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Research Note

Afferents to the Cortical Pupillo-Constrictor Areas of the Cat, Traced with HRP

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Summary. Afferents of the cortical pupillo-constrictor areas (PCAs) of the cat were studied using the horseradish peroxidase method. PCAs receive heavy cortical inputs from areas 7, 19, 21, the lateral suprasylvian area, the splenial visual area, and subcortically from the claustrum, the intralaminar nuclei, the pulvinar-lateral posterior nuclear complex.

Key words: Pupillo-constrictor areas – Afferents – HRP – Cat

We previously reported that electrical stimulation of the most ventral part of the posterior suprasylvian gyrus of the cat revealed two separate and independent foci of low thresholds for pupillary constriction (Shoumura et al. 1982). Comparing the extent and location of the cortical pupillo-constrictor areas (PCAs) with the map of visual areas defined electrophysiologically (Tusa and Palmer 1980), it can be said that both areas are located in area 20 on the lateral surface of the brain. The present communication reports some observations on the afferents of the PCAs of the cat by using the retrograde axonal transport of Horseradish peroxidase (HRP).

Methods

Experiments were performed in a total of ten adult or young adult cats, which were anesthetized by intramuscular injection of ketamine hydrochloride (35–40 mg/kg) and placed in a stereotaxic head holder. The occipital cortex of one hemisphere was exposed under sterile conditions. Anteroventral(av-PCA) and posterodorsal(pd-PCA) pupillo-constrictor areas were identified by the method described in the previous paper (Shoumura et al. 1982).

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An injection of 0.05–0.1 µl of 50% HRP (Miles or Sigma type VI) dissolved in 2% dimethylsulfoxide was made into the center of the av-PCA, pd-PCA or silent region of area 20 through a glassmicropipette attached to a microsyringe mounted on a micromanipulator. After a postinjection period of 48–72 h, the cats were reanesthetized deeply and perfused through the ascending aorta with 0.5 l of physiological saline followed by 1.5–2.0 l of 1.0% paraformaldehyde and 1.5% glutaraldehyde in 0.1 M phosphate buffer at pH 7.4. The brains were removed and immersed in cold buffer containing 20% sucrose, and 50 µ sections were cut in the frontal plane on a freezing microtome. Every second section was treated for peroxidase histochemistry by the diaminobenzidine (Streit and Reubi 1977) or tetramethyl benzidine (Mesulum 1978) method, and the alternative sections were reacted for acetylcholinesterase (AChE) to identify the boundaries of the posterior thalamic nuclei (Graybiel and Berson 1980). The sections were mounted on gelatinized slides and diaminobenzidine reacted sections were lightly counterstained with thionine. Both light- and darkfield illuminations were employed to identify HRP-labeled neurons.

Results and Discussions

In this communication, we show chiefly two representative cases which received an injection into the pd-PCA (case A) or av-PCA (case B). In both cases the injected enzyme was found to be restricted to one of the PCAs although it was diffused into most of the cortical layers. The distributions of retrogradely labeled cells were essentially similar in both cases, however, a few differences were observed between them.

In the ipsilateral cerebral cortex, many HRP-labeled cells were distributed in the crown of the posterior part of the suprasylvian gyrus, the medial and lateral banks of the lateral sulcus, the lateral suprasylvian area (LS, Palmer et al. 1978) and the splenial visual area (SVA, Kalia and Whitteridge 1973).

In case A (Fig. 1), which received an injection into the pd-PCA, the distribution of HRP-labeled

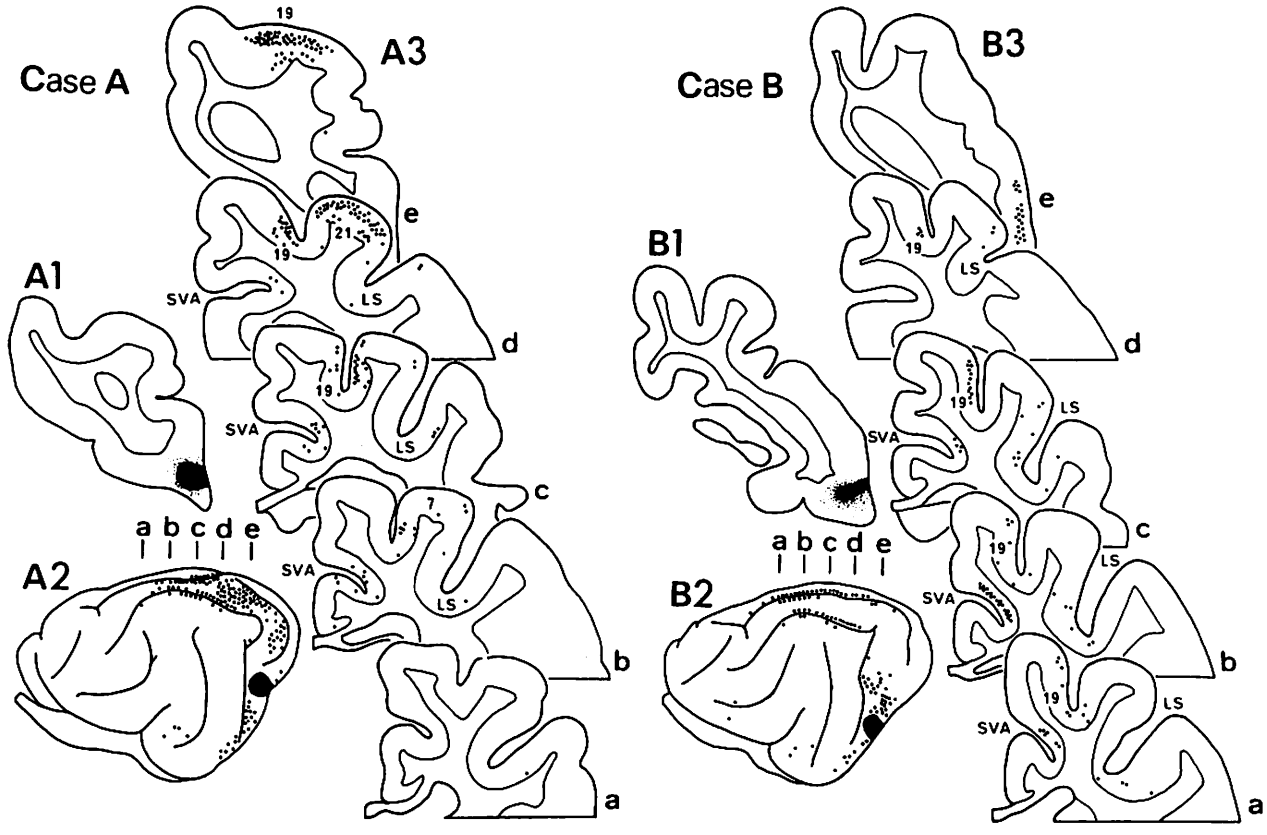

Fig. 1. Distribution of HRP-positive cells in the cerebral cortex after an injection into the pd-PCA (case A) and the av-PCA (case B). A1, B1: Coronal sections to show injection sites. A2, B2: Lateral view of the cerebral hemisphere to show the distribution of the labeled cells. Dots aligned along sulci show the distribution of the cells within the banks of the lateral and suprasylvian sulci. A3, B3: Coronal sections to show the distribution of labeled cells in the cerebral cortex. The levels of the sections are indicated in A2 and B2. Abbreviations as in text

cells extended from the posterior part of the crown of the posterior suprasylvian gyrus rostromedially to the medial and lateral banks of the lateral sulcus at its intermediate levels. Most of these cells appeared to fall in areas 19 and 21 (Tusa et al. 1979; Tusa and Palmer 1980). However, labeled cells were not observed at the rostral levels of area 19. On the other hand, in case B which received an injection into the av-PCA, HRP-positive cells were not identified in the crown of the posterior part of the suprasylvian gyrus (Fig. 1). Instead, many labeled cells were distributed in the rostral part of area 19. Thus, there was a tendency that the more dorsal HRP injection (pd-PCA) resulted in labeling in area 19 at more caudal levels and the more ventral injection (av-PCA) at more rostral levels. The patterns of distributions of labeled cells in the LS and SVA are similar to that in area 19. These results suggest that the PCAs receive topographically different inputs from areas 19, 21, LS and SVA.

In addition, a small number of labeled cells were observed in the ventral part of the posterior ectosylvian gyrus, the ventral part of the posterior sylvian gyrus, the fusiform gyrus of Papez, the posterior rhinal sulcus, the medial septal nucleus and the nucleus of the diagonal band of Broca in both cases. Furthermore, after an injection into the pd-PCA, HRP-labeled cells were seen in the parasplenial gyrus and the crown of the middle suprasylvian gyrus (area 7). Essentially, the largest number of labeled cells in the cortex appeared in layer III, but quite a few were in layers V and VI, especially in areas 19, LS and SVA. In the contralateral cerebral hemisphere, many HRP-positive cells were observed in an area homotopical to the injection and a few HRP-labeled cells were seen in areas 19, SVA, LS and the fusiform gyrus of Papez.

Many HRP-labeled cells were observed ipsilaterally in the caudal half of the dorsal claustrum after an injection into the pd-PCA or av-PCA (Fig. 2). It was noted that the pd-PCA received claustrocortical input from the central to lateral part of the dorsal claustrum at its caudal half and also from the ventral part at the most caudal level. The av-PCA received

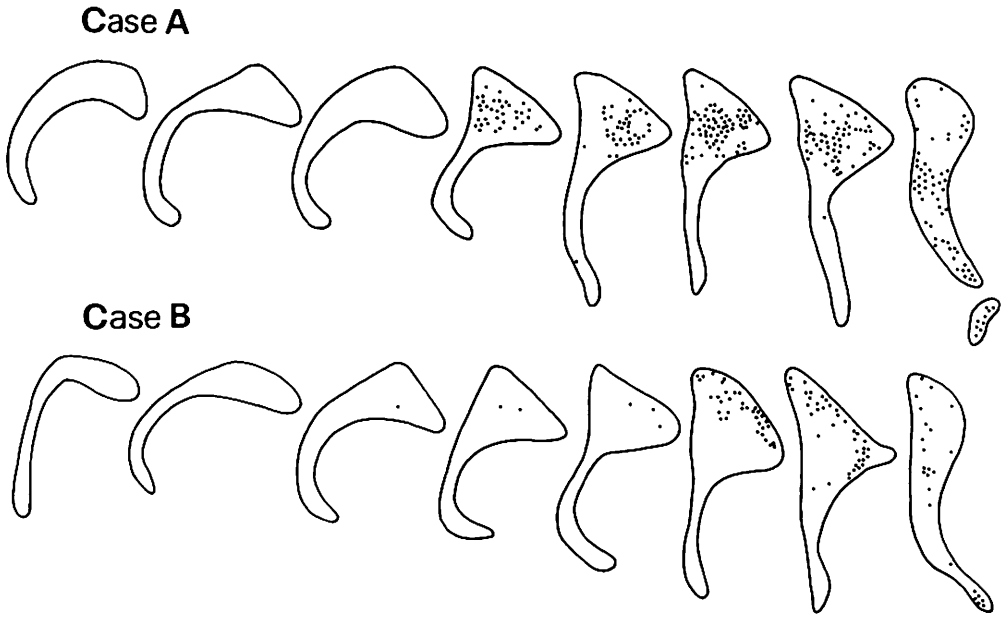

Fig. 2. Coronal sections showing the distribution of HRP-positive neurons in the ipsilateral claustrum in case A and B

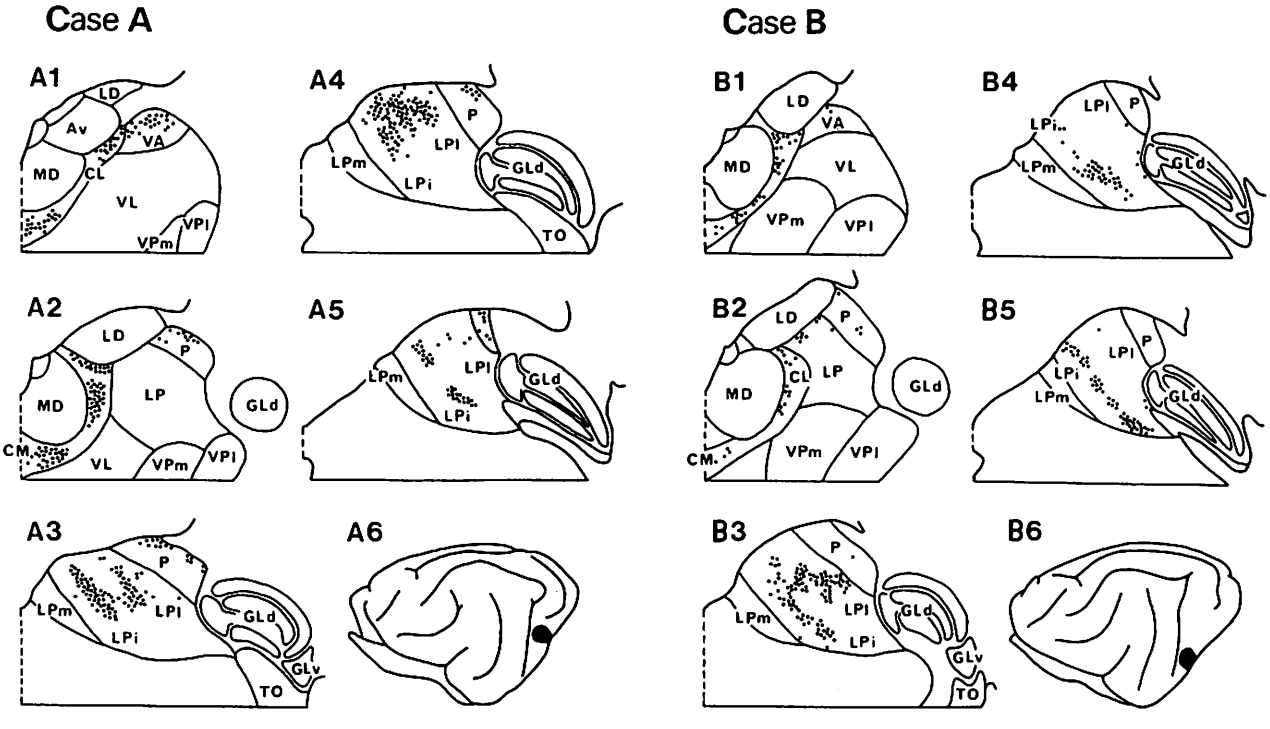

Fig. 3. Coronal sections showing the distribution of HRP-positive cells in the thalamus in case A and B (A1-5, B1–5), and the injection sites (A6, B6). The nomenclature of the subdivisions of the lateral posterior nucleus was compiled by Updyke (1977). LD: Nucleus lateralis dorsalis; Av: Nucleus anteroventralis; MD: Nucleus medialis dorsalis; VA: Nucleus ventralis anterior; VL: nucleus ventralis lateralis; VPl, m: Nucleus ventralis posterior lateralis et medialis; GLd, v: Nucleus geniculatus lateralis dorsalis et ventralis; LPm: Nucleus lateralis posterior pars medialis; TO: Tractus opticus; P: Pulvinar; CL: Nucleus centralis lateralis; CM: Nucleus centralis medialis. Other abbreviations as in text

fibers from the dorsolateral part of the nucleus at its caudal half and from the ventral part at the most caudal level. The visual claustrum (Sherk and LeVay 1981) was largely included in the labeled region. A few HRP-positive cells were also encountered in the globus pallidus in both cases.

In the diencephalon, numerous HRP-labeled cells were observed ipsilaterally in the pulvinar-lateral posterior nuclear complex (Pul-LP complex), the lateral central nucleus, the paracentral nucleus and the medial central nucleus (Fig. 3). In the Pul-LP complex, labeled cells were observed in the interjacent division (LPi) and the rostral part of the lateral division (LPl) of the lateral posterior complex of Updyke (1977). However, only a few HRP-positive cells were identified in the caudal part of LPl (Fig. 3; A5, B4, B5). According to the neighboring AChE stained sections, the densely packed cells in the rostral part of LPl and LPi (Fig. 3; A3, A4, B3) fell in the region which corresponds to the caudal division of the lateral intermediate nucleus (LIc) of Graybiel and Berson (1980), which receives an ascending input from the pretecto-tectal border zone and a descending projection from the parietal cortex, including area 7. Labeled cells in the caudal part of LPi (Fig. 3; A5, B4, B5) appeared to fall in the medial division of the lateral posterior nucleus (LPm) of Graybiel and Berson (1980), which receives input from the superficial layers of the superior colliculus. A tendency was noted that the pd-PCA received projections from the dorsal part of LP and the av-PCA from the ventral part of the nucleus. Furthermore, many HRP-positive cells appeared in the region ventrolateral to the caudal part of LPi (LPv of Graybiel 1972) after an injection into the av-PCA. A substantial number of labeled cells were also seen in the pulvinar nucleus (Fig. 3).

Besides these subcortical structures, labeled cells were identified in the dorsal portion of the anterior ventral nucleus, the dorsal central nucleus and the hypothalamus after an injection into either pd-PCA or av-PCA. A few small HRP-labeled cells were also observed in the parvocellular C-lamina of the dorsal lateral geniculate nucleus as reported by Raczkowski and Rosenquist (1980).

In another case (not illustrated), which received an injection into the silent region in area 20 (rostral to the pd-PCA), the distribution pattern of labeled neurons was essentially similar to that of case A.

The present results indicate that the PCAs receive multiple inputs from various cortical and subcortical structures related to visual functions including areas 7, 19, LS, SVA, claustrum and Pul-LP complex. All these structures have demonstrated retinotopic representation of the visual field (Palmer and Rosenquist 1978; Tusa et al. 1979; Raczkowski and Rosenquist 1981; Sherk and LeVay 1981), except area 7.

Considering the sources of afferents to the PCAs, it is very probable that the PCAs are largely concerned with visuo-motor functions. Since the pupillary light reflex is not impaired by large destruction of the cerebral cortex (unpublished observation), the PCAs can be excluded from the light reflex pathway. It is quite possible that the PCAs are in close relation to pupillary constriction accompanied with a proximity reflex, because the PCAs are reciprocally interconnected with the LS where Bando et al. (1981) observed lens accomodation by electrical stimulation. The PCAs may receive visual information from the above-mentioned multiple sources and regulate pupillary constriction accompanied with accomodation and convergence via certain brain stem nuclei.

In the present study, no essential differences were noted between the afferents of PCAs and that of the silent region in area 20. Therefore, further detailed studies are needed to investigate whether there are any hodological differences between them, so we are now studying the efferents of the PCAs with autoradiography.

Very recently Cavada and Reinoso-Suarez (1983) published a paper on the afferent connections of area 20 in the cat. However, their HRP injections appear so extensive, involving most of area 20, that there are several gaps between their observations and ours, especially with respect to labeling in the proreal gyrus, the anterior rhinal sulcus, the entorhinal cortex, postsubiculum, the dorsal portion of the subiculum, the caudal portion of the orbital gyrus, the anterior sylvian gyrus and the corpus amygdaloideum. In some cases which received a somewhat larger injection into av-PCA, we observed labeling in the caudal portion of the orbital gyrus, the anterior sylvian gyrus and the corpus amygdaloideum. This labeling appears to be caused by the uptake of the enzyme from the rostroventral or rostromedial corticies to the av-PCA.

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