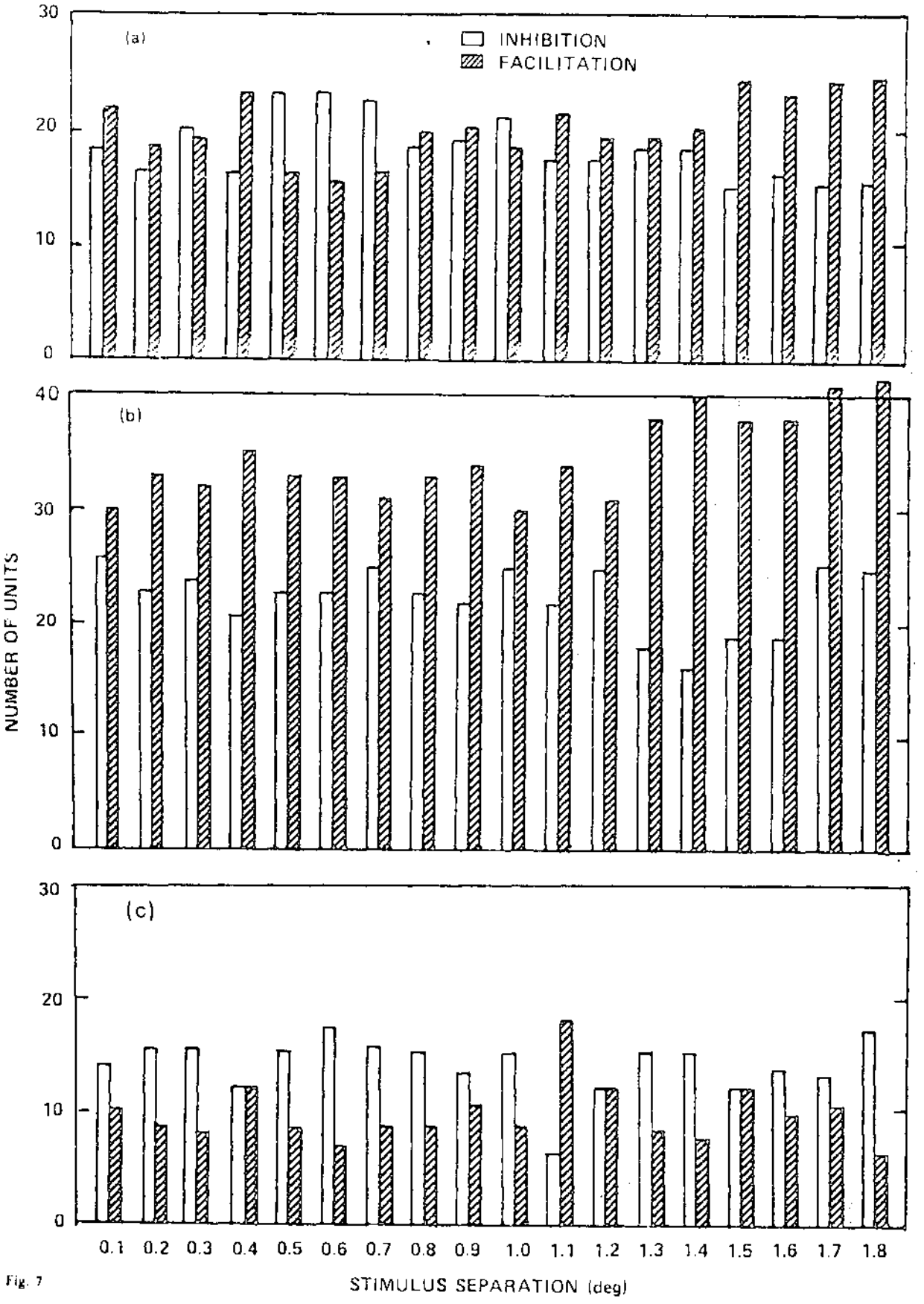
(a)
INHIBITION
FACILITATION
30
20
10
0
(b)
40
30
20
10
0
NUMBER OF UNITS
(c)
30
20
10
0
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8
STIMULUS SEPARATION (deg)

Fig. 7

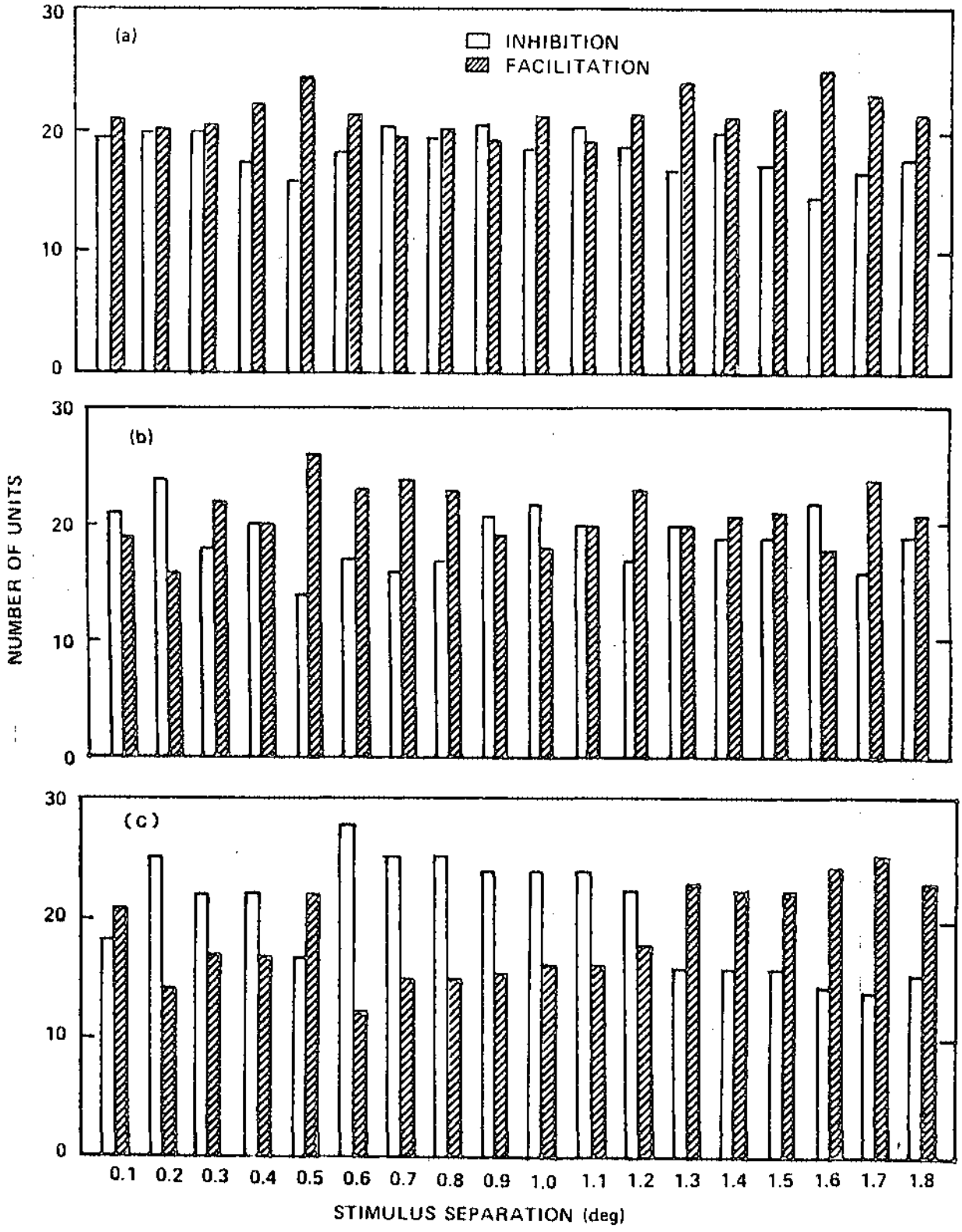

Fig. 8a–c. Graph of the number of cells in which facilitation and inhibition is produced for all receptive field properties and combinations of properties by the interaction of two lines moving at the preferred orientation, direction and velocity. a During visual stimulation only: number of cells studied = 40. b During gyrus proreus electrical stimulation: number of cells studied = 40. c During gyrus compositus electrical stimulation: number of cells studied = 39. Abscissa: stimulus separation in degrees: Ordinate: number of units

1. Putamen and Caudate Stimulation. Figure 7 presents the effect of electrical stimulation of caudate and putamen on all the units studied ($N_{CN} = 56$; $N_p = 23$). No overall change could be observed during putamen stimulation ($Z = 0.94$, $p > 0.5$) but a general excitatory influence was found during caudate stimulation ($Z = 3.6$, $p < 0.01$).

However, it can be seen from Fig. 7 that the number of cells showing facilitation during caudate stimulation is increased for all parts of the histograms as shown in Fig. 7 ($Z = 3.4$, $p < 0.01$; $Z = 3.6$, $p < 0.01$; $Z = 2.0$, $p < 0.05$). On the other hand, putamen stimulation increases the number of receptive fields which show inhibitory sub-regions in the first (0.1°–0.4°) and second (0.5°–1.2°) parts of the histograms ($Z = 2.1$, $p < 0.05$; $Z = 1.87$, $p < 0.05$). The terminal region (1.3°–1.8°) however, shows an inverse effect ($Z = 2.10$, $p < 0.05$).

In an additional analysis, the cells were divided according to their simple/complex properties and the effect of stimulation on each category was evaluated. No significant differences were found.

2. Cortical Stimulation. Figure 8 illustrates the effects of stimulation of proreus and compositus on all units ($N_{Proreus} = 40$; $N_{Compositus} = 39$). Only stimulation of gyrus compositus produced an overall change and this was inhibitory ($Z = 2.75$, $p < 0.01$). Stimulation of gyrus proreus produced no overall change. However, when the three segments of the histogram were considered separately (that is, 0°–0.4°; 0.6°–1.2°; 1.3°–1.8°), it could be seen that proreus stimulation increases the magnitude of the facilitatory effects in the middle segment of the histogram ($Z = 2.63$, $p < 0.01$) leaving the other parts unaffected by the stimulation ($Z_{1st\ third} = 1.05$, $p < 0.5$; $Z_{3rd\ third} = 1.12$, $p < 0.5$). The effects of compositus stimulation were restricted to the first two segments of the histogram ($Z_{1st\ part} = 2.65$, $p < 0.01$; $Z_{2nd\ part} = 2.76$, $p < 0.01$) leaving the third part relatively unaffected. Finally, no significant differences were found between cells showing simple and complex properties as to their responses to the double-line interaction before and during stimulation.

III. Stimulation of Other Cerebral Structures

Some electrode tips inadvertently hit the Capsula Interna (CI), the stria medullaris of the thalamus (SMT), the gyrus ectosylvian anterior (GEA), and claustrum. Statistical analyses similar to those used above were applied. The results show that stimulation of CI (ipsi- or contralateral), GEA (ipsi- or contralateral) and SMT (contralateral) had no significant effect on any of the tested variables. However,

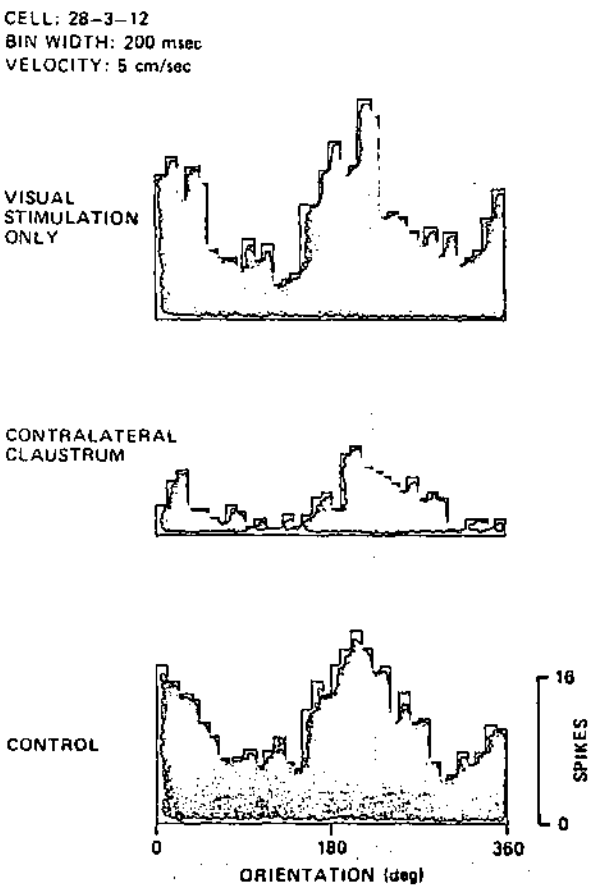

Fig. 9. Effects of electrical stimulation of the claustrum on the increase in firing level above spontaneous activity of a unit in the visual cortex. First histogram: mean optimal firing rate of the unit in response to the presentation of the stimulus in 36 orientations. Second histogram: during stimulation of contralateral claustrum, the cell's response dropped drastically. Third histogram: in the final control run, in the absence of electrical stimulation, there was a return to pre-electrical stimulation level. Abscissa: orientation of the line stimulus in deg.; Ordinate: unit's firing in spikes/s

electrical stimulation of the claustrum (contra or ipsilateral) has a statistically significant effect on spontaneous activity, optimal firing level, and receptive field size essentially identical to putamen stimulation, i.e., a decrease in spontaneous activity and optimal firing level and a diminution of the receptive field.

The effects of claustrum stimulation on optimal firing rate are represented in Fig. 9. The first PSTH represents the mean response of the cell to each of 36 directions (preferred orientation: 210°). In the second histogram, electrical pulses applied to ipsilateral claustrum induced a drop in the cell's firing level and finally in the last PSTH the cell returns to the pre-electrical stimulation level.

Table 5. Effect of claustrum stimulation on spontaneous activity, optimal firing rate, and receptive field size

	Spontaneous activity	Optimal firing rate	Receptive field size
Number of cells	17	17	17
Mean change	−3.32	−1.24	−0.19
Standard deviation	7.52	6.27	2.27

Table 5 reports the effects of claustrum stimulation on spontaneous and optimal firing rates as well as on the receptive field size.

IV. Autonomic Measures

To test whether the amount and parameters of electrical stimulation of the basal ganglia and cortex was affecting autonomic functions, heart rate and GSR were recorded during and before electrical stimulation. Heart rate was monitored in all experiments and GSR in several additional ones. Neither heart rate nor the number of deflections nor mean amplitude of the GSR were affected by these particular parameters of the stimulation sites.

Discussion

The experiments performed in this study devolved on determinations of the effects of electrical stimulation of the basal ganglia (caudate or putamen) and of cortex (gyrus proreus and gyrus compositus) on the properties of visual receptive fields. To this end, quantitative baselines of these properties had to be delineated. The set of properties described in the previous report (Pribram et al. 1981) was used to characterize the receptive fields of neurons in the visual cortex: orientation; direction and velocity of movement; spontaneous and optimal firing rates; receptive field size; and responses to stationary and drifting gratings.

Our results indicate that electrical stimulations of the basal ganglia and cortex have different effects. Fundamental to this difference is the fact that basal ganglia (including claustrum) stimulations influence the spontaneous activity of neurons in the visual cortex, while cortical stimulations do not. Thus, whatever other effects electrical stimulations of the basal ganglia produce, the results must always be considered as possibly due to some overall activation or reduction of spontaneous activity, while those of cortical stimulation can be considered independent of any such effect.

With this caveat in mind, important similarities in the effects of stimulations of the basal ganglia and cortex can also be noted. The reciprocal balance between frontal and posterior brain mechanisms to which the current experiments were addressed has been supported by the results. Thus stimulations of the caudate nucleus increased, and those of the putamen decreased, the spontaneous activity of cells in the visual cortex. Further, optimal firing rates were increased by stimulations of gyrus proreus or the caudate nucleus; whereas stimulations of gyrus compositus or putamen decreased them. These results confirm previous findings (Smerin 1981; Spinelli and Pribram 1966, 1967) in which it was found that stimulations of the basal ganglia and cortex modify responses in the lateral geniculate nucleus in similar fashion: fronto/caudate stimulations have an excitatory effect and posterior cortex-putamen stimulations have an inhibitory one.

The only exception to this front-back reciprocal effect of the stimulations were those on receptive field size. In this instance, ipsilateral stimulations of both proreal and composit cortex (and only of cortex) produces enlargement of the receptive fields while contralateral stimulation shrinks them.

A beginning can be made in understanding these diverse effects by noting that none of the electrical stimulations of subcortical and cortical structures which were undertaken influenced the orientation selectivity or the overall spatial tuning characteristics of the visual cortical cells. In keeping with the analysis made in the previous report (Pribram et al. 1981) this suggests that such extra geniculo-striate stimulations do not influence the invariant properties of receptive field organization of striate cortex neurons which arise from sensory input.

Next, recall that only basal ganglia stimulations, not those of cortex, influenced spontaneous activity. Conversely, optimal firing rate and receptive field size are altered by cortical stimulation in the absence of changes in spontaneous activity. Changes in sensitivity to stimulation and in receptive field size can thus occur independently of changes in the level of activation.

These differences observed between the effects of stimulating basal ganglia and cortex suggest that different pathways are responsible for the differential effects. The massive effect observed on the spontaneous activity, the optimal firing rate and the receptive field size following basal ganglia stimulation could be attributed to a change in the level of general activation in a manner analogous to the model presented

by Deutsch and Deutsch (1963). Caudate stimulation would "raise" the level of general activation such that both the noise (spontaneous activity) and signal (optimal firing rate) would be amplified. Alternatively, putamen stimulation would "lower" the level of general activation such that both the noise (spontaneous activity) and signal (optimal firing rate) would be greatly reduced.

The basal ganglia thus act in accord with a system responsible for general activation such as the mesencephalic reticular activating system (Deuel et al. 1971; Jouvet 1967). Both the caudate and the reticular systems have, in turn, been shown to modify the activity of the nucleus reticularis of the thalamus whose activity generally influences the visual pathway (Yingling and Skinner 1975).

By contrast, cortical stimulation specifically modifies the optimal firing rate and receptive field size of the cells in the visual cortex without influencing the spontaneous activity level. This influence on optimal firing rate and receptive field size could be exerted through lateral or recurrent inhibitory processes. The mechanism by which the cortex affects such control might well be mediated by intra- and inter-hemispheric cortico-cortical connections as suggested by the behavioral neuropsychological studies of Deuel et al. (1971). However, an alternative possibility is that cortico-thalamic pathways to the specific nuclei of the diencephalon are involved (Skinner and Yingling 1976).

In an essential respect, the results of the current experiment support the proposal made by Pribram et al. in the companion study (submitted): Network properties rather than currently described cell types are optimal candidates for classification. In the current series of experiments the overall (excitatory) reactivity of the network is influenced by basal ganglia stimulations raising the question as to whether sustained-transient properties are subject to change by such stimulations. The interactive (inhibitory) properties of the network clearly respond to cortical stimulations and are only indirectly influenced by basal ganglia stimulations. The properties classified as independent in the companion report remain invariant when subject to either basal ganglia or cortical stimulations in the current series of experiments.

The results of these experiments support the conception that the primary visual system can be influenced by the action of related non-primary systems. The evidence presented suggests that the cortico-cortical influences operate on lateral or recurrent inhibition, but it is not clear whether this effect transpires at the lateral geniculate nucleus or at the cortex. Nor has it been established anatomically what the pathways might be for overall activation: Are they, as suggested above, basal ganglia → mesencephalic reticular formation → reticular nucleus of the thalamus – or are the more direct routes from basal ganglia to centrum medianum, or even to visual cortex (as for example in the case of the claustrum (Sanides and Buechold 1979; Ptito and Miceli in prep.)), involved? Or both? These questions are now under consideration in our laboratories.

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