ACTA NEUROBIOL. EXP. 1981, 41: 467-476

TWO-UNIT RECORDINGS FROM THE LATERAL GENICULATE NUCLEUS OF THE CAT. SOME INHIBITORY INTERACTIONS

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Key words: Lateral geniculate nucleus, two-unit recordings, receptive fields, inhibitory interactions

Abstract. Pairs of units were recorded by single electrodes from cat's LGN. Three types of pairs were distinguished. Two of them were classified as retinogeniculate pairs with positive cross-correlograms (ON center — ON center, and OFF center — OFF center); the third type consisted of negatively correlated pairs of LGN neurones. In each case the spatiotemporal organizations of both receptive fields (RFs) were analyzed at several levels of background luminance. An increase of background illumination induced more pronounced compression of the retinal than of the related geniculate ON-center RFs; a strong, central stimulation evoked oscillatory responses only in the LGN cells. The LGN neuron pairs showed a significant overalap of their RFs antagonistic areas. Potentiation of inhibition at the LGN level is discussed in relation to a proposed functional model.

INTRODUCTION

Single unit data analyzed in a preceding paper (7) have shown the reorganization of the receptive fields of the LGN cells using light-adaptation level as a changing factor. The implication of those data for the models of retino-geniculate convergence as proposed by other autors (3, 4, 6) was discussed. It is obvious, however, that the intrinsic, functional circuitry within the LGN should be studied directly using a multi-unit recording method. An attempt at such an analysis is presented here.

METHODS

The experimental procedure was indentical to that described in a preceding paper (7). The multiple-unit data were obtained using single electrode recordings from the lateral geniculate nucleus (LGN) of the cat. Action potentials were sorted using two window discriminators and analyzed on-line to obtain spontaneous contour planes representing the spatiotemporal structure of the receptive fields (RFs). The contour plane integrated along the space axis formed a sum-PST-histogram. A detailed description of such analysis was presented in the preceding paper (7).

The relation between two spike trains was examined by means of a PST analyzed where the spikes of one train triggered the time base while the spikes of the second train were counted. Such a histogram represents the time-density of the second train action potentials with respect to the occurence of the spikes of the first one, i.e., it constitutes the positive-going half of a cross-correlation histogram (with some inefficiency and data loss). The negative-going half could be obtained separately by interchanging the inputs to the PST analyzer.

Great care was taken to distinguish the optic tract (OT) fibers from the LGN-cell spikes. The frequency of firing and the shape of the action potential were initially used for identification. The characterisitc features of the contour plane were examined later. Ambigous cases were discarded.

RESULTS

Over 30 correlated pairs of units with non-flat crosscorrelograms of spikes occurring during spontaneous activity were analysed partially or fully. Two-thirds of them were classified as OT fiber — LGN cell pairs. Nine pairs were fully analysed and are presented here. Six of them were retino-geniculate duplets with positive cross-correlograms, and had RFs of the same type. Two pairs had ON center fields for both units and four showed OFF center organization. The remaining three were LGN cell — LGN cell pairs, all of them reciprocally organized (ON center vs. OFF center). Figures 1–3 are representative examples of the three types of pairs.

OT—LGN unit double recordings. OT and LGN spikes are shown on the oscilloscope trace in Fig. 1. Cross-correlograms of the corresponding spike trains are presented to the right. A group of the geniculate impulses which were time-related to the retinal spikes, form a narrow peak with a 0.5 ms latency. This fits the criterion of a usual synaptic

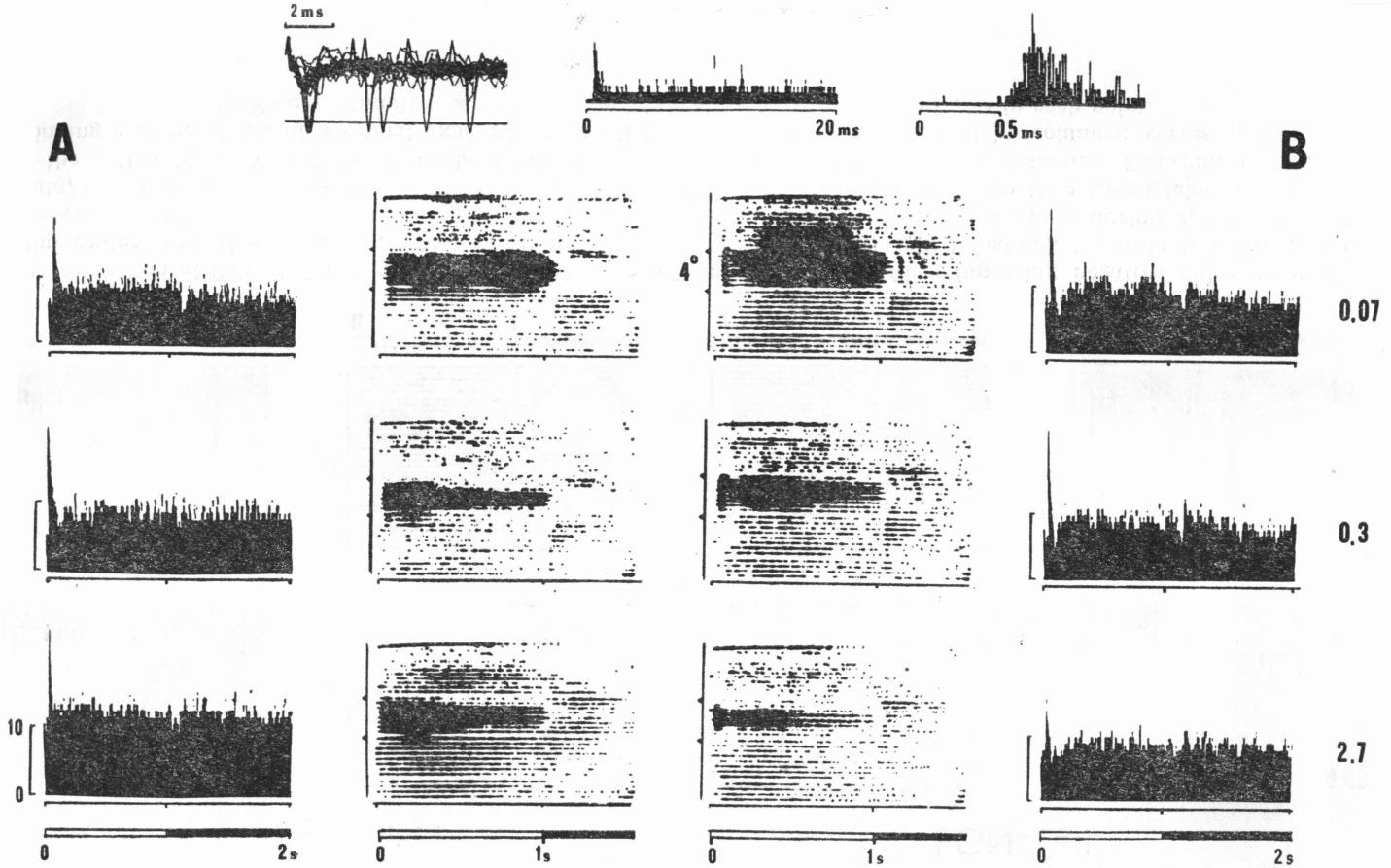

Fig. 1. Analysis of double recording of OT (A) and LGN (B) spikes. Both spikes triggered by separate discriminators. Top row, left side: a compound osciloscope trace showing OT fiber spikes (upward deflections, negative impulses) and action potentials of a LGN cell (downward deflections); both spikes retouched. Several superimposed sweeps were triggered by retinal spikes. Top row, center: cross-correlogram of spikes A→B, bin width 0.01 ms; right: same correlogram expanded. *A* (left two columns): PST-sum-histograms and corresponding contour planes of a retinal axon RF at three light adaptation levels. *B* (two right columns): contour planes and apropriate PST-sum-histograms for a LGN cell RF. Stimulus: bar of light subtending 0.5°×1°, luminance of 5 cd/m². The values of background luminance are indicated in cd/m² on the right side of each row and apply to both A and B units. Contour planes are obtained after 6 repetitions of stimulus in each of the 31 points along the RF axis.

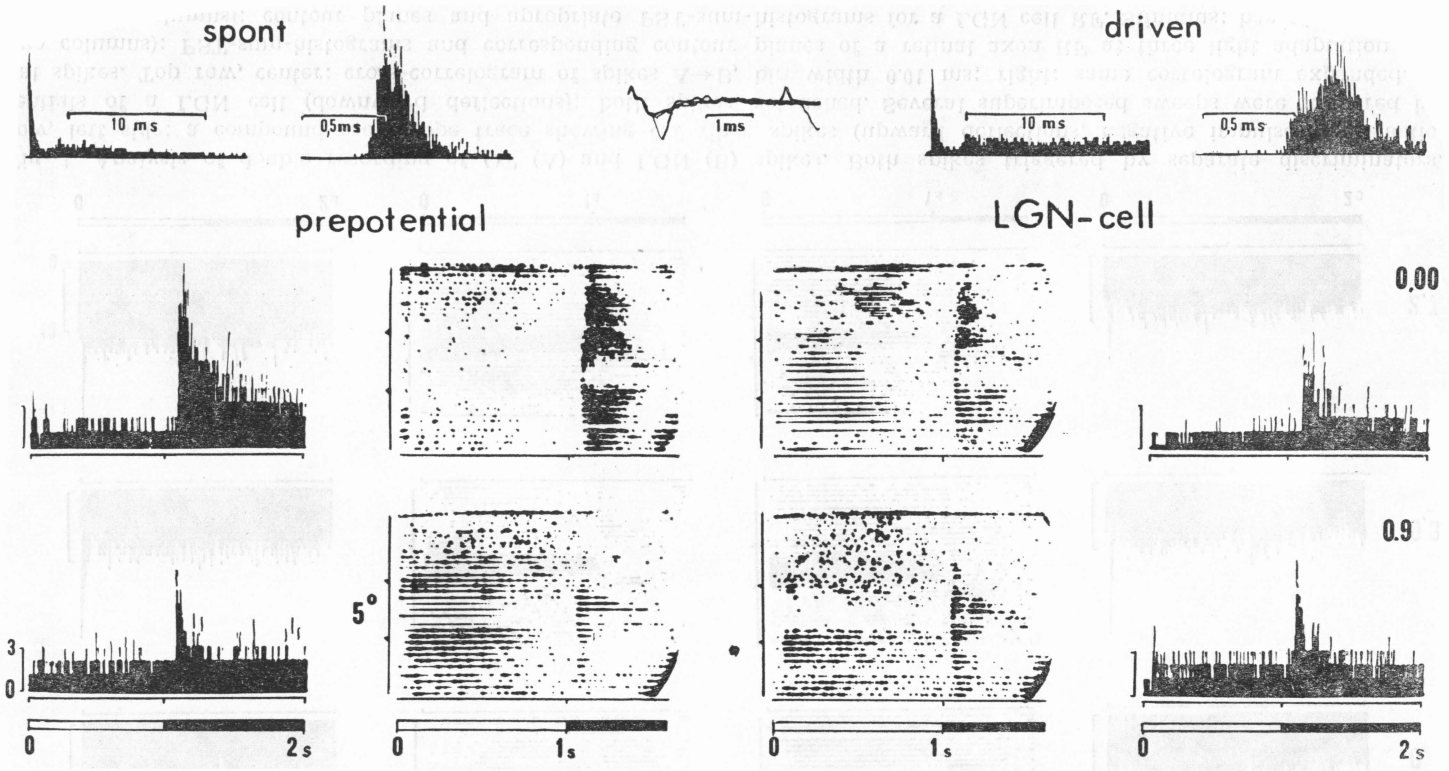

Fig. 2. Organization of RFs of simultaneously recorded spikes of an OT afferent fiber (up-going negative pulse on osciloscope trace, top center) and of a LGN cell, at two light adaptation levels (0.00 cd/m² and 0.9 cd/m²). Separate triggering. Top row, left side: cross-correlogram between the prepotential (OT spike) and LGN-cell spike trains taken during spontaneous activity. Same data, two time bases, b. w. — 0.01 ms. Top row, right side: driven cross-correlogram (two time bases) taken during stimulation of the retina by diffuse flash of 8 cd/m² intensity and frequency 1 Hz. Two left columns: PST-sum-histograms and corresponding contour planes of a retinal axon RF at two light adaptation levels. Two right columns: corresponding data for LGN-cell. Stimulus parameters same as on Fig. 1. Two repetitions in each point.

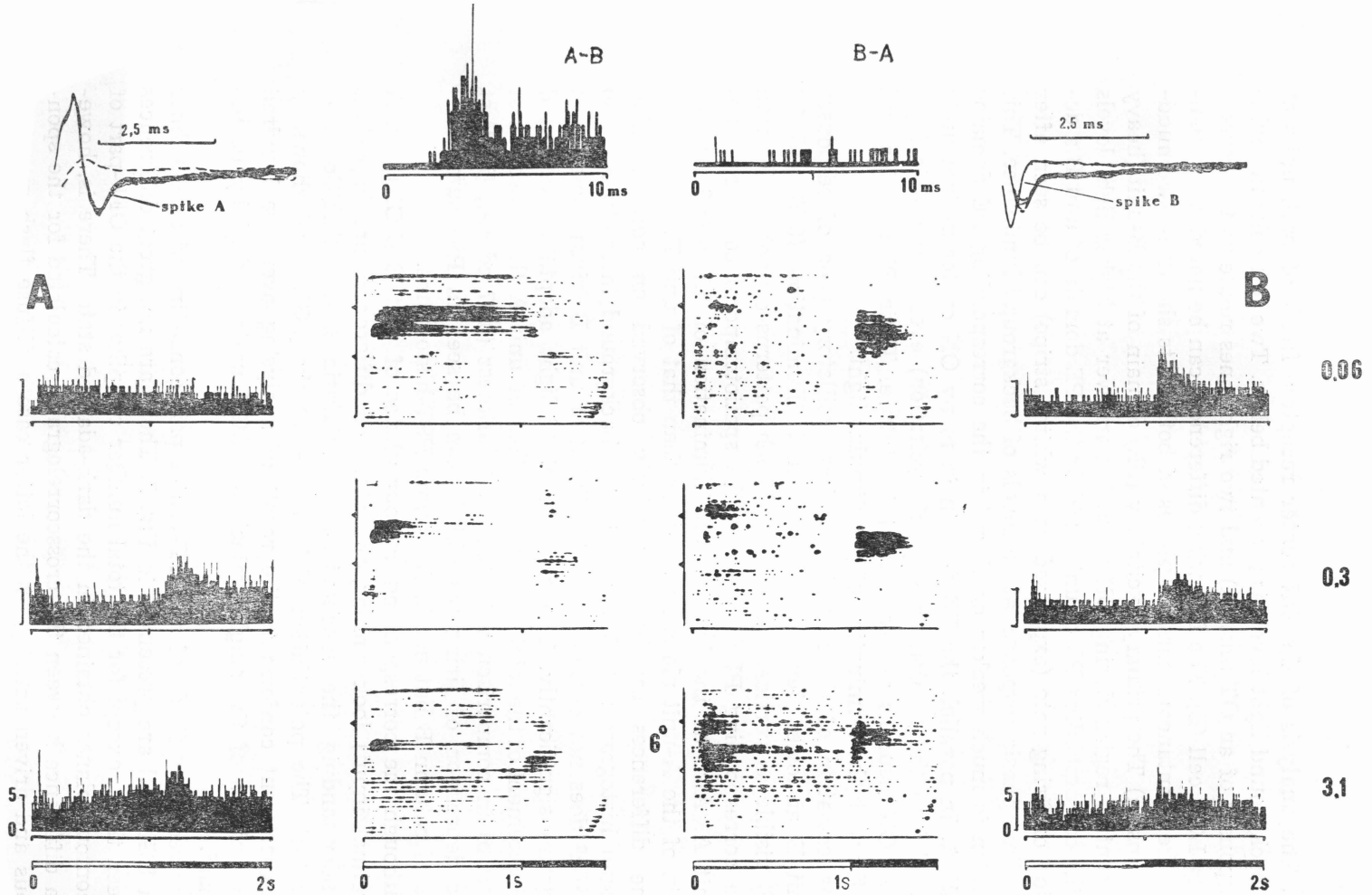

Fig. 3. Organization of RFs of simultaneously recorded spikes (A and B) of two LGN neurons. Top row in the middle: cross-correlograms between both spike trains (A to B and B to A) 1536 counts of source spikes in each case. A (two left columns): PST-sum-histograms and corresponding contour planes of unit A RF. B (two right columns): analysis of B cell RF. Stimulus: 0.5°×1° bar of light of 5 cd/m² luminance. Four repetitions at each point. Three levels of light adaptation (in cd/m²) are marked on right side of each row. Adaptation level was achieved by 0.5°×2° adapting spot placed in the field center. The full dead time of the discrimination is shorter than 1 ms.

delay. The analysis of the ON center receptive fields of both units at three background light levels is presented below. Two left columns exhibit responses of an OT unit (A) and two right ones relate to the corresponding LGN cell (B). The following differences can be noted when comparing the spontaneous contour planes of both units shown in two middle columns: (i) The primary excitatory (PE) domain of the B-unit (heavy black central region during ON time) is narrower at higher light levels than the corresponding PE of unit A; (ii) In the PE domain of unit B a depression of firing rate (expressed as a whiter stripe) can be seen after the earliest phasic response, at all levels of background luminance. This depression is much weaker or absent in the corresponding PE domains of unit A. In parallel, the PE domain in many ON center retinal units extended into the PI domain (tab of excitation) even at mesopic light levels. LGN neurons rarely show this feature. Their PI domains end abruptly with the termination of the stimulus light.

The cessation of the stimulus evokes oscillatory type of responses of unit B at lower levels of background illumination (0.07 and 0.3 cd/m^2) visible as vertical dark stripes. Such patterns cannot be detected in the corresponding PI domains of the spatiotemporal contour planes of unit A. Also at the background illumination of 2.7 cd/m^2, the PI domain of the A-unit plane lasts longer than that of unit B.

The differences can be consecutively observed on corresponding PST-sum histograms: (1) The rise in the background intensity level to 2.7 cd/m^2 does not change the total firing of unit B (right lower-most histogram) significantly. The same level of light adaptation produced an enhancement of the total number of spikes of unit A (left lower-most histogram) in comparison with the semi-darkness (0.07 cd/m^2); (ii) Post phasic depression of firing probability can be seen in PST-sum-histograms of column B but not in A column PST-histograms.

Although the corresponding contour planes of unit B (LGN) and A (its retinal input) look similar, the observed differences are important for understanding the mechanisms of intrinsic LGN inhibition (see Discussion). The potentiation of inhibition at the LGN level shown in this experiment conform to the result of analysing over one hundred contour planes of the single retinal and LGN units studied by us beforehand.

The receptive fields of an OFF-center pair consisting of an OT fiber and a LGN cell are presented in Fig. 2. There are not great differences between them, except for the total number of spikes in the OFF-part of the contour planes obtained in the dark-adapted state. There is, however, a difference between the crosscorrelograms calculated for the spontaneous and driven activity (in the latter case a diffuse flash was used

as the stimulus — uppermost row of Fig. 2). The cross-correlogram on the left, taken during spontaneous activity is unimodal in its main peak part whereas that on the right side on the figure (taken during stimulation) showed at least two modalities, the second having a longer delay time. This suggests the existence of other (e.g. inhibitory) inputs to the LGN-cell which enhance their activity during massive stimulation of the retina.

LGN unit pairs. Responses of two neuronally-related cells are presented in Fig. 3. The initial segment inflection on spike A indicates its origin from a cell body. The cross-correlogram of spike A with respect to B (B-A) does not exhibit any significant correlation between these spike trains. (A histogram with 1s time of analysis not shown in the figure, was also evenly distributed). The A-B cross-correlogram shows a deficit of B-spikes during 2.5 ms following each action potential A. The time-density of B-spikes becomes high immediately after this period and returns to a random level after subsequent 2.5 ms.

The contour planes taken for both units at three light adaptation levels showed the reciprocal arrangment of their RF domains. The spatiotemporal extent of the PE domain of unit A receptive field (ON-center, second column) corresponds to the sparsely dotted regions on the unit B contour plane. On the other hand PE domain of unit B receptive field (OFF center, third column) fits the spatiotemporal extent of PI domain on A contour planes. These data allow the assumption that an occurrence of spike A inhibits the activity of unit B for 2.5 ms and probably enhances its probability of firing afterwards. Such interaction strongly support the hypothesis of intrageniculate interneurones (2, 6).

DISCUSSION

The results relating to the organization of the retinal and geniculate receptive fields presented above and in a preceding paper (7) can be discussed with the aim to analyze the enhancement of inhibition in LGN-cells RFs comparing to the retinal ones (3, 4).

A physiological model of the LGN-cell receptive field should then explain:

a) Smaller, background-dependent changes of spontaneous firing rates of LGN cells in respect to retinal units;
b) Larger spatial extent of the inhibitory than the excitatory domains of the RFs of LGN cells;
c) More pronounced narrowing of the RF center of the LGN ON-cells than that observed for the ON-retinal units;
d) The lack of primary domain tabs (domain extension after switching

the stimulus ON or OFF) at higher background levels for LGN units and the presence of such tabs in light-adapted retinal fields (more retinal data in preparation);

e) The oscillations of the LGN-cell responses elicited from the RF center and the absence of such oscillations in the heterogeneous retinal RFs. Inhibitory post-phasic period in the responses of heterogeneous ON center LGN cells;

f) The persistence of weak inhibitory domains in dark-adapted LGN-cells and their presence in the central region of the field;

g) Reciprocal inhibitory interactions between the ON- and OFF-center type IGN neurones.

In the preceding paper (7) three models of LGN RF organization postulated in the literature were discussed. Findings (a) and (b) of the above list fit all three of them. So colled "zone" model was, however, excluded since it does not explain the enlargement of RF center in the dark observed for LGN fields (c). Finding (d) is not contradictory with the two other models. Data of (e) and (f) support, however, the "pool" model which postulates recurrent negative feedback from interneurons with large ON-OFF RF types whereas (g) agrees with the "reciprocal" model.

Experiments supporting the "pool" and "reciprocal" models were published by other authors. Singer at all (5) using quasi-intracellural recording suggested that area from which shortly delayed (2–10 ms) inhibition can be elicited is coextensive in space with the central excitatory area. This agrees with the finding presented above (f). Levick et al. (3) found large (at least 6 degrees in diameter) suppresive surround (similar to (b)) which, as they postulated, might be the result of activation of interneurones getting their inputs from both ON and OFF center relay cells. Such interneurones might form a base for the "pool" model. On the other hand, Stevens and Gerstein (6) have reported 9 neurally-coordinated pairs exhibiting deficit of spike counts on both sides of the origin of their cross-correlograms. The corresponding, opposite type RFs of these neuron pairs overlapped each other.

Lately Dubin and Cleland (2) and Ahlsen and Lindström (1) using electrical stimulation of OT and visual cortex have classified two types of LGN interneurones: intrageniculate and perigeniculate. To visualise all the data presented above, a schematic neuronal circuit is shown on Fig. 4. Two proposed LGN models: "pool" (3) and "reciprocal" (6) are here integrated using interneurons described by Dubin and Cleland as connecting elements. It should be stressed, however that this circuit represents a functional abstract of this discusion rather than a specific morphological reality.

The ON-center cell is presented on Fig. 4 as being central for all other conncections. Both relay cells (white circles) and intrageniculate interneuron (black) of an OFF-type, receive their main inputs of the same type from the retina. This inputs can consist of several retinogeni-

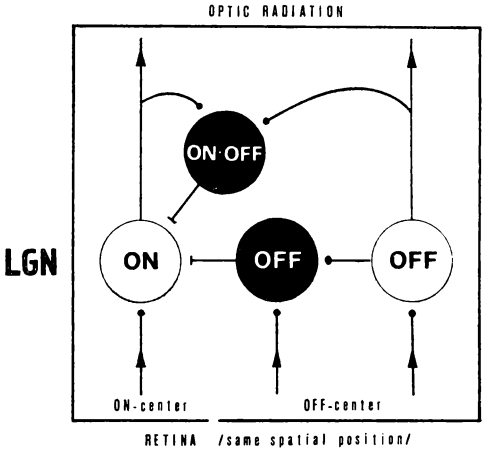

Fig. 4. Functional diagram of connections between LGN cells. White circles, relay cells. Black circles, interneurons. See text for details.

culate fibers. The reciprocal inhibition is mediated by the OFF-interneuron. The perigeniculate interneuron of an ON-OFF type (since it receives inputs from many ON- and OFF-center neighboring RFs) produces a negative feedback onto the relay cell.

Further experiments are needed for evaluating the mechanisms of enhancement of inhibitory influences at the LGN level.

I thank Miss D. Stumpło and Mrs B. Stachelska for technical assistance; Mr W. Gawor for photography; Dr. R. Tarnecki and dr. A. Michalski for reading this manuscript and helpful discussions.

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Accepted 15 May 1981