Neuroscience Letters, 43 (1983) 143–147
Elsevier Scientific Publishers Ireland Ltd.

LAMINAR ORIGIN OF THE TECTO-THALAMIC PROJECTIONS IN THE ALBINO RAT

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(Received October 19th, 1983; Revised version received November 10th, 1983; Accepted November 11th, 1983)

Key words: tecto-geniculate projection - tecto-lateroposterior thalamic nucleus projection - superior colliculus - wheat germ agglutinin - horseradish peroxidase

Cells of origin of the tecto-LP (lateroposterior nucleus of the thalamus) projection and the tecto-LGNd (dorsal nucleus of the lateral geniculate body) projection were studied in the albino rat by means of retrograde transport of wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP). Tecto-LGNd neurons with small spindle form were located in the stratum griseum superficiale of the superior colliculus (SC), whereas tecto-LP neurons with polygonal shape were found in the stratum opticum of the SC.

Anatomical studies using degeneration [4] or autoradiographic techniques [5, 14] as well as electrophysiological studies [9, 11] have given reliable evidence for the existence of ascending projections from the superficial layers of the superior colliculus (SC) to the dorsal nucleus of the lateral geniculate body (LGNd) and to the lateroposterior nucleus of the thalamus (LP). Recent investigations with retrograde axonal transport of horseradish peroxidase (HRP) have further disclosed that the upper and the lower layers of the superficial gray of the SC (SGS) project to the LGNd and to the LP-pulvinar complex, respectively [1–3, 6–8, 12, 13, 15, 16]. However, little is known about the cells of origin of these tecto-thalamic projections in the rat. In the present study, tecto-LP and tecto-LGNd projection neurons in the rat were examined by retrograde tracing technique.

Forty-one male albino rats weighing 200–250 g were anesthetized with sodium amobarbital (60 mg/kg) and injected stereotaxically with a small amount (0.01–0.02 μl) of either 5% HRP conjugated with wheat germ agglutinin (WGA-HRP, Sigma) or 30% HRP (Boehringer, Grade I) solution into the LP and the LGNd after aspirating the overlying cerebral cortex. After a postoperative period of 21–24 h, the

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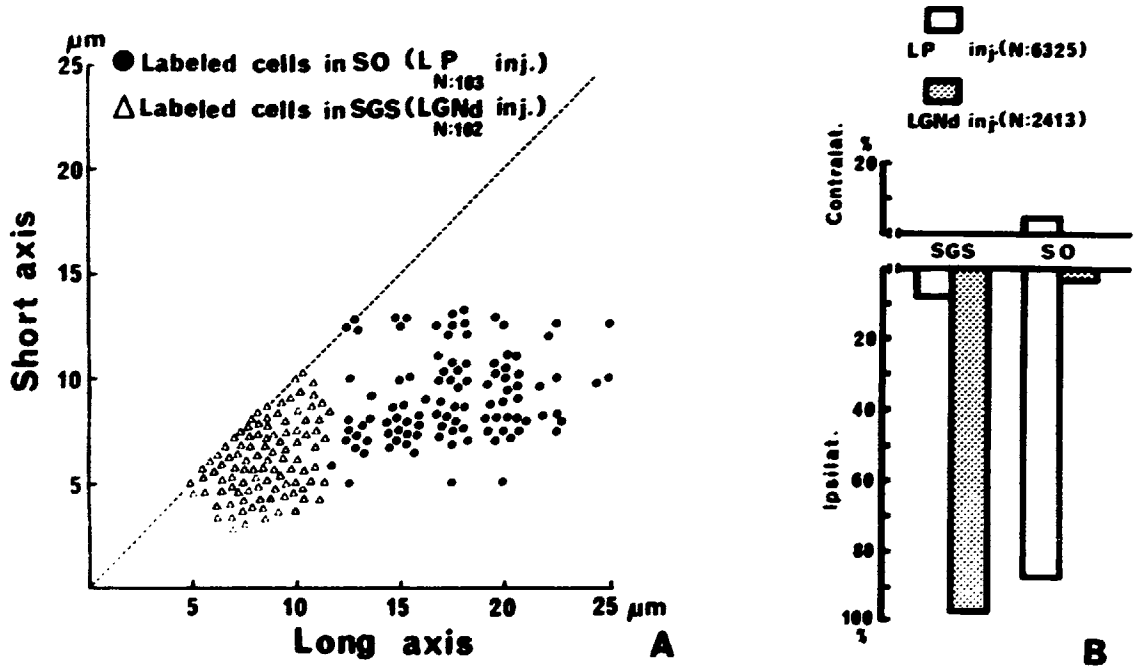

Fig. 1. A: distribution of labeled cell sizes in the superficial gray (SGS) and optic layer (SO) of the rat superior colliculus (SC) after WGA-HRP injections into the dorsal nucleus of the lateral geniculate body (LGNd) or the lateroposterior nucleus of the thalamus (LP). Cell size of labeled neurons was obtained randomly from the 5 successful injections (LP: 2 rats, LGNd: 3 rats). B: histogram of the distribution ratio of labeled neurons in SGS and SO after WGA-HRP injection in the LP (open column: mean of 2 successful cases), or LGNd (stippled column: mean of 3 successful cases). Z, stratum zonale; SGS, stratum griseum superficiale; SO, stratum opticum.

rats were perfused intracardially with 500 ml of 0.1 M phosphate buffer (pH 7.4) containing 10% sucrose, followed by a mixture of 500 ml of 1% paraformaldehyde and 1.25% glutaraldehyde in phosphate buffer (pH 7.4). Coronal sections were serially cut at 45 μm on a freezing microtome, and every second section was treated with tetramethylbenzidine (TMB) [10].

Unilateral injection of the tracers into the LP (Fig. 2A) labeled neurons in the SGS ipsilaterally, and in the optic lamina of the SC (SO) bilaterally (Fig. 2C, D). About 92% of the total number of labeled SC neurons were observed in the SO; 87% ipsilaterally and 5% contralaterally. The labeled neurons in the SO were medium-sized (long axis, 17.5 ± 3.3 μm; short axis, 9.0 ± 2.3 μm; n = 103, see Fig. 1A, B), and had triangular or polygonal cell bodies with 3 or more dendrites extending in a radial fashion (Figs. 2C and 3A, C). The HRP-positive neurons in the SGS were only 8% of the total labeled SC neurons (Fig. 1B). They were small in size (long axis, 8.0 ± 1.8 μm; short axis, 5.5 ± 1.0 μm; n = 33) and round or fusiform in shape (Fig. 2C).

Unilateral intra-LGNd injection (Fig. 2B) resulted in labeling of neurons in the SGS and the SO ipsilaterally (Fig. 2E). No labeled cells were detected contralaterally. The majority of labeled neurons were found in the SGS (97%); these were small in size (long axis, 8.3 ± 1.3 μm; short axis, 6.3 ± 1.3 μm; n = 102, see Fig. 1A, B),

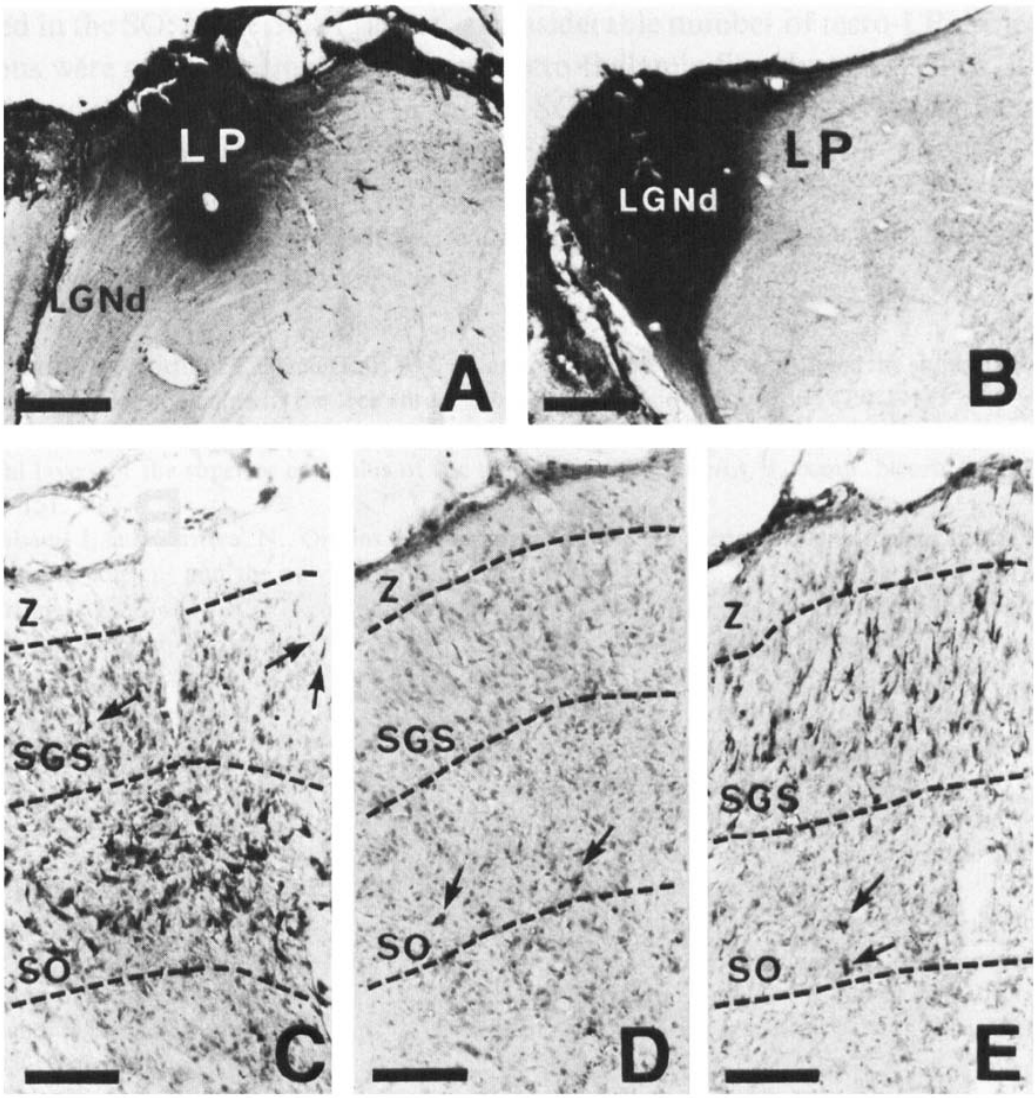

Fig. 2. Injection sites in the LP (A) or LGNd (B). After LP injection, many medium-sized, multipolar neurons were labeled in the ipsilateral SO (C), but only a few neurons were labeled in the ipsilateral SGS (arrows in C) and the contralateral SO (arrows in D). LGNd injection resulted in the labeling of many small fusiform neurons ipsilaterally in the SGS (E); a few medium-sized multipolar neurons were also labeled in the ipsilateral SO (arrows in E). Calibration bars = 500 μm in A and B; 100 μm in C–E. Abbreviations as in Fig. 1.

and spindle-form in shape, orienting their long axis perpendicular to the SC surface and issuing one or two thick proximal dendrites perpendicularly from each pole of the soma (Figs. 2E and 3B, D). A small number of medium-sized multipolar neurons (3%, long axis, 18.3 ± 3.0 μm; short axis, 9.0 ± 2.5 μm; n = 42) were labeled in the SO ipsilaterally (Fig. 2E).

On the basis of profile and orientation of dendritic field, Tokunaga and Otani [17] classified SC neurons into 4 types: the horizontal, cylindrical, vertical conical and multipolar neurons. The SGS and the SO consist mainly of the cylindrical neurons with fusiform cell body and dorsoventrally oriented dendrites, and of the

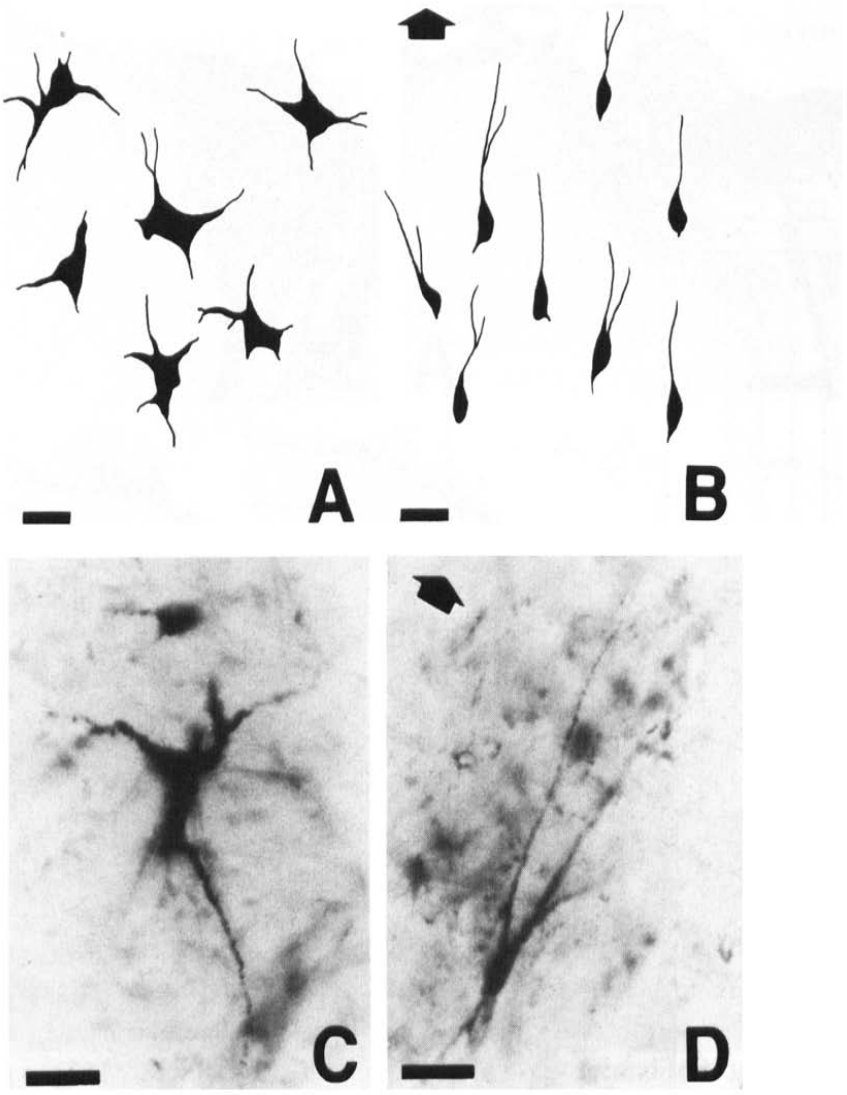

Fig. 3. Camera lucida drawings and photomicrographs of retrogradely labeled SC neurons after HRP injection into the LP (A and C) or LGNd (B and D). Calibration bars = 20 μm. Arrows indicate direction perpendicular to the surface of the SC.

wide-field multipolar neurons with polygonal cell bodies. The tecto-LP projection neurons with medium-sized multipolar soma, as revealed in the present study, are probably equivalent to the wide-field multipolar neurons in the SO [17]; the small, round or fusiform tecto-LGNd projection neurons may correspond to the cylindrical cells in the SGS [17].

Anatomical studies in the tree shrew [1, 2], rabbit [3], cat [7, 8] and squirrel monkey [6] exhibited that the tecto-LGNd projection neurons were located in the upper two-thirds of the SGS, while cells of origin of the projection from the SC to the LP-pulvinar complex were mainly distributed in the lower one-third of the SGS. In the present study, however, the tecto-LGNd projection neurons of the rat were distributed evenly in the SGS, and the tecto-LP projection neurons were mainly

located in the SO; in the SC of the rat, a considerable number of tecto-LP projection neurons were scattered among optic and tecto-thalamic fiber bundles. Thus, it may be inferred that the SGS and SO in the rat SC correspond respectively to the upper and the lower sublayers of the SGS in the SC of other animals.

The authors wish to thank Mr. K. Miyama, Mrs. F. Saito and Mrs. T. Saito for their expert technical assistance.

1 Albano, J.E., Norton, T.T. and Hall, W.C., Laminar origin of projections from the superficial layers of the superior colliculus in the tree shrew, *Tupaia glis*, Brain Res., 173 (1979) 1-11.
2 Graham, J. and Casagrande, V.A., A light microscopic and electron microscopic study of the superficial layers of the superior colliculus of the tree shrew (*Tupaia glis*), J. comp. Neurol., 191 (1980) 133-151.
3 Graham, J. and Berman, N., Origins of the projections of the superior colliculus to the dorsal lateral geniculate nucleus and the pulvinar in the rabbit, Neurosci. Lett., 26 (1981) 101-106.
4 Harting, J.K., Hall, W.C., Diamond, I.T. and Martin, G.F., Anterograde degeneration study of the superior colliculus in *Tupaia glis*: evidence for a subdivision between superficial and deep layers, J. comp. Neurol., 148 (1973) 361-386.
5 Harting, J.K., Casagrande, V.A. and Weber, J.T., The projection of the primate superior colliculus upon the dorsal lateral geniculate nucleus: autoradiographic demonstration of interlaminar distribution of tectogeniculate axons, Brain Res., 150 (1978) 593-599.
6 Huerta, M.F. and Harting, J.K., Sublamination within the superficial gray layer of the squirrel monkey: an analysis of the tectopulvinar projection using anterograde and retrograde transport methods, Brain Res., 261 (1983) 119-126.
7 Kawamura, S. and Kobayashi, E., Identification of laminar origin of some tecto-thalamic fibers in the cat, Brain Res., 91 (1975) 281-285.
8 Kawamura, S., Fukushima, N., Hattori, S. and Kudo, M., Laminar segregation of cells of origin of ascending projections from the superficial layers of the superior colliculus in the cat, Brain Res., 184 (1980) 486-490.
9 Leiby, III, C.C., Bender, D.B. and Butter, C.M., Localization and detection of visual stimuli in monkeys with pulvinar lesions, Exp. Brain Res., 48 (1982) 449-454.
10 Mesulam, M.-M., Tetramethyl benzidine for horseradish peroxidase neurohistochemistry: a non-carcinogenic blue reaction-product with superior sensitivity for visualizing neural afferents and efferents, J. Histochem. Cytochem., 26 (1978) 106-117.
11 Molotchnikoff, S. and Lachapelle, P., Evidence of a collicular input to the dorsal lateral geniculate nucleus in rabbits-electrophysiology, Exp. Brain Res., 40 (1980) 221-228.
12 Mason, R. and Groos, G.A., Cortico-recipient and tecto-recipient visual zones in the rat's lateral posterior (pulvinar) nucleus: an anatomical study, Neurosci. Lett., 25 (1981) 107-112.
13 Makey-Sim, A., Sefton, A.J. and Martin, P.R., Subcortical projections to lateral geniculate and thalamic reticular nuclei in the hooded rat, J. comp. Neurol., 213 (1983) 24-35.
14 Perry, V.H., A tectocortical visual pathway in the rat, Neuroscience, 5 (1980) 915-927.
15 Pasquier, D.A. and Villar, M.J., Subcortical projections to the lateral geniculate body in the rat, Exp. Brain Res., 48 (1982) 409-419.
16 Robson, J.A. and Hall, W.C., Projections from the superior colliculus to the dorsal lateral geniculate nucleus of the grey squirrel (*Sciureus carolinensis*), Brain Res., 113 (1976) 379-385.
17 Tokunaga, A. and Otani, K., Dendritic patterns of neurons in the rat superior colliculus, Exp. Neurol., 52 (1976) 189-205.