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RECEPTIVE FIELDS OF CAT'S NON-RELAY LATERAL GENICULATE AND PERIGENICULATE NEURONS

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Abstract. Two groups of neurons are postulated to serve as inhibitory interneurons for principal lateral geniculate cells: intrageniculate interneurons and the perigeniculate neurons. We analysed the spatiotemporal characteristics of receptive fields (RFs) of cells from both groups identified by their anatomical position and responses to electrical stimulation of the optic chiasm and visual cortex. Intrageniculate interneuronal RFs resembled in all respects those of relay cells. One third of perigeniculate neurons had erratic responses to visual stimuli. Those which responded well to flashing stimuli possess large (up to 20 degrees) spatially heterogeneous ON/OFF type RFs. Spatiotemporal extents of excitatory domains of both intrageniculate interneurons and perigeniculate neurons RFs correspond to the extents of inhibitory domains in the principal cell RFs which were described previously.

INTRODUCTION

It is generally assumed that the function of the lateral geniculate nucleus (LGN) is crucially dependent on its inhibitory systems (6, 8, 17, 20). Recent anatomical (1, 4, 11) and physiological (2, 3, 7, 14, 16, 23) results provide convincing evidence for the existence of two such inhibitory systems acting on relay cells in the LGN. According to these results, the principal cells receive inhibition of feed-forward type from the retinal ganglion cells as well as recurrent inhibition. It is postula-

ted that the feed-forward inhibition is mediated by inhibitory interneurons located within the main layers of the LGN, while the recurrent inhibition is mediated by perigeniculate nucleus (PGN) neurons excited by axon collaterals of principal cells. The receptive fields (RFs) of both those groups of inhibitory neurons and their functional connections have not been sufficiently studied, however. The aim of these experiments was to characterize in more detail the RFs of postulated intrageniculate interneurons and perigeniculate neurons (24). We have previously shown (22, 25) that intrageniculate interneurons monosynaptically inhibit the principal cells and therefore should strongly influence their RFs characteristic. With respect to the recurrent loop there are some data for convergence of excitation from both ON- and OFF-center type principal LGN cells onto an individual perigeniculate neuron. The RFs of these cells may play an important role in an attention control system (16, 17) and therefore their visual input should be carefully studied with specific visual stimuli. We expected that spatiotemporal characteristics of RF-excitatory domains of both postulated inhibitory neurons would be similar to inhibitory domains observed in RFs of the principal LGN cells (19, 21).

METHODS

The experiments were performed on 10 adult cats with pretrigeminal brain stem sections. Animals were immobilized by Flaxedil and artificially ventilated with continuous monitoring of the tidal CO_2. Atropine neosynephrine mixture was applied to the eyes, and refraction was corrected by + 1D contact lenses. Tungsten in lacquer microelectrodes were used for recording and marking with small electrolytic lesions the beginning and final points of the vertical tracks. Conventional criteria (3, 10) based on spike shape were used for differentiation between soma and axon-origin recordings. The physiological features (15) and histological verification of the tracks were used for precise localization of analysed cells. All neurons with uncertain features were not analysed. For electrical stimulation an array of four tungsten macroelectrodes positioned rostro-caudally (2 mm apart) was inserted 2.5 mm below the surface of the visual cortex (VCx) as shown in Fig. 1*A*. Another two electrodes were placed in the optic chiasm (OX). Single rectangular pulses (and occasionally pulse trains) were used for identifying the activation of cells recorded. The strength of pulses only sporadically exceeded 20 μA for OX, and 200 μA for VCx stimulation. Visual stimuli were bars of light (5 cd/m^2 luminance) or black spots from 0.25 to 20° of visual angle, flashing or moving upon a perimeter-like screen. The white

screen (60° diameter) was illuminated by an additional source of light to mesopic range (1–3 cd/m^2). Diffuse flashing was used during searching for neurons and as the first stimulus characterizing the RFs (Fig. 1*C*). We used the procedure of Stevens and Gerstein (19) for RFs analysis with response planes, which is, from our experience, a powerful tool for studying even a subtle changes of receptive field organization. The response plane is a stereoscopic view of thirty PSTHs obtained "simultaneously" for cyclic stimulation of 30 separate points spread over the RF axis (Fig. 3, left column). The slices cut off from a response plane at different levels of probability of firing result in "contour planes" pictures (Fig. 3, middle and right hand column). On the "spontaneous contour planes" (slices cut off at the spontaneous probability of firing — Fig. 3, middle column) dark and white "domains" correspond to excitatory and inhibitory spatiotemporal areas of the cell activity. To get fast, but still reliable spatiotemporal image of the RF we produced the "contour planes" on the screen of the storage oscilloscope by means of the dot-diagram method. On such contour plane (Figs. 1*D, E* and 2) each spike is presented as a dot correspondingly to the point of stimulation (ordinate axis) and time from the onset of the stimulus (abscissa axis). This method of analysis was described in detail in the previous paper (21).

RESULTS

Sampling. We have recorded from 154 neurons in 11 electrode tracks, localization of which was confirmed by anatomical reconstructions and physiological properties. The search was usually started 2 or 3 mm above the expected border of lamina A. The activity of each unit which was recognized as of soma origin was first tested by visual stimuli (diffuse flash, white and black spots of different sizes) and then by electrical stimulation of the OX and VCx. In agreement with Sanderson's results (15) the first cells recorded at the upper border of lamina A were only slightly visual or nonresponsive to any of the visual stimuli. The closer to lamina A, the more definite visual responses were obtained. It was noted that every visually responsive cell could be activated by diffuse flash, smaller flashing or moving stimuli were less effective. We were unable to define the localization of six RFs of cells, found in this region, which responded to diffuse flashing (see unit 2, Fig. 1*C*). These units and six other visually nonresponsive cells were not activated by OX stimulation and four of them were driven by VCx stimulation with rather long latencies (2.4–8 ms). We have classified this group of twelve neurons as reticular cells according to Ahlsen et al. (3) classification.

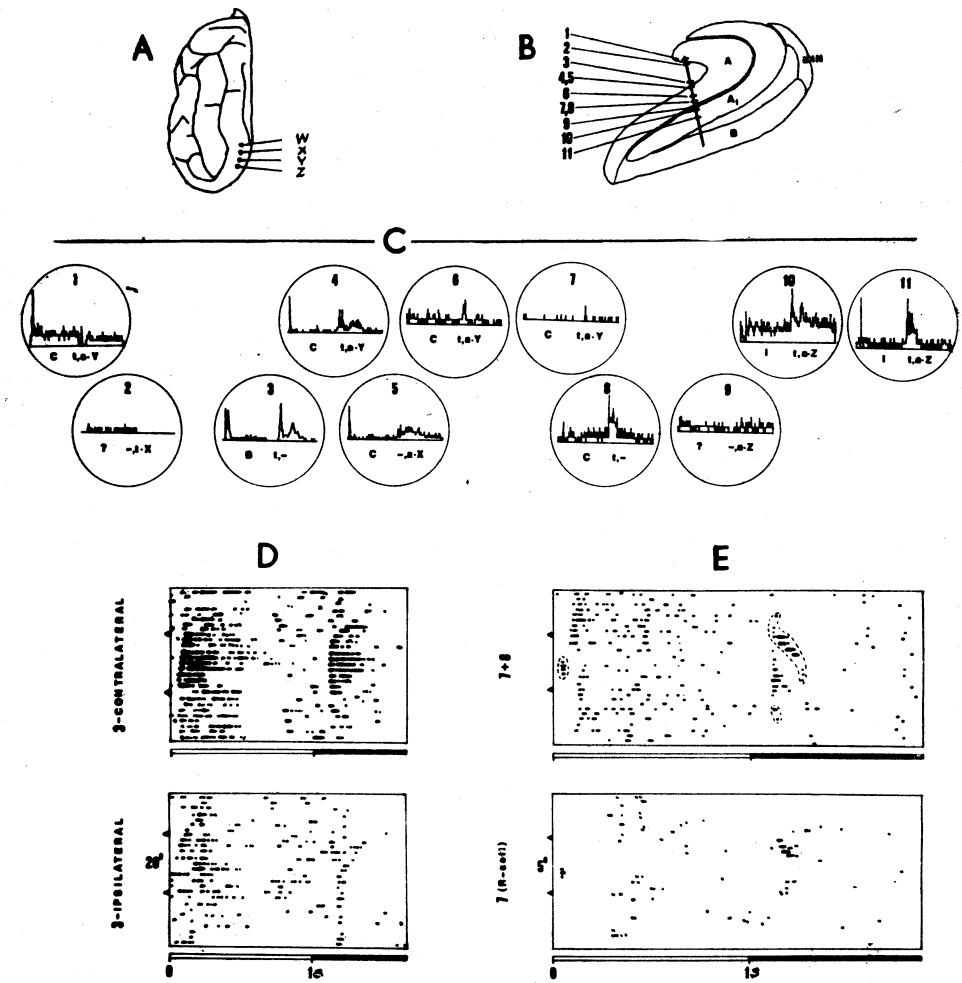

Fig. 1. A, positions of stimulating electrodes in the visual cortex; B, histological identifications of the microelectrode track. The points from which the appropriate cell responses were recorded are labelled by numbers; C, diffuse flash (of 10 cd/m² luminance) responses of the cells found during the penetration. The first half of histograms correspond to ON-time, the second to the OFF-time of the stimulus. The probability axis scale of histograms 3.4 and 5 is twice that in other histograms. Histograms in the upper row show the responses of relay cells. In the lower row the responses of other neurons are shown. Notation letters: B, C, I, below each histogram indicate: binocular, contralateral and ipsilateral inputs from retinae, respectively; t, cell responded transsynaptically; a, cell activated antidromically from points X, Y, Z as indicated in A. The OX and VCx pattern of responses are separated by a comma; D, the contour planes of RF of the perigeniculate neuron localized at position "3" as obtained by stimulating contra- and ipsilateral retinae respectively. Stimulus: 2° × 4.5° bar of 5 cd/m² luminance; E, lower contour plane shows the RF organization of relay cell "7". Upper contour plane shows the sum

The remaining 31 neurons localized above lamina A, responding to OX stimulation (but not activated antidromically by VCx) and possessing definable RFs were called perigeniculate cells, and were studied in detail.

Entering the geniculate laminae A and A1, we recorded from 90 cells, all of which showed clear, monocular concentric type of receptive fields. Eight of these cells, however, were not antidromically activated from VCx in contrast to their neighbours in the column with the same RF positions. We shall refer to the cells of this group as to the intrageniculate interneurons. The percentage of such neurons in our sample of geniculate cells does not exceed that found by antomical investigations (9, 13). Three other neurons with unusual RFs were found on the border in between laminae A and A1: two with binocular input and one with non-defined RF (cell 9 in Fig. 1C). We did not study these cells by means of response planes similarly to the other 18 cells from lamina B from which two were also binocularly driven.

Perigeniculate neurons RFs. Fourteen perigeniculate neurons found during vertical penetration were clustered between 80 to 500 μm above the dorsal border of lamina A. The remaining 11 cells were localized between 600 to 1100 μm above lamina A with exception of six cells found at a distance up to 2400 μm. The centers of all perigeniculate receptive fields sampled in this study were positioned in the contralateral, upper quarter of the visual field. This might explain the higher location of some of our PGN cells as compared to other studies (3), since several penetrations were going through the rostral tail of perigeniculate nucleus before entering the lamina A (e.g., Fig. 3). All but one PGN neuron were found below the reticular neurons in appropriate vertical tracks. The neurons closest to lamina A had their RF centers 0 to 5 degress higher than the first relay cell found. All of the perigeniculate fields (see Fig. 1–3) were approximately circular with a mean diameter of 15 degrees (range 8 to 50°). With exception of two cells, all others showed ON–OFF type of organization of their RFs with the most active responses near the center of the field. Nine of them showed, however, rather erratic responses (e.g., Figs 2C, E). Once activated, such a cell usually responded with a burst of spikes. The borders of these

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of responses of both units: "7" and "8" (intrageniculate interneuron). Dashed lines limit the spatiotemporal domains of activity of cell "7". Stimulus: 0.5° × 1° bar of 5 cd/m² luminance. Two repetitions of the stimulus in each point of the RFs shown on D and E contour planes. The white and black bar under the contour planes show the ON- and OFF-time of the stimulus, respectively.

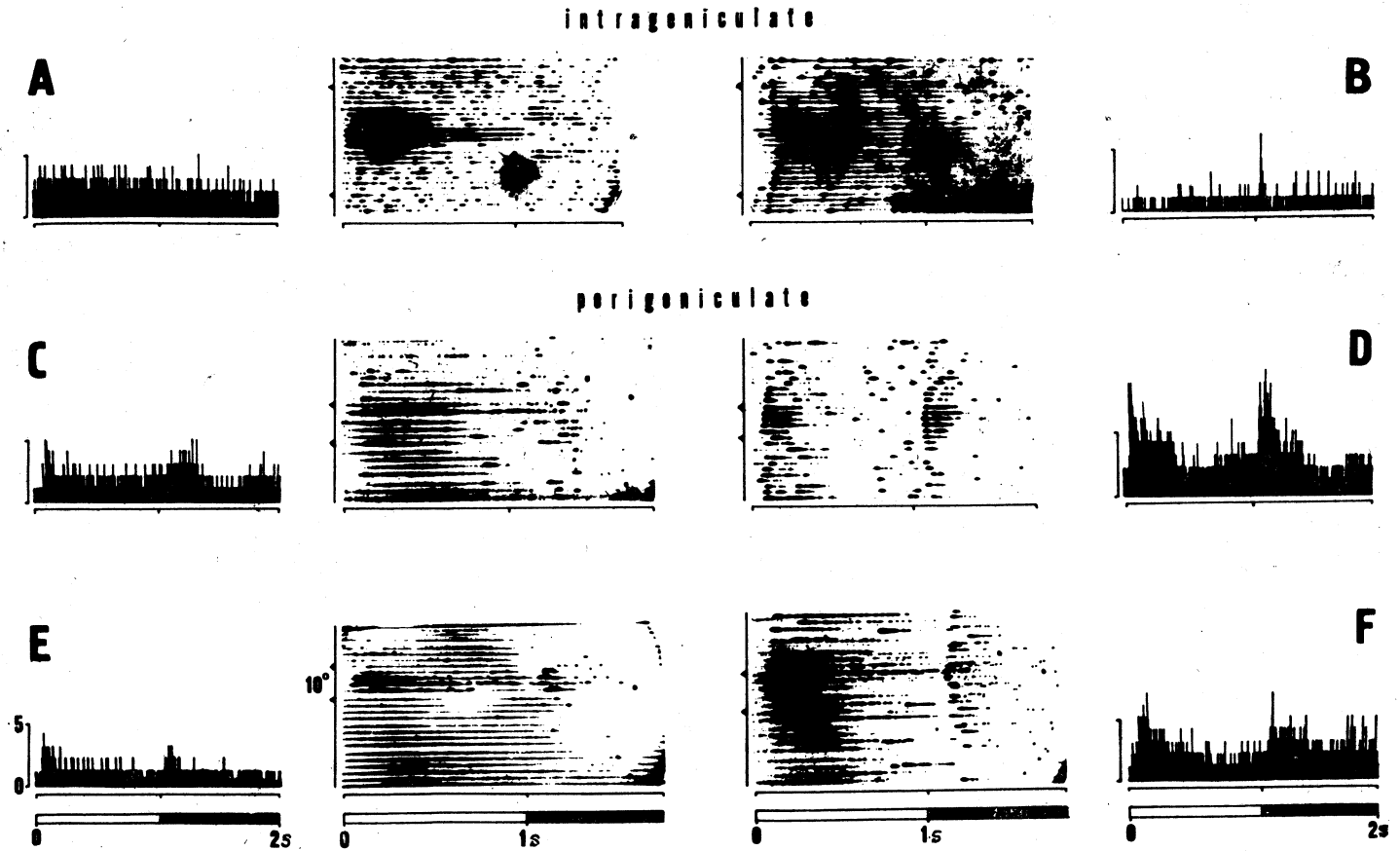


Fig. 2. Examples of contour planes of RFs of intrageniculate interneurons (A, B) and perigeniculate cells (C–F). Close by are sum-PST-histograms representing numbers of spikes from all responses integrated in space (21).

nine fields were hard to define and not every stimulation by small spot evoked the response from the center. Three of such neurons were weakly inhibited by a visual stimulus applied at any point of their RFs. The other 21 neurons responded repetitively to each stimulation mostly with phasic-like discharges (Figs. 2*D, F* and Fig. 3*A–C*). Usually the small bar of light of 0.5×1 degree of visual angle was adequate to evoke the cell response; seven units, however, were activated only by bigger spots of 2–8 degrees of diameter (Figs. 2*C, E* and Fig. 3*C*). To obtain the contour planes we used such a bar of light, which evoked the most vigorous response of the cell, the step between the neighbouring points of stimulation being equal to the stimulus size (compare Figs. 1–3). Most of the cells studied in the nucleus perigeniculate responded to visual stimulation of both retinae with one of the inputs being always stronger. Among the 31 perigeniculate neurons, we have found four units with only contralateral and two others in which only ipsilateral inputs were detected.

The response latencies of perigeniculate neurons for OX stimulation were in the range of 1.6–2.8 ms (plus two measurements of 3.2 ms) which fits well the data of Dubin and Cleland (7) and Ahlsen et al. (3). In two perigeniculate neurons, however, we have registered the first spike after 1.3 ms of OX stimulation (compare 16). The latencies for VCx stimulation were measured only for 14 perigeniculate neurons and all of them were in the range of 1.0–2.3 ms with characteristic variances and frequency limits as expected for monosynaptic linkage.

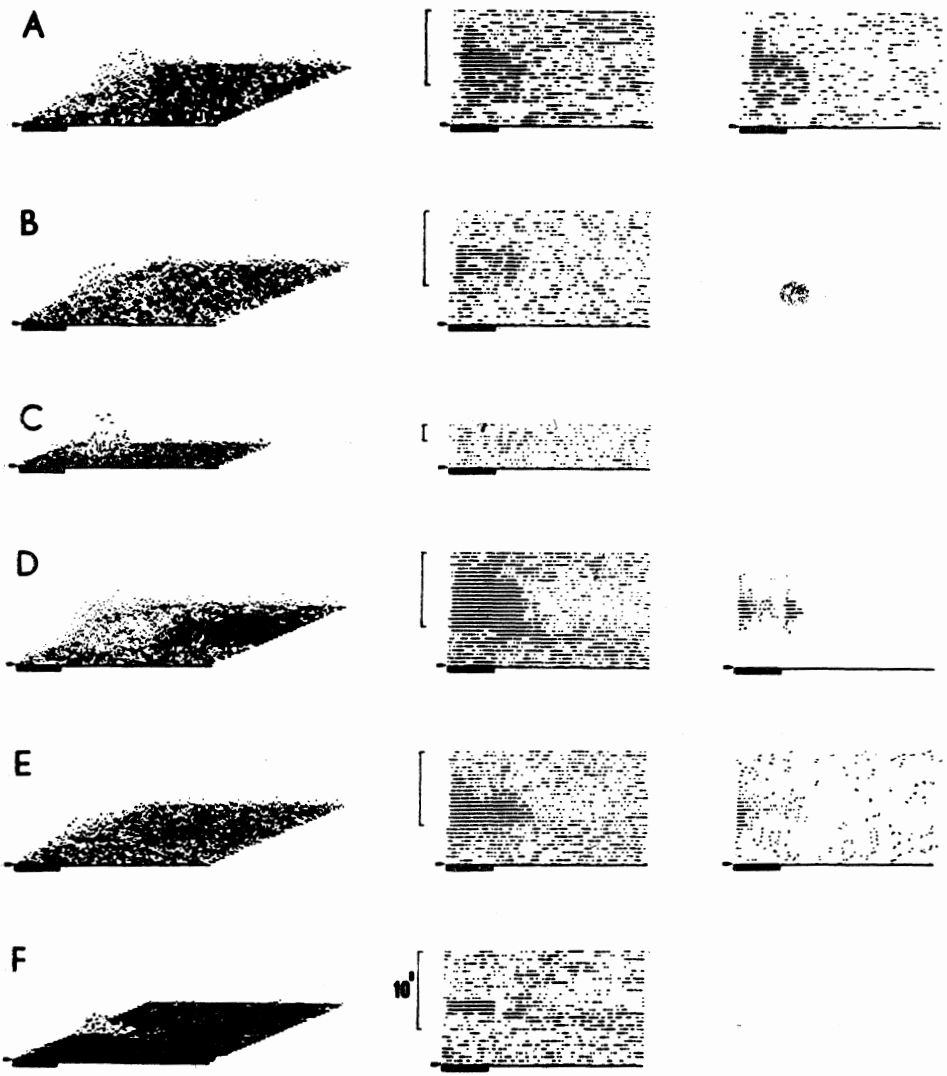
RFs of intrageniculate interneurons. We were able to classify eight intrageniculate interneuronal RFs according to classification used earlier for relay cells (19, 21) e.g.: heterogeneous ON (X_{ON} type, Fig. 2*A*), heterogeneous OFF (X_{OFF} type) and homogeneous OFF (Y_{OFF} type, Fig. 2*B*). The lack of example of homogeneous ON RF which was not correspondingly found might be due to our small sample of cells. In one case we registered the pair (Fig. 1*E*) of neighbouring relay cell and intrageniculate interneuron with reciprocally organized spatiotemporal domains of their RFs. It has previously been shown with crosscorrelation technique (22, 25) that the interneuron of such a pair may inhibit the activity of the relay cell by monosynaptic input, thus producing the reciprocal organization of spatiotemporal domains.

The intrageniculate interneurons responded to OX stimulation with latencies similar to those of relay cells (the average latencies measured in relay neurons for OX stimulation were in our sample 1.5 ms for transient type and 2.0 ms for sustained type). In most cases we were unable to get any facilitation of intrageniculate interneurons by VCx stimu-

lation. This might be due to the fact that we did not attempt hard to drive them with threshold and repetitive stimuli. In two measured cases, however, the latencies were 3.2 and 4 ms and the response venished when the frequency exceeded 5 Hz. These latencies fall within the range reported by Dubin and Cleland (7).

DISCUSSION

The present study describes the receptive field organization of identified perigeniculate neurons and non-relay geniculate cells. As far as we know such detailed data were not presented in the literature al-



though the visual responses of both groups of cells were mentioned before in several papers. According to these data the perigeniculate neurons show ON–OFF type of RFs (3, 7, 15, 16, 23) and they are usually binocularly driven (3, 15, 16, 23). These features also characterize the most perigeniculate RFs shown in our study. The higher percentage of binocular units counted in our data might be due to our special effort to find even the slightest response, combined with a very sensitive method of the contour planes.

Most of the units recorded in this study responded to visual stimuli in a strongly phasic manner, suggesting their main input from Y-type cells (7, 16); however, units with tonic responses were also found (e.g., Fig. 3*A*, *D*). Although we have also used the pretrigeminal preparation we have registered many RFs that were not clearly definable; this is in disagreement wth Ahlsen et al. (3). Moreover, we have still found cells with erratic type of responses with tonic excitatory and/or inhibitory influences (see Fig. 2*C*, *E*). Neither different visual stimuli nor changing the background light intensity could evoke more regular responses from these cells. The RFs of such cells can not be simply considered as built up mainly from geniculate projections. We think that other inputs probably via nucleus reticularis thalami (see 5, 16) are playing a crucial role in organizing such RFs. As far as intrageniculate interneuronal RFs are concerned we have confirmed the report of Dubin and Cleland (7) that these fields do not differ from regular LGN relay cell RFs.

Dubin and Cleland (7) first proposed a model of a dual inhibitory

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Fig. 3. The response planes (first column) and appropriate contour planes of consecutive perigeniculate (A–E) and relay (F) cells recorded in one electrode penetration. In the second column the cut of the response planes was made on the neous probability level. To show the ON and/or OFF peaks, higher probability cuts are presented for three cells in the third column.

The characteristics of the cells are presented in the Table.

	Distance from the first recorded relay cell (μm)	Ocular dominance	RF center azimuth/elevation
A	1800	Bilateral	115/+31.5
B	1700	with contralateral input	120/+31
C	1660		110/+17
D	400	stronger	112/+17
E	120		112/+17
F	—	contralateral	112/+17

For A, B and D–F analysis the stimulus was 0.5° × 1° bar of light of 5 cd/m² luminance. 2° × 4° stimulus was applied to get C response plane. Ten repetitions of the stimuli in each point of the RFs axes. The black bar under the response- and contour-planes shows the ON-time of the stimulus. Arrows indicate the first histogram obtained without stimulus for estimating the spontaneous activity level.

pathway upon the LGN relay cell via intra- and perigeniculate inhibitory cells serving as interneurons. This model was further confirmed by both anatomical (4, 11) and physiological (3, 14, 23) findings. We were able to classify both groups of potential interneurons by applying the criteria established by Dubin and Cleland (7). Moreover, we have also characterized the spatiotemporal extent of their receptive fields to compare them with inhibitory influences within the geniculate relay cells. Our data seem to support the hypothesis that intrageniculate interneurons are responsible for enhancing the inibitory domains in geniculate relay cell RF, which originally reflect the domains of ganglion cell activity suppression; and that perigeniculate neurons might influence the relay cell RF by providing a large ON–OFF "suppressive field" (12, 18).

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