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Direct synaptic connections between superior colliculus afferents and thalamo-insular projection neurons in the feline suprageniculate nucleus: A double-labeling study with WGA-HRP and kainic acid

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ABSTRACT

The suprageniculate nucleus (Sg) of the feline thalamus, which subserves largely unimodal sensory and orientation behavior, receives input from the deep layers of the superior colliculus (SC), and projects to the suprasylvian cortical areas, such as the anterior ectosylvian visual area and the insular visual area (IVA), which contain visually responsive neurons. Through a double tract-tracing procedure involving the injection of wheat germ agglutinin conjugated with horseradish peroxidase (WGA-HRP) into the IVA and the injection of kainic acid into the SC, this study sought to determine the nature of the synaptic relationship between the SC afferents and the thalamo-cortical projection neurons. WGA-HRP injections labeled numerous neurons in the Sg, while kainic acid injections destroyed many tectothalamic terminals in the Sg. The distributions of the WGA-HRP-labeled neurons and the degenerated axon terminals overlapped in the dorsal part of the Sg. Electron microscopic observations demonstrated that the degenerated axon terminals made synaptic contacts with the dendrites of the WGA-HRP-labeled neurons in this overlapping region of the Sg. These results provide the first anatomical evidence that the Sg may play a role in the key relay of visual information from the SC to the IVA, within an identified extrageniculo-cortical pathway.

1. Introduction

There are two major visual projection pathways from the retina to the cerebral cortex in the cat: one of these is the geniculo-striate system, which conveys information to the primary visual cortex by way of the lateral geniculate nucleus. The other is the extrageniculo-extrastriate system, in which information flows first to the superior colliculus (SC), and then to the nucleus lateralis posterior-pulvinar (LP-Pul) complex of the thalamus, from where projections lead to what has traditionally been called the associational cortices, including such structures as the lateral suprasylvian cortex (LS) and the associational cortices along the anterior ectosylvian sulcus that include the anterior ectosylvian visual area (AEV), and the insular visual area (IVA) (Benedek et al., 1988). Physiological and anatomical studies have demonstrated that the suprageniculate nucleus (Sg) of the posterior thalamus is another relay nucleus of the tectal extrageniculo-extrastriate visual information toward the associative cortical areas.

The Sg receives input from subcortical areas, most intensively so from the SC (Graham, 1977; Huerta and Harting, 1984; Takada et al., 1985; Hicks et al., 1986; Katoh and Benedek, 1995; Sato and Ohtsuka, 1996), but also from brainstem regions such as the pedunculopontine tegmental nucleus (PPT) (Edley and Graybiel, 1983; Hoshino et al., 1997) and the substantia nigra (Takada et al., 1984; Hoshino et al., 2009). It is also known that neurons of the Sg project to extrastriate cortices such as the LS (Norita et al., 1996; MacNeil et al., 1997), the AEV (Olson and Graybiel, 1987; Benedek et al., 1988) and the IVA (Benedek et al., 1986; Hicks et al., 1988a,b; Norita et al., 1991). Electrophysiological studies have revealed that the Sg subregion has neurons that are sensitive primarily to visual stimuli (Hicks et al., 1984; Krupa et al., 1984). The deep layers of the SC, which sends projection fibers to the Sg, have constituent neurons whose activity is related largely to the orientational behavior of the eye and head in relation to concomitant visual, auditory and somatosensory stimuli (Schiller, 1984; Sherk, 1986). This is interesting in the context that the IVA, a cortical area closely connected with the Sg, contains visually responsive neurons that express considerable directional selectivity (Benedek et al., 1986; Hicks et al., 1988a). It has therefore been widely assumed, though never proven, that the afferent fibers of the SC neurons make synaptic contacts with thalamo-cortical Sg projection neurons that have axons leading to the IVA.

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The present study was undertaken to evaluate the hypothesis that there are anatomically direct connections between the afferents of the SC and these thalamo-insular projection neurons. A combination of degeneration and retrograde tracing techniques at the light and electron microscopic levels was used to determine the distribution of degenerated fibers from the SC simultaneously with the distribution of retrogradely labeled neurons from the IVA, and to describe the synaptic contacts between the afferent fibers from the SC and the projection neurons of the Sg.

2. Materials and methods

2.1. Surgery and perfusion

The brains of 4 adult cats weighing 1.6–2.3 kg were used in this study. All experimental procedures undertaken were as approved by the Animal Care Committee of Niigata University. The animals were anesthetized with sodium pentobarbital (30 mg/kg, i.p.) and received unilateral injections of kainic acid (Sigma–Aldrich, St. Louis, MO, USA) dissolved in sterile saline and brought to a concentration of 1 μg/μl. Small injections (0.8 μl) of this solution were made via a Hamilton syringe into near the middle of the rostrocaudal extent of the SC (AP level 3.0–2.5 mm). Three days later, the animals were again anesthetized and, via a glass micropipette injection system, employing a needle tip diameter of about 70 μm, received 0.03 μl injection volumes of 3% wheat germ agglutinin conjugated with horseradish peroxidase (WGA-HRP, Sigma–Aldrich) into the ipsilateral portion of the insular cortex previously indicated electrophysiologically to be involved in the visual motor function (Hicks et al., 1988a; Norita et al., 1991).

2.2. Histochemical procedures

Two days following the WGA-HRP injection, the animals were again anesthetized deeply with sodium pentobarbital and perfused through the ascending aorta with isotonic saline, followed by 4% paraformaldehyde and 0.1% glutaraldehyde in 0.1 M sodium phosphate buffer, pH 7.6. The brains were immediately removed from the skull and sectioned into 50 μm coronal serial sections with a Vibratome (Oxford Instrument). These sections were divided into four groups. The sections in the first and second groups were processed for WGA-HRP histochemistry with the tetramethylbenzidine (TMB) method. Following the TMB reaction, the sections in the first group were mounted on gelatin-coated slides and counterstained with neutral red for light microscopic observation. The sections in the second group were processed with the HRP-electron microscopic method of Carson and Mesulam (1982). They were post-fixed in 1% osmium tetroxide in 0.1 M sodium phosphate buffer (pH 6.0) at 45 °C for 1 h, dehydrated in a graded series of alcohols, and embedded in Epon. The ultra-thin sections, cut with an LKB ultramicrotome, were collected onto copper grids, stained with uranyl acetate and lead citrate, and examined with an H-7100 electron microscope.

The sections in the third group were processed by the silver impregnation method to reveal degeneration (Yamadori, 1975) and counterstained with Nissl, while those in the fourth group were used for acetylcholine esterase (AChE) histochemistry (Hardy et al., 1976) in order to identify the different subregions of the LP-Pul complex.

3. Results

As described above, the kainic acid injections were in all cases situated near the middle of the rostrocaudal extent of the SC, and the WGA-HRP injections were administered into the portion of the IVA previously indicated by electrophysiological experiments to be involved in the visual motor function (Fig. 1). In all cases, a number of degenerated axonal fibers and terminal-like puncta and numerous retrogradely labeled neuronal somata were found in the Sg. Although the distributions of the degeneration and the retrograde labeling differed slightly from case to case, only Case 140 will be described in detail, so as to avoid unnecessary repetition.

3.1. Light microscopic observations

The lesions produced by injections of kainic acid into the SC were centered mainly in the deep four layers, with slight involvement of the superficial three layers. Their extents were clearly delineated by Nissl staining as areas of reactive gliosis that contained no intact neurons and which included a needle track. The border of a lesion was characterized as an area that exhibited a rapid shift from normal tissue to an area completely devoid of normal elements. Fig. 2 presents a photomicrograph of a typical injection in Case 140. The injection of kainic acid into the SC produced many degenerated fibers and terminal-like puncta within the Sg (Fig. 3B and D). Similarly as in a previous study (Katoh et al., 1995), these puncta were distributed bilaterally, with an ipsilateral predominance in the Sg. The distribution of degenerated terminal-like puncta was not centered on the Sg, but rather produced a patchy profile close to the boundary between the LP, pars medialis (LPm) and the Sg (Fig. 4).

In Case 140, the WGA-HRP injected into the IVA was located mainly in the gray matter of the cortex (Fig. 2B and D) and labeled numerous neurons within the ipsilateral Sg (Fig. 3C and E), in accordance with the reports of previous studies (Norita and Katoh, 1988; Norita et al., 1991; Clascá et al., 1997). The distribution of these retrogradely WGA-HRP-labeled neurons throughout the Sg was not homogeneous. They formed a rather patchy pattern

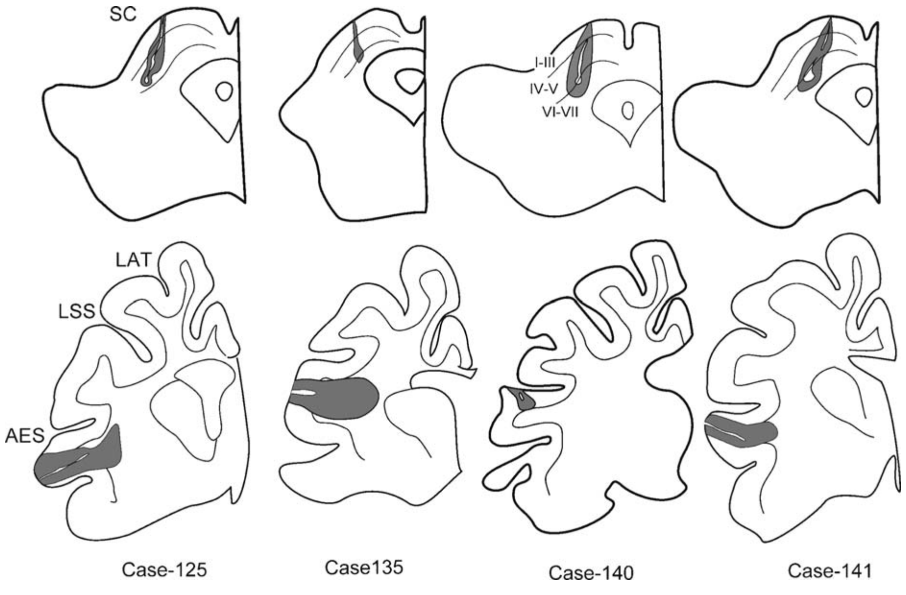

Fig. 1. Diagrams of coronal sections through the SC and IVA, depicting the center of kainic acid (upper) and WGA-HRP (lower) injections, respectively. The solid lines in SC denote the boundary of superficial (I–III), intermediate (IV–V) and deep layers (VI–VII). AES, anterior ectosylvian sulcus; LAT, lateral sulcus; LSS, lateral suprasylvian sulcus.

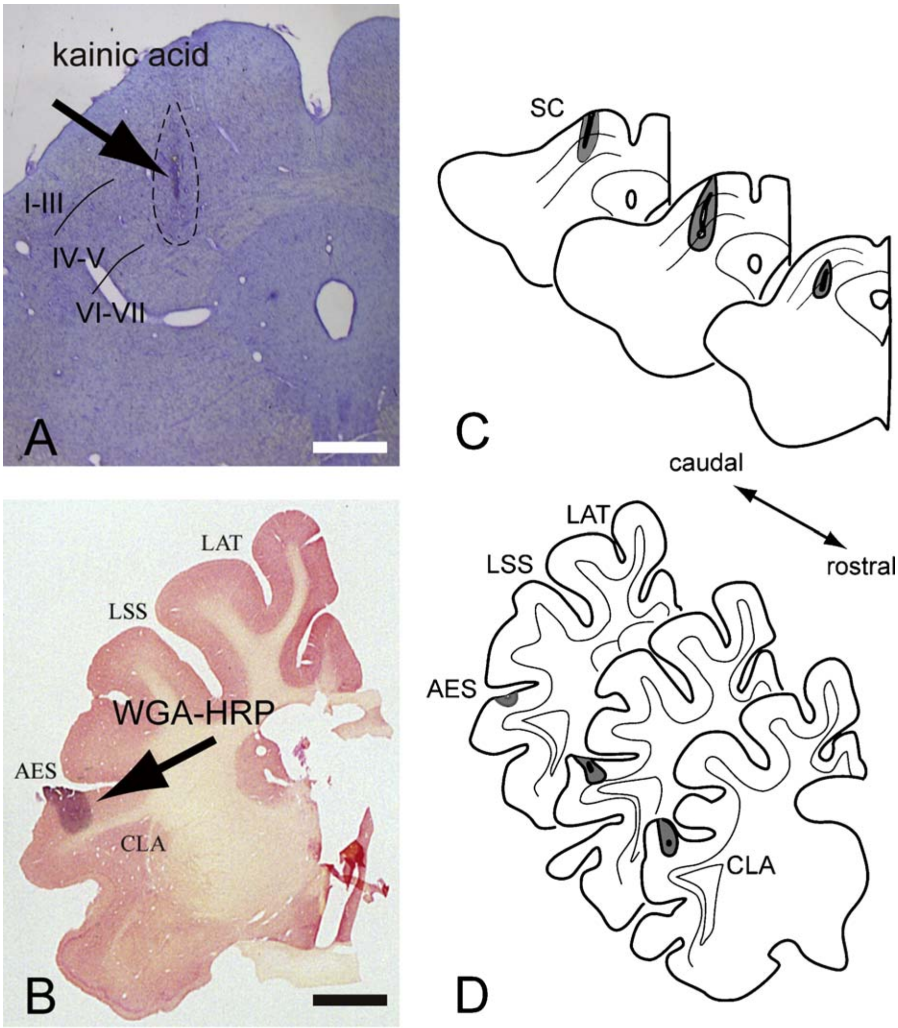

Fig. 2. Photomicrographs and illustrations showing the sites of injection of kainic acid (A and C) and WGA-HRP (B and D) in Case 140. (A) A photomicrograph demonstrating a transverse section through the injection site of kainic acid (arrow) into the SC. A dotted line shows the extent of the lesion on the injection of kainic acid. (B) A photomicrograph of the site of injection of WGA-HRP (arrow) into the IVA. (C and D) Schematic drawings indicating the sites of injection (shaded areas) of kainic acid into the SC (C) and of WGA-HRP into the IVA (D). CLA, claustrum; Scale bars, 1 mm in (A), 0.5 mm in (B).

(Fig. 4). Furthermore, terminal-like puncta were mainly found in the close vicinity of the labeled neurons. The WGA-HRP-labeled neurons and terminals were distributed in a manner favoring the ventral part of the Sg and the medial part of the nucleus lateralis medialis (LM) and as a whole they were located slightly more ventrally than were the terminals originating from the SC. However, the distributions of the WGA-HRP-labeled neurons and of the degenerated terminals overlapped within the dorsal part of the Sg, on the ipsilateral side in relation to the injection sites.

In the AChE-stained thalamic tissue, the Sg was labeled heterogeneously, i.e. higher (darkly stained portion) and lower (lightly stained portion) intensities of staining were observed (Fig. 3A). On the whole, the distributions of the degenerated fibers and of the WGA-HRP-labeled neurons corresponded to the lightly stained portion of the Sg (Fig. 4).

3.2. Electron microscopic observations

Ultrastructural inspection of the tissue revealed degenerated axon terminals exhibiting typical characteristics of different stages at a given survival time. These could be recognized because they demonstrated different degrees of atrophy, electron-dense axoplasm, and broken organelles. Although some of them (perhaps because they were in the early stages of degeneration) could be identified as small-sized (RS) or large-sized (RL) axon terminals, most of them were unclassified. These degenerating terminals also sometimes contained mitochondria and made asymmetrical synaptic contacts on small-diameter dendrites (Fig. 5A and B), or occasionally, on medium or large-diameter dendrites (Fig. 5C).

Following the injection of WGA-HRP into the insular cortex, many retrogradely labeled neurons were found in the Sg. The WGA-HRP-labeled neurons could be distinguished from unlabeled neurons by the tracer reaction product crystal contents of the former. There were also numerous anterogradely labeled terminals, similar to those which originated from the SC in that they were small, contained round synaptic vesicles, and made asymmetrical contacts with small-diameter dendrites. The WGA-HRP-labeled terminals could be identified with the labeled-crystal contents.

The region of overlap of the degenerated terminals and the WGA-HRP-labeled neurons in the Sg was observed through the electron microscope. In this region, the profiles of a portion of the degenerated terminals from the SC were found to make direct synaptic contact with dendrites of WGA-HRP-labeled, thalamocortical neurons that projected their axons to the insular cortex (Fig. 5).

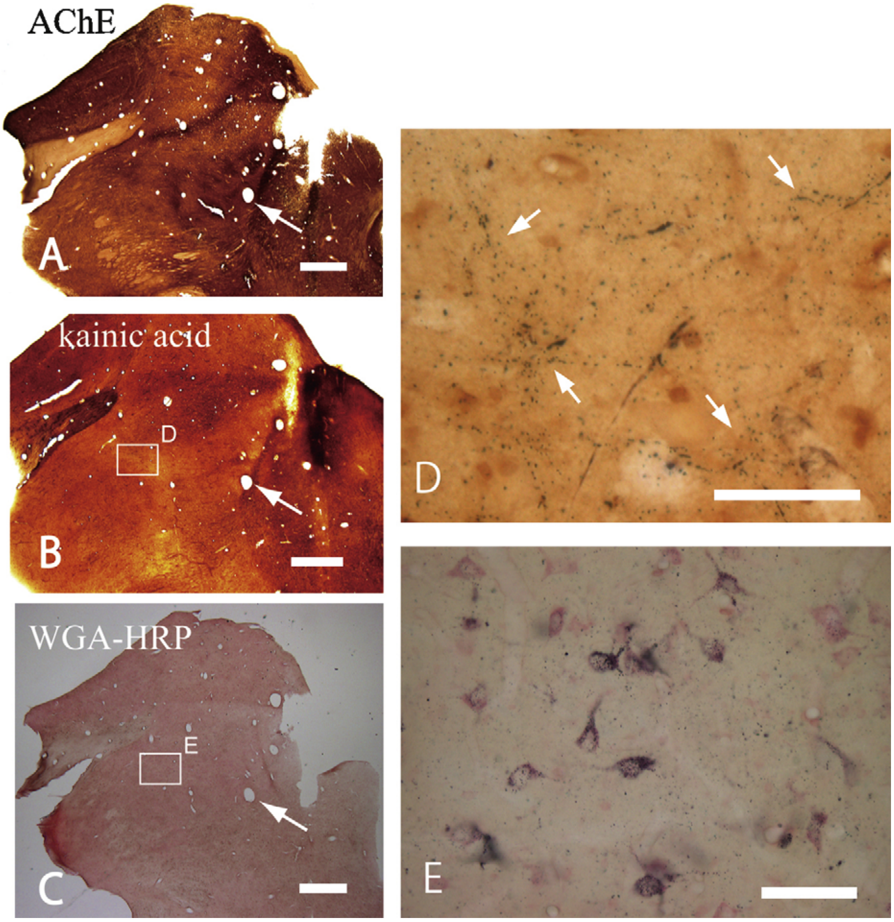

Fig. 3. Photomicrographs of transverse serial sections through the Sg in Case 140. (A) AChE staining. (B) Silver impregnation for degeneration. (C) TMB reaction for WGA-HRP. (D and E) Higher magnification photomicrographs of the boxed areas in B and C, respectively. Arrows in A, B and C denote the same blood vessel. A number of anterogradely degenerating terminal-like puncta originating from the SC (arrows in D) and retrogradely labeled cells projecting to the IVA (in E) are seen. Scale bars, 1 mm in (A–C), 100 μm in (D and E).

4. Discussion

4.1. The distributions of degenerated axon terminals and WGA-HRP-labeled cells in the Sg

In AChE-stained sections, the label found in the Sg was expressed unevenly, as shown in Fig. 3A; it exhibited a patchy profile featuring both darkly and lightly stained portions (Graybiel and Berson, 1980; Hoshino et al., 2000a,b). The AChE activity was especially intense in the medial part of the LM and the ventral part of the Sg. The distributions of degenerated terminals originating from the SC and retrogradely WGA-HRP-labeled neurons from the IVA also featured a patchy pattern of labeling. However, the degenerated terminals were situated in the dorsal parts of the Sg and close to the boundary zone between the LM and the LPm. This densely labeled portion of degenerated terminals corresponded to the lightly labeled region of AChE staining. The distribution of WGA-HRP-labeled neurons was most concentrated in the middle and ventral parts of the Sg and the medial part of the LM. Overall, the positions of these labeled neurons were more ventral than the degenerated terminals. This distribution was repeated in the lightly labeled portions of the AChE-stained Sg.

The feline SC consists of seven layers (Kanaseki and Sprague, 1974), which can be subdivided into two functionally different groups: the upper three superficial layers (Kanaseki and Sprague, 1974) and four deeper layers. The superficial three layers receive direct visual input from the retina and indirect visual input from the primary visual cortex (Beckstead and Frankfurter, 1983). Cells there project to the LP, pars lateralis (LPl) and the LPm in the thalamus (Abramson and Chalupa, 1988). Cells of the deep four layers also receive indirect visual input from visual association areas as well as from the superficial three layers (Behan and Appell, 1992). In addition, the deep four layers receive input from the substantia nigra (Harting et al., 1988; Hall et al., 1989; Wallace et al., 1990) and PPT (Hall et al., 1989) and project to the Sg. We earlier reported that the Sg receives cholinergic fibers from the PPT and that many of these terminals are distributed comparatively ventrally in the Sg, in the darkly staining portion of the AChE-labeled material (Hoshino et al., 2000b). As described above, the PPT also sends cholinergic fibers to the deep layers of the SC (Hall et al., 1989) and it is cells in these layers that send numerous fibers to the Sg. Many of these terminals from the SC are distributed throughout the dorsal part of the Sg, corresponding to the lightly stained portions in the AChE-labeled material. Thus, the direct input from the PPT to the Sg is concentrated in the darkly stained portions of the AChE-labeled material, whereas the indirect input from the PPT via the SC enters through the lightly stained areas.

The Sg is topographically connected with regions of cortex formerly described simply as “associational cortex”, such as the IVA and the AEV. The IVA communicates with the more dorsal parts of the Sg and the central-medial portions of the LM (Clascá et al., 1997, 2000). The AEV also has connections with the more dorsal parts of the Sg, but shares fiber connections with the more lateral parts of the LM (situated close to the LPm), and additionally within

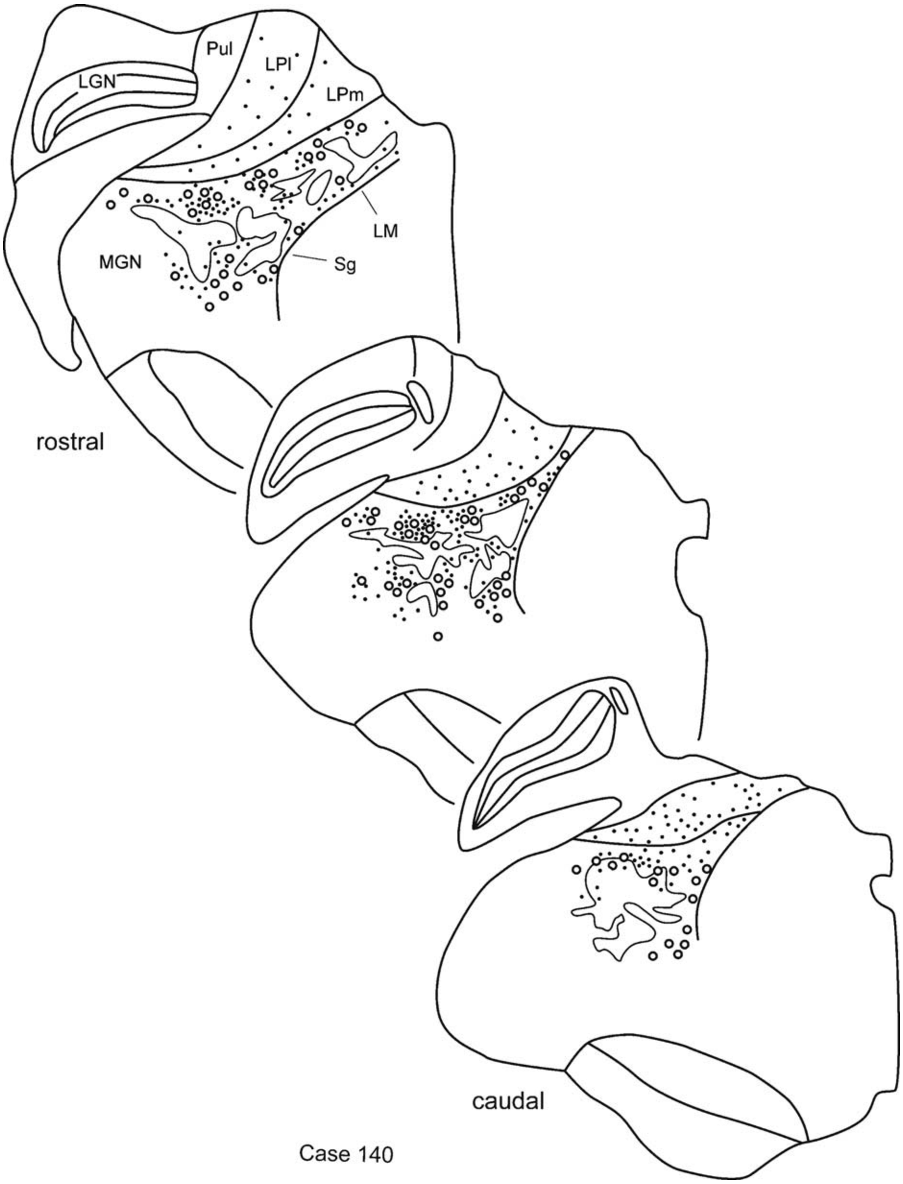

Fig. 4. Schematic illustrations of the distributions of degenerated terminal-like puncta (small dots) and WGA-HRP-labeled neuronal somata (circles) in the transverse sections at various rostrocaudal levels of the Sg in Case 140. The zones with high activity of AChE are enclosed by thin, solid lines. Each dot represents from 20 to 40 puncta, and each circle represents three cells. LGN, lateral geniculate nucleus; MGN, medial geniculate nucleus.

the LPm itself (Roda and Reinoso-Suárez, 1983; Olson and Graybiel, 1987). This region corresponds to the lightly stained portions of the AChE-reacted material.

There are topographical connections between the LP-Pul complex and the visual cortex in the cat. A medial-to-lateral progression in the LP-Pul complex corresponds to a rostrocaudal axis in the cortex (i.e. anterolateral division of LS-to-posterolateral division of LS, or area 17) (Naito and Kawamura, 1982; Rosenquist, 1985; Norita et al., 1996). In this sense, the constituent nuclei of the LP-Pul complex, including the Sg, have topographical relations with various visually responsive regions of the cortex. A projection continuum can be described between the axis of Sg-to-LPm-to-LPl-to-Pul, and the axis of IVA-to-AEV-to-LS-to-area 17.

4.2. Relationship of structure and function of the Sg

Within the present material that we observed electron microscopically, we found two types of terminals from the SC: RS and RL types. In a previous study of terminals originating from the PPT (Hoshino et al., 2000b), we also distinguished RS and RL. The RS terminals from the PPT were distributed throughout the Sg, but the distribution of RL in the Sg was not uniform. The RL terminals were denser in the darkly stained portion of the AChE-stained tissue than in the lightly stained portions. Furthermore, synaptic glomeruli were observed more than twice as often in the dark portions as in the light portions, while some of the RL terminals arriving from the PPT fibers were components of glomeruli (Hoshino et al., 2000b). In the present study, both types of degenerated axon terminal from the SC made simple contacts with small-diameter dendrites, and we did not encounter any of these in the glomeruli. Thus, we suggest that many of the fibers from the SC take part in simple transmission and not in the precise modulation of local-circuit processing, as some terminals from the PPT appear to do through their participation in the glomeruli.

Visual structures in the mammalian brain serve a double function, perception and action (Milner and Goodale, 2008). The ascending and descending pathways originating from the deep four layers of the SC serve visuomotor actions (Ingle, 1975). This is

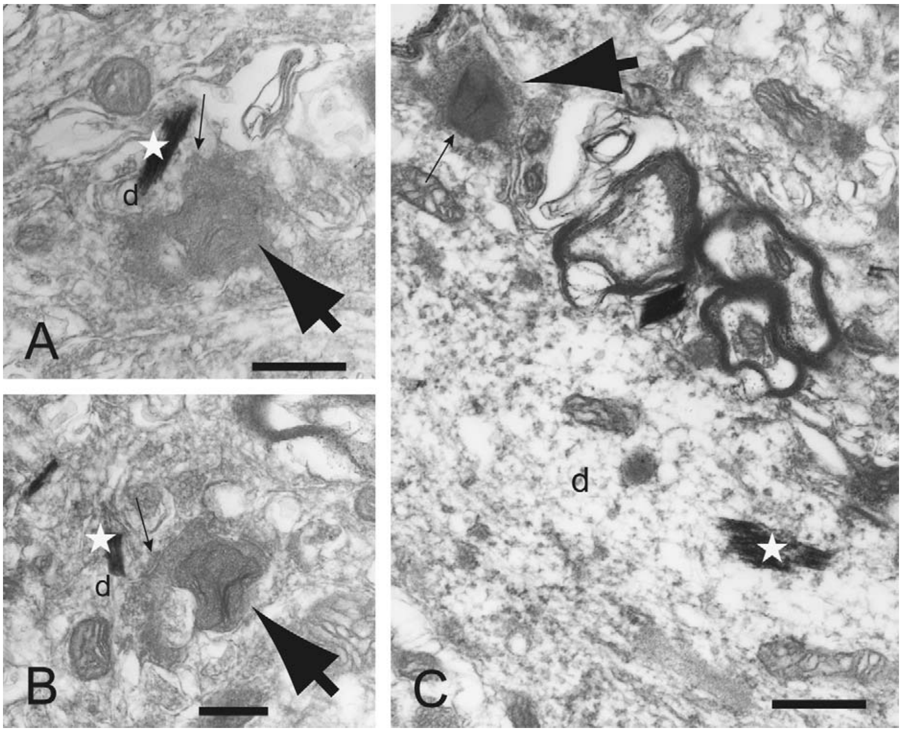

Fig. 5. Electron micrographs showing WGA-HRP-labeled neuronal profiles and degenerated axon terminals in the Sg in Case 140. (A and B) Two examples indicating an electron-dense degenerated tectothalamic axon terminal (large arrows) making a synaptic contact (small arrows) with a WGA-HRP-labeled dendrite (d) containing crystal-like HRP reaction product (asterisks). (C) A WGA-HRP-labeled large dendrite (d) containing crystal-like HRP reaction product (asterisk), making an axodendritic synaptic contact (small arrow) with a degenerated tectothalamic axon terminal (large arrow). Scale bar, 0.5 μm.

obvious as concerns the descending (tectonigral and tectobulbar) pathways and is presumably true for the ascending tectothalamic pathways that provide connections to the basal ganglia (Takada et al., 1985). The tectothalamic pathway is likely to transmit complex information containing both sensory and motor components toward the basal ganglia, supporting their integrative function in visuomotor actions such as the generation of saccades or the orientation of behavior.

Up to the present the connections between the SC-Sg and the Sg-IVA have been investigated individually. The directness of the possible interaction of these two pathways has been inferred only through physiological and functional studies, where behavioral or receptive-field analyses were performed (Benedek et al., 1996; Márkus et al., 2009). The neurons of the deep four layers of the SC, the Sg and the IVA possess strongly similar physiological properties that suggest a functional relationship of these structures. The neurons have huge visual receptive fields. The units display high sensitivity to visual stimuli moving in a particular direction, and are only weakly sensitive to stationary visual stimulation. These structures are multisensory in the sense that their neurons may be sensitive to both auditory and somatosensory modalities. Multisensory units with multisensory cross-modal integration ability have been described in each structure (Meredith and Stein, 1986, 1990; Benedek et al., 1986, 2004). The SC-Sg-IVA axis seems to be involved in motion and novelty detection, and in such ways this system takes part in multisensory processing and sensory-motor integration (Nagy et al., 2003; Eördegh et al., 2005; Paróczy et al., 2006). Moreover, a population of neurons located within the IVA is functionally and anatomically organized in a sensory mosaic pattern (Hicks et al., 1988a,b). Furthermore, the IVA has connections with the suprasylvian visual field, a region prominently involved in visually guided orientation behavior (Hardy and Stein, 1988; Payne et al., 1996). In this study, our ultrastructural observations revealed that the afferent terminals from the SC are in direct contact with thalamo-cortical projection neurons that send their axons to the IVA, their somata residing principally within the dorsal part of the Sg. Accordingly, at least a portion of the Sg may play a role in the direct transmission of visual information from the SC to the IVA. This transmission may be essential in ensuring that the sensory-motor information from other subcortical regions, such as the PPT or substantia nigra, is integrated with the ongoing tectal visual signal in the Sg and processed toward the associative cortical regions.

Acknowledgments

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