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Direct projection from the visual associative cortex to the caudate nucleus in the feline brain

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ABSTRACT

Recent morphological and physiological studies support the assumption that the extrageniculate ascending tectofugal pathways send visual projection to the caudate nucleus (CN) in amniotes. In the present study we investigate the anatomical connection between the visual associative cortex along the anterior ectosylvian sulcus (AES) and the CN in adult domestic cats. An anterograde tracer – fluoro-dextrane-amine – was injected into the AES cortex. The distribution of labeled axons was not uniform in the CN. The majority of labeled axons and terminal like puncta was found only in a limited area in the dorsal part of the CN between the coordinates anterior 12–15. Furthermore, a retrograde tracer – choleratoxin-B – was injected into the dorsal part of the CN between anterior 12 and 13. We detected a large number of labeled neurons in the fundus and the dorsal part of the AES between the coordinates anterior 12–14. Based upon our recent results we argue that there is a direct monosynaptic connection between the visual associative cortex along the AES and the CN. Beside the posterior thalamus, the AES cortex should also participate in the transmission of the tectal visual information to the CN. This pathway is likely to convey complex information containing both sensory and motor components toward the basal ganglia, which supports their integrative function in visuomotor actions such as motion and novelty detection and saccade generation.

The caudate nucleus (CN) is the main structure that receives sensory motor information arriving to the basal ganglia. It is involved in visuomotor behavior and contributes to the control of visually guided oculomotor and skeletomotor functions [1,14,18,38].

A number of studies have been carried out to clarify the role of the CN in visual and visuomotor processing [5,13,17,24,32,36,39], there is some uncertainty concerning the pathways conveying sensory information to the basal ganglia. Earlier morphological findings stressed the overwhelmingly dominant role of the geniculostriatal pathway to provide visual input to the CN in cats and rabbits [15,41], however recent morphological and physiological studies support that the extrageniculate ascending tectofugal system also projects to the CN in reptiles, birds and mammals. Harting and colleagues [10,11] postulated that the CN receives efferents from all of the extrageniculate visual and intralaminar thalamic nuclei [11]. Furthermore, the dorsolateral, visual part of the CN in the cat receives visual afferentation from the posterior thalamus – including the suprageniculate nucleus (Sg) – that is strongly connected to the visual associative cortex along the anterior ectosylvian sulcus (AES cortex) with thalamo-cortico-thalamic loops [8–11,20,24,25]. Beyond the morphological connection among these structures, they possess very similar sensory properties, which suggest their functional connection and their common role in visuomotor action and multisensory information processing. In the present study we ask whether there is a direct anatomical connection between the visual associative cortex and the striatal region of the feline brain. Based on the results of the present study, where combination of anterograde and retrograde tracing techniques were used, we suggest the existence of direct cortical input form the AES cortex to the CN.

The brains of one male and one female adult cat weighing 2.5 and 2.8 kg, respectively were used in this study. All experimental procedures followed the European Communities Council Directive of 24 November 1986 (S6609 EEC) and the National Institutes of Health guidelines for the care and use of animals for experimental procedures. The experimental protocol was accepted by the Ethics Committee for Animal Research of Faculty of Medicine at the University of Szeged.

The animals were initially anaesthetized with ketamine hydrochloride (30 mg/kg i.m., Calypsol, Richter Gedeon, Budapest, Hungary). The subcutaneous injection of 0.2 ml 0.1% atropine

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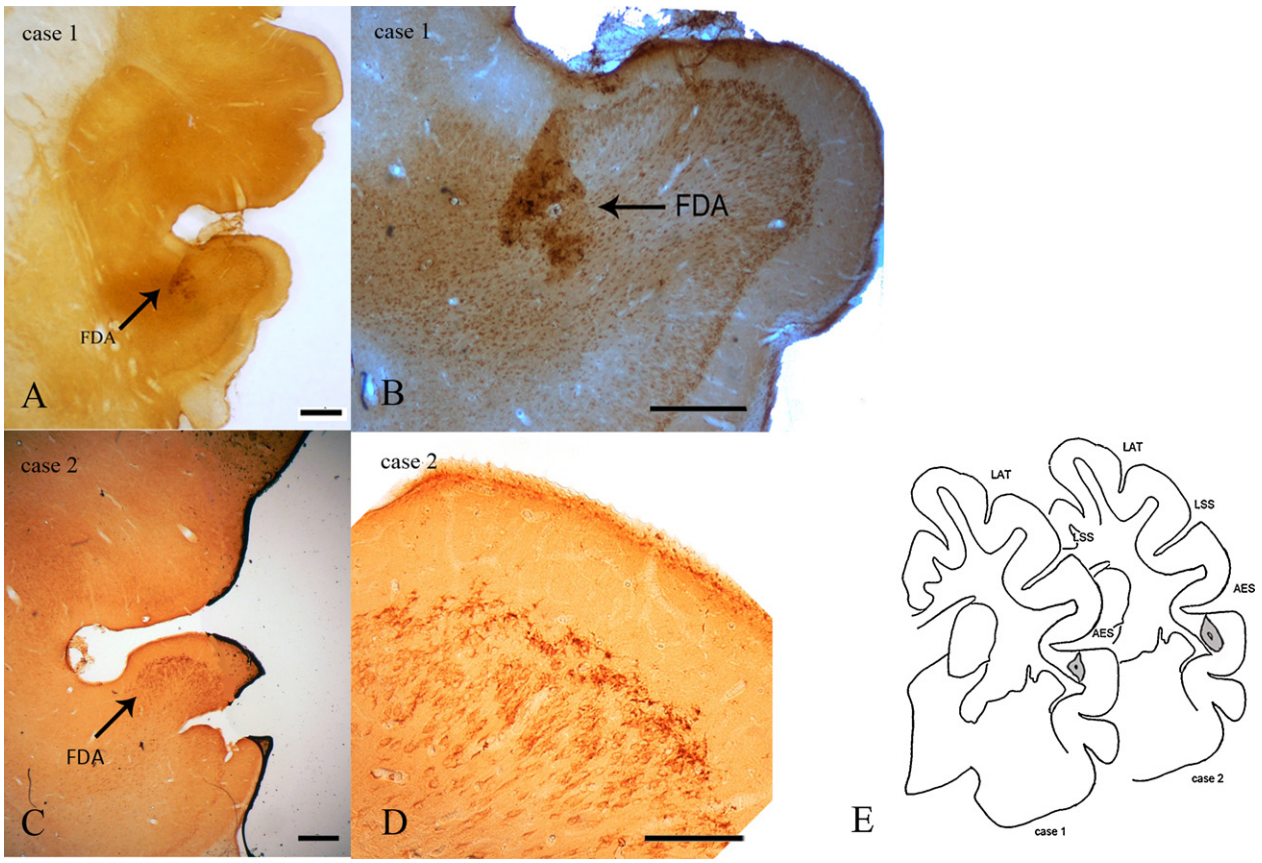

Fig. 1. The sites of FDA injections in the AES cortex. The arrow denotes the position of the tracer on the photomicrograph at about anterior 13 in both cases (A, C) and the FDA labeled cells in the AES cortex (B, D), while the gray areas on the schematic illustrated coronal sections (E) show the localization of the deposits. *Abbreviations*: LAT, lateral sulcus, LSS, lateral suprasylvian sulcus, AES, anterior ectosylvian sulcus. Scale bars: (A–C) 1 mm, (D) 800 μm.

sulphate was administered preoperatively to reduce salivation and bronchial secretion. The trachea was intubated, the femoral vein was cannulated and the animals were placed in a stereotaxic headholder. All wounds and pressure points were routinely infiltrated with local analgesic (procaine hydrochloride, 1%). Throughout the surgery the anaesthesia was maintained with halothane (1.6%, Narcotan, Zentiva, Prague, Czech Republic,) in air. The animals were immobilized with gallamine triethiodide (20 mg/kg). During the positioning of the deposits in the brain, gallamine triethiodide (8 mg/kg/h), glucose (10 mg/kg/h) and dextran (50 mg/kg/h) were infused with Ringer lactate solution at a rate of 4 ml/h. Atropine sulphate (1–2 drops, 0.1%, Egis, Budapest, Hungary) and phenylephrine hydrochloride (1–2 drops, 10%) were applied locally to dilate the pupils, block accommodation, and retract the nictitating membranes. The end-tidal concentration of halothane, MAC values and peak CO_2 concentrations were monitored with a capnometer (Capnomac Ultima, Datex-Ohmeda, Inc.). The heart rate and brain activity (ECG and EEG) were also monitored continuously. During the length of the anaesthesia the EEG indicated slow wave sleep. The peak expiratory CO_2 concentration was kept in the range of 3.8–4.2%. The body temperature was maintained at approx. 37 °C using a warm-water heated blanket with thermostat.

The coordinates of the injection sites and the position of the labeled axons, terminal like puncta and neurons were determined according to the Reinoso-Suárez topographical atlas [33]. The animals received unilateral injection of 10% fluoro-dextran-amine (FDA, Molecular Probes) as an anterograde tracer, dissolved in 0.1 M sodium phosphate buffer (PB), pH 7.6. Two μl of this solution was injected via a Hamilton syringe in the AEV. Choleratoxin (List Biological Laboratories, Lot number: 10426B) was applied as a retrograde tracer. The animals received 2 μl 0.5% choleratoxin injection in the CN previously determined to be involved in the visual function via electrophysiological testing [12,24,29].

One week following the injection of the deposits, the animals were deeply anesthetized with sodium pentobarbital and perfused transcardially with isotonic saline (0.9%), followed by 4% paraformaldehyde and 0.1% glutaraldehyde in 0.1 M sodium phosphate buffer, pH 7.6. The brains were removed from the skull and cut into 50 μm coronal serial sections with a vibratome. These sections were divided into two groups. The sections in the first group were processed for the FDA histochemistry. In order to visualize the FDA, the following three-day-long protocol was used:

On the first day sections were washed in 0.1 M PB, then for 30 min in 10% H_2O_2 followed by PB rinses again. As a following step, the sections were washed in 10% normal rabbit serum (Vector Lab.), then were incubated in anti-fluorescein first antibody diluted to 1:2000 in 0.1 M PB overnight on 4 °C. On the second day sections were rinsed in PB, and then were incubated overnight in rabbit anti-goat secunder antibody diluted to 1:300 in 0.1 M PB. Sections were then rinsed in PB on the following day and incubated at room temperature for 2 h in avidin–biotin complex. Sections were finally washed in PB and in Tris-buffer.

The second group of the sections was processed for the choleratoxin-B immunohistochemistry. In order to visualize the CTB, the following three-day-long protocol was performed: on the first day sections were washed in 0.1 M PB, then 30 min in 10% H_2O_2, then in PB again. Finally, the sections were washed in 10% normal rabbit serum (Vector Lab.), then incubated in

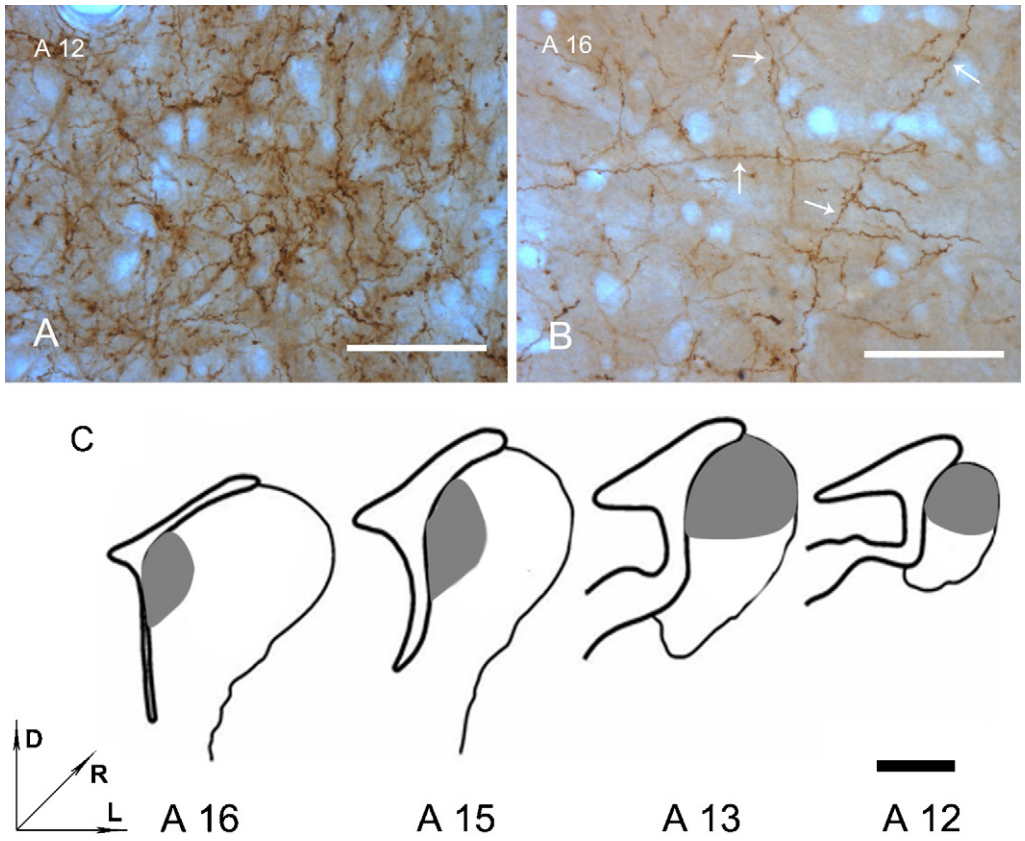

Fig. 2. FDA labeled axons and terminal like puncta in the CN. Photomicrographs of the FDA labeled axons in the dorsal part of the CN on the coronal sections (parts A and B). Part A is showing the labeling in the CN at the coordinate anterior 12, where high density of labeled axons and terminal like puncta can be seen. In part B the arrows demonstrate the labeled axons in the more anterior part of the CN (anterior 16). The black dots on the schematic drawing of the CN (part C) indicate the localization of the anterogradely labeled axons in the CN between the coordinates anterior 12–16. Dots are indicating the density of the FDA labeled axons. Note the high density of labeled axons between anterior 12–13 in the CN and the decreasing density of labeled axons in the more anterior part. Scale bars on part A and B are 50 μm.

anti-choleratoxin antibody as primary antibody diluted to 1:2000 in 0.1 M PB overnight on 4 °C. On the next day sections were first rinsed in PB then were incubated overnight in rabbit anti-goat antibody as secondary antibody diluted to 1:300 in 0.1 M PB. Sections were rinsed in PB on the following day, then were incubated at room temperature for 2 h in avidin–biotin complex, then finally washed in PB and in Tris-buffer. After the FDA and choleratoxin-B immunohistochemistry, in order to visualize both reactions, the sections were treated by diaminobenzidine (DAB). Following the DAB reactions, the sections were mounted on gelatin-coated slides for light microscopic observation.

First, we observed the injection site in the AES cortex. Photomicrographs show clearly the position of the FDA deposits, between anterior 12 and 13 in the AES cortex in each cat (Fig. 1). We have detected large number of FDA labeled axons and also terminal like puncta in the CN. The distribution of labeled axons was not uniform in the CN. We found only a limited area, in the dorsal part of the CN where FDA labeled axons and terminal like puncta were found (Fig. 2A, B). Fig. 2C shows the position of the FDA labeled axons in the CN. The labeled axons were found from anterior 12 to anterior 16. We did not find any more labeled axons in the more anterior parts of the CN. These results suggest that the AES cortex sends strong projections to the dorsocaudal part of the CN, while the projections to the central and rostral parts are weak.

Furthermore, FDA labeled axons were also detected in the frontal cortex at anterior 22–24 and throughout the whole extent of the suprageniculate nucleus (Sg) of the posterior thalamus.

CTB, which was applied as a retrograde tracer, was injected in the CN at anterior 12 and 13, respectively. Fig. 3A, C demonstrates the photomicrograph of the choleratoxin injection site and the schematic illustrations of the positions of injection sites in the CN (Fig. 3B, D). The examination of the AES cortex demonstrated high density of choleratoxin labeled neurons (Fig. 4A, B). Fig. 4C illustrates the labeled neurons in the AES cortex located between the coordinates anterior 12–14 (Fig. 4C).

Furthermore, choleratoxin labeled neurons were also found in the posterior thalamus. An investigation of the occurrences of the FDA labeled axons and choleratoxin labeled neurons in the thalamus showed that the position of retrogradely labeled neurons overlap with the anterogradely labeled axons in the posterior thalamic nuclei, i.e. suprageniculate nucleus (Sg) and posterior pulvinar complex (LP-Pul).

In the present study based upon our anterograde and retrograde tracer studies in the feline brain we give the first evidence of a direct monosynaptic connection between the visual associative cortex along the AES and the CN. Anterograde tracer – fluoro-dextrane-amine – was deposited in the AES cortex and a large number of labeled axons were found in the dorsal part of the CN. Choleratoxin-B as a retrograde tracer was inserted in the dorsal part of the CN and we detected large number of labeled neurons in the AES cortex.

A possible direct interaction between the ascending tectofugal system and the CN was observed in physiological studies, where behavioral or receptive-field analyses were performed [3,19]. The neurons of the intermediate and deep layers of the SC, the Sg and the AES cortex and the CN exhibit similar physiological properties,

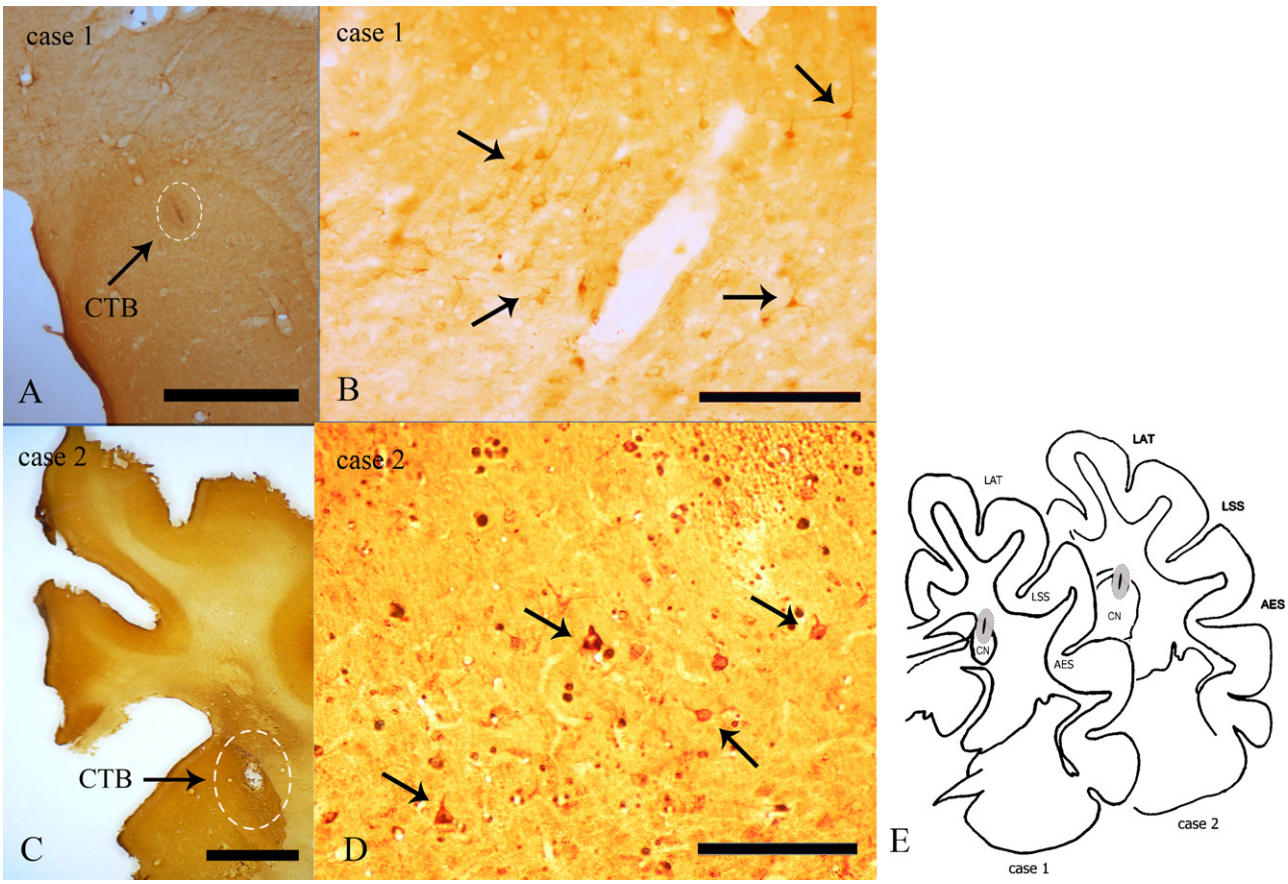

Fig. 3. The sites of choleratoxin-B injections in the CN. The arrow denotes the position of the tracer on the photomicrograph at about anterior 12 in the CN (A, C) and choleratoxin labeling in the CN (B, D), while the gray areas on the schematic illustrations (E) show the localization of the deposits on the coronal sections. *Abbreviations*: LAT, lateral sulcus, LSS, lateral suprasylvian sulcus, AES, anterior ectosylvian sulcus. Scale bars: (A, C) 1 mm, (B, D) 200 μm.

which suggests a functional relationship between these structures. The neurons of these structures have similarly large visual receptive fields. These structures are multisensory neurons may be sensitive to both auditory and somatosensory stimulus modalities. Multisensory units with cross-modal integration ability have been described in each structure [2,4,21,22,26]. The similar spatio-temporal visual receptive field properties of the neurons in SC, Sg, AES cortex and CN suggest their similar function in visual information processing [35]. These neurons respond optimally to low spatial and high temporal frequencies and exhibit narrow spatial and temporal frequency tuning. These characteristic visual features in combination with the classical visual receptive field organization (extensive overlapping visual receptive fields, strong direction selectivity and preference to small stimuli moving at high velocities) of these neurons make them capable of motion and novelty detection, and this way this system takes part in multisensory processing and sensory-motor integration [8,24,31].

Some visual structures in the mammalian brain serve dual function, that is, perception and action at the same time [23]. The descending tectonigral and tectobulbar pathways originating in the intermediate and deep layers of the SC serve visuomotor actions [16], which is presumably true also for the ascending tecto-thalamic pathways that provide connections to the basal ganglia [41]. As it was described earlier, the ascending tectofugal system seems to be one of the sources of visual information to the basal ganglia where the posterior thalamus plays a key role in relaying of this information. The posterior thalamus is topographically connected with regions of cortex formerly described simply as “associative cortex” along the AES, such as the insular visual area (IVA) and the anterior ectosylvian visual area (AEV) [34]. The IVA communicates with the more dorsal parts of the Sg and the central-medial portions of the lateralis medialis nucleus (LM) [6,7]. The AEV also has connections with the dorsal parts of the Sg, but shares fiber connections with the more lateral parts of the LM (situated close to the medial division of lateralis posterior nucleus (LPm), and additionally within the LPm itself [30,32]. Furthermore, 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 rostro-caudal axis in the cortex (i.e. anterolateral division of lateral suprasylvian areas (LS)-to-posterolateral division of LS, or area 17) [27,28,37]. In this sense, the constituent nuclei of the posterior thalamus including LP-Pul complex and the Sg, have topographical connections with various visually responsive regions of the cortex.

The tecto-thalamic 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. This input to the CN could be directly from the posterior thalamus [40]. On the other hand sensory input to the CN may arrive from the AES cortex. While the intermediate and deep layers of the superior colliculus project via the posterior thalamus to the AES cortex we argue that this AES cortex-CN pathway might be one of the sources of the tectal visual information to the CN. The direct visual neural input arriving from the AES cortex – in a manner analogous to other modalities from other cortical areas – provides a full spectrum of feedback from the external environment. This may allow the CN to adjust the motor actions of the animal more properly, according to the changes of the environment.

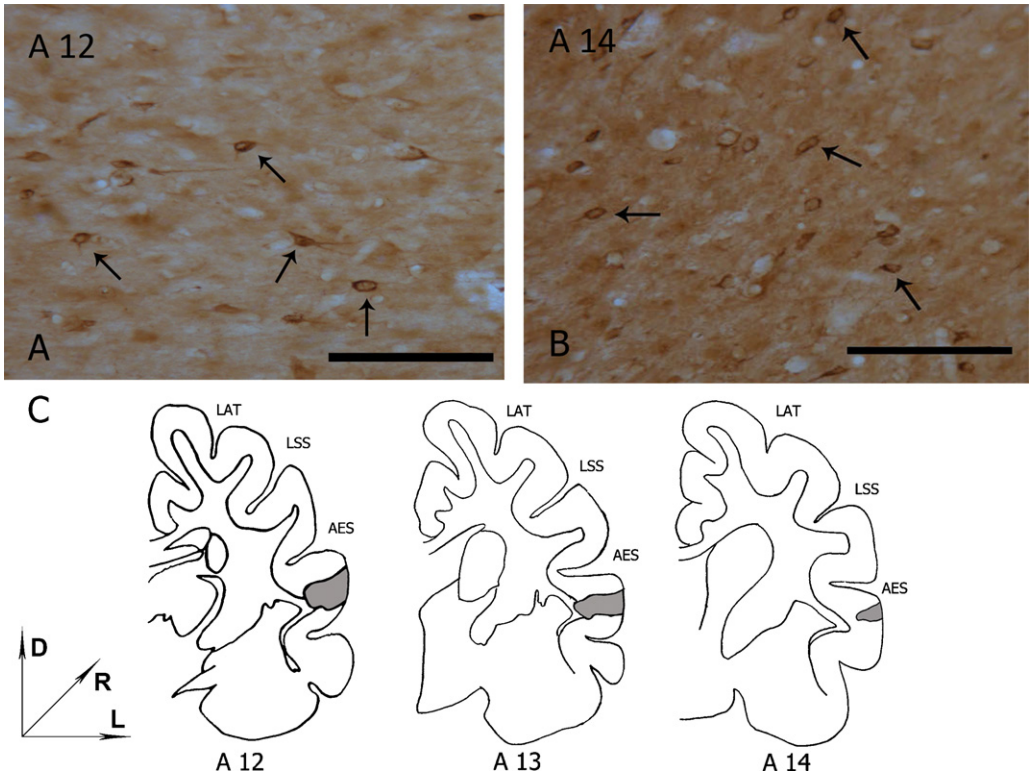

Fig. 4. Choleratoxin labeled neurons in the AES cortex. Photomicrographs of the choleratoxin labeled neurons in the AES cortex on the coronal sections (A, B), where arrows denote the retrogradely labeled neurons in the AES, originated from the CN. Part A shows the labeled neurons at anterior 13 while part B at anterior 12. The extent of the gray shading in schematic sections in C indicates the location of the high density clusters of the AES neurons retrogradely labeled with the choleratoxin (C). Scale bars in A and B are 200 μm.

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