17. **Location and Function of So-called Interneurons of Rat Lateral Geniculate Body**

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In 1966 Burke and Sefton reported that interneurons (I-cells) of the rat lateral geniculate body (LGB) were identifiable as the units showing repetitive discharges to single shock stimulation of either optic nerve or visual cortex. This response pattern of I-cells was clearly distinguishable from that of principal cells (P-cells) which were fired mostly once by optic nerve stimulation and antidromically by visual cortical stimulation. Several pieces of evidence, though indirect, led these workers to assume that I-cells might be inhibitory neurons acting upon P-cells and intercalated between the latter and their axon collaterals.

Although several workers noted that Burke and Sefton's I-cells were recordable when unit discharges were searched for in and around LGB, no works have been published on their location. In the present experiment a systematic exploration for I-cells was made and it was found that this type of cells were clustered in a zone separate from but immediately neighboring to the one containing P-cells exclusively. This anatomical arrangement of P- and I-cells made it possible to examine effects of electrical stimulation of the cluster of I-cells upon individual P-cells. The results were that activity of P-cells, either spontaneous or evoked by optic nerve stimulation, suffered suppression upon activation of I-cells.

**Methods.** Rats, weighing 200–300 g, were used. After initial anesthesia with an intraperitoneal injection of urethane (1 g/kg), the rats were fixed to a stereotaxic apparatus by Fidková and Maršala's method. Subsequently a small dose of urethane was given intraperitoneally as frequently as required. One per cent procaine was injected to all pressure points.

A bipolar stimulating electrode, consisting of singly aligned insulated wires with exposed tips separated by 0.5 mm, was introduced each into the optic tract (OT) at the optic chiasm and into the optic radiation (OR) about 2 mm below the visual cortex. Stimulus pulses

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applied through these electrodes were 0.01–0.05 msec square waves with intensities less than 50 V. Unit discharges were recorded extracellularly by means of glass pipette microelectrodes filled with 3 M KCl. For recording field responses gross electrodes, made of insulated wires of 0.1 mm in diameter, were introduced into LBG and nearby areas. In some experiments electrical stimulation was applied to the area where I-cells were clustered. Its details will be described later.

Results. Typical examples of responses of P- and I-cells to stimulation of OT and of OR are shown in Fig. 1A. Identification of the cell types was made with the following criteria based on the description of Burke and Sefton1) and other workers.4)-6)

P-cells. In response to single OT shocks P-cells discharge mostly once with latencies ranging from 1.0 to 6.0 msec. More than 100 msec later this short-latency discharge is followed by two or three bursts of spikes which are spaced by 100 msec or more. The response pattern to OR stimulation is very similar to that to OT stimulation, except that the earliest discharge to OR stimulation is an antidromic firing.

I-cells. I-cells show to single OT shocks a burst of more than five spikes, the first one being elicited with latencies ranging from 2 to 10 msec. Usually the spike burst is repeated twice or more at about the same interval of more than 100 msec. Responses to OR shocks are approximately the same as those to OT shocks.

1. Locations of P- and I-cells. By orienting microelectrodes systematically in and around LGB it was found that P- and I-cells were clustered in separate zones (P- and I-zones) which were immediately neighboring to each other. This is clearly seen in Fig. 1B which shows projections onto the midsagittal plane of anteroposterior and dorsoventral coordinates of 112 P- and 28 I-cells assembled from several rats. Ordinates represent depths from the cortical surface and abscissae distances from the frontal zero plane of Fīfková and Maršala. It is seen that the P- and I-zones are sharply bounded at 3.2 to 3.3 mm posterior to the frontal zero plane. Taking it into account that the frontal zero plane of Fīfková and Maršala7) is set so as to pass the anterior commissure and referring to other stereotaxic maps of rat brain,8),9) the boundary of the P- and I-zones is judged to coincide approximately with the rostral limit of LGB. From this boundary the I-zone extends anteriorly by about 0.5 mm and the P-zone posteriorly by about 1.3 mm. Dorsoventrally a majority of P-cells are contained in an extension of about 1.2 mm thickness, indicating that they were recorded from the dorsal nucleus.10),11) The dorsoventral extension of the I-zone is smaller than that of the P-zone and the former is displaced slightly ventrally to the latter. Medio-
laterally P-cells occupy an area of about 1 mm width with the center at about 4.0 mm lateral to the midsagittal plane. The mediolateral extension of the I-zone is much smaller than that of the P-zone.

Field responses to OT stimulation were recorded from the P- and I-zones separately. The P-zone field response was a positive-negative sharp deflection of presynaptic origin followed by two or three postsynaptic negative waves. This potential pattern is in accord with the one described by previous workers\textsuperscript{12,13} as recorded from LGB. In contrast to this, the I-zone field response was a burst of multiple discharges of small amplitude lasting 20 to 30 msec. This potential pattern is interpreted as resulting from summation of repetitive discharges of many I-cells. Histological examination of the sites of recording revealed that the P-zone field response was obtained from the dorsal nucleus of LGB and the I-zone field response from the nucleus reticularis thalami immediately anterior to LGB.

2. Effects of electrical stimulation of the I-zone upon activity of P-cells. By placing a macroelectrode in the I-zone for stimulation and introducing a microelectrode in the P-zone for recording unit discharges, it was examined how excitability of individual P-cells was influenced by electrical stimulation of the I-zone.

First, single shock stimulation of the I-zone was found to result
in suppression of responsiveness of P-cells to single OT shocks. I-zone stimulation was made with rectangular pulses of 0.01 msec duration. The intensities were set not so as to excite target P-cells and mostly less than 10 V. The intensities of OT shocks were twice the threshold of the short-latency discharges of each P-cell. Changes in responsiveness of P-cells due to conditioning I-zone stimulation were assessed with the response probability to testing OT stimulation. It was determined in successive ten trials of the combined stimulation of the I-zone and OT. The results obtained from seven P-cells are summarized in Fig. 2A which shows that the response probabilities of P-cells decreased within several msec after condition-

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**Fig. 2.** Inhibitory effects of I-zone stimulation upon P-cells. A: a plot of the response probabilities of 7 P-cells as functions of the interval between single shock stimulation of I-zone and of OT. The abscissa axes from 0 to 10, from 10 to 100 and from 100 to 250 msec are scaled differently. B: suppression of spontaneous discharges of a P-cell by continuous stimulation of I-zone at 10 Hz. A record of about 3.5 sec length was cut off.
ing I-zone stimulation, remained reduced up to 70–100 msec and then recovered the control level with variable speeds.

The inhibitory effect of I-zone stimulation was also proved with spontaneous discharges of P-cells. In P-cells discharging at high rates the inhibitory effect was readily obtained by stimulating the I-zone at low rates. This is exemplified by the record of Fig. 2B. This P-cell was discharging at about 20 impulses/sec in the control stage. After the start of I-zone stimulation at 10 Hz, the spontaneous discharge was immediately stopped and remained so as long as I-zone stimulation continued. It is notable that a time of more than 200 msec was required for the spontaneous discharge to recover the control level after the end of I-zone stimulation.

Conclusion. The present experiment established that cells encountered in LGB, particularly in its dorsal nucleus, were exclusively of P-type and I-cells were recordable only outside LGB. This makes it unlikely that I-cells may be interneurons of LGB as originally assumed by Burke and Sefton.2)3) Studying Golgi-Kopsch and Cox preparations of the rat LGB Grossmann et al.14) distinguished two classes of cells, A and B. They assumed class A cells to be geniculo-cortical cells which are identical with P-cells defined electrophysiologically. Class B cells were claimed to be intrinsic neurons and assumed to correspond to I-cells of Burke and Sefton. Since I-cells are not encountered in LGB, their identification of class B cells as I-cells awaits a revision. Also there remains a problem to be solved as to what patterns of electrical responses class B cells of Grossmann et al. show in response to stimulation of OT and of OR.

Burke and Sefton’s I-cells were located in the nucleus reticularis thalami immediately anterior to LGB and were found to exert a powerful inhibitory action upon P-cells of LGB. This finding is consistent with the general notion that dorsal thalamic cells receive inhibitory actions from the thalamic reticular complex.15) However, a question as to whether I-cells are inhibitory neurons in a strict sense still remains unanswered. This may be solved by measuring transmission times of the inhibitory action from I-cells to target P-cells. An experiment toward this objective is now in progress.

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