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Evidence for corticocortical connections between areas 7 and 17 in cerebral cortex of the cat

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Abstract

This study provides the first evidence of direct corticocortical connections between areas 7 and 17 of the cat. Wheat germ agglutinin horseradish peroxidase (WGA-HRP) was administrated by micro-electrophoresis and micro-injection, respectively, into area 17 and area 7 in different hemispheres in eight cats. WGA-HRP labeled pyramidal neurons were observed primarily in layer 5 of areas 7 and 17 indicating that there are reciprocal connections between these areas. Optical imaging was used to guide WGA-HRP injections to single orientation columns in area 17. After such restricted injections labeled pyramidal cells were observed in layer 5 of area 7. These pyramidal cells were arranged as discontinuous patches extending across a broad region of area 7. These results suggest that feedback from area 7 to area 17 may arise from specific functional columns in area 7.

Keywords: Visual cortex; Area 7; Suprasylvian gyrus; Area 17; Reciprocal projection

In the mammalian visual system, there are many areas that process visual information, from the retina through the dorsal lateral geniculate nucleus (LGN) in the thalamus to the cortex. In monkey cortex, neurons in more than 30 visual areas are arranged in two feedforward hierarchies of areas, the ventral and dorsal streams which have been proposed to be important for form and motion processing, respectively [21,8,5]. Recently there has been increasing interest in the role of feedback projections from the high-order areas to lower-order areas [4,3,13,22]. Data indicates that cortical visual areas within each hierarchy communicate with each other almost exclusively through reciprocal connections arising from pyramidal neurons, which send excitatory inputs to their target areas [20,2,15,16]. These connections, together with projections from local inhibitory interneurons, the LGN feedforward input and cortical horizontal axons, construct local circuitries in each target area.

Like monkey, cat cortex consists of a number of visual areas. However, there is still controversy about how many visual areas exist in this species and which areas belong to the visual hierarchy. Area 7, an area located in the crown of the suprasylvian gyrus, was initially defined by Gurewitsch and Chatschaturian [10]. It is located anterior to visual area 21a and posterior to area 5, medial to area 22 and the posteromedial lateral suprasylvian (PMLS) area, and lateral to visual area 19 (Fig. 1A and B). Traditionally, area 7 has not been considered as a visual area because some neurons in area 7 respond best to somatic and auditory stimuli. However, increasing evidence indicates that neurons in the crown of the middle suprasylvian gyrus, including areas 5, 7 and 21a respond to visual stimulation and to eye movements [14,18,9,23]. Most of those neurons have relatively restricted visual receptive fields and many of them are directionally selective [7]. A classical work by Symonds and Rosenquist [20] on corticocortical connections among many visual areas demonstrated that area 7 has strong reciprocal connections with area 19, weak connections with areas 20a and 21a, possible connections with area 18, but no connections with area 17. Pigarev and Rodionova [19], however, reported that the receptive fields of the neurons in area 7 in alert cats were clearly visual and restricted to the lower part of the contralateral visual field, and that these cells could mainly be classified into four types according to their cell location in area 7 and the shape and distribution of their visual receptive fields. Therefore, it is of interest to reconsider whether there are any direct connections between area 7 and area 17 in the cat. In this study we used retrograde labeling of WGA-HRP to elucidate this issue.

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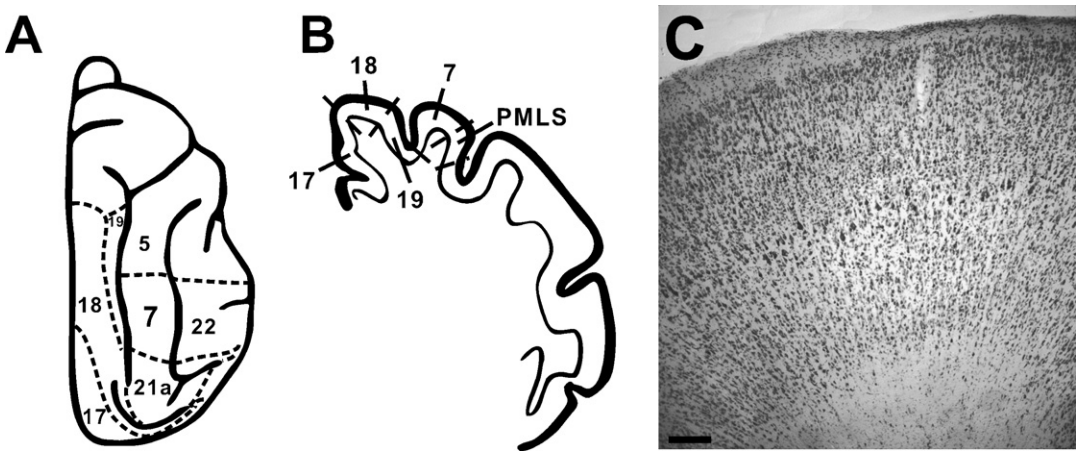

Fig. 1. Schematic drawings for the location of areas 7, 17 and neighboring areas: (A) top view of the right hemisphere of a cat; (B) a coronal view of a section at Horsley–Clarke coordinates A4. Numbers in A and B represent the names of cortical areas. PMLS, posterior medial lateral suprasylvian area; (C) a coronal Nissl stained section of area 7. Scale bar: 200 μm.

Eight adult cats of either sex were used in the current study. All procedures were performed in strict accordance with the Guide for the Care and Use of Laboratory Animals described by the United States National Institutes of Health. All experiments were designed to minimize the number of animals used. The procedures were previously reported elsewhere [6,11,12] and are only briefly described here. Animals were initially anaesthetized with ketamine (25 mg/kg). During the remainder of the experiment, anesthesia was maintained with *i.v.* infusion of sodium pentobarbital with a dose of 3 mg/(kg h). Gallamine triethiodide (8–10 mg/(kg h)) was then used for immobilization and animals were artificially respired. The end-tidal CO_2 was kept at about 4%. The animals' physiological condition was monitored and kept in normal range throughout the experiment. Contact lenses were used to protect the cornea and provide power to focus the eyes on a stimulus screen. Three millimeter artificial pupils were used.

In some cases, a stainless steel imaging chamber was fixed with dental cement on the skull over area 17. After removal of the dura, the chamber was filled with silicone oil and sealed with a glass window for optical imaging orientation maps which were used to guide small WGA-HRP iontophoretic injections.

Drifting sinusoidal gratings (contrast 90%, temporal frequency of 2 Hz) were presented binocularly on a screen (FlexScan F931, EIZO NANAO, Japan) located 57 cm from the cat's eyes. A higher spatial frequency of 0.58 cycles/degree was used to differentiate area 17 from area 18 [17,11].

An intrinsic signal optical imaging system was used to record optical images from the exposed area 17 [6,11,12]. The blood vessel map was obtained by shining of green light (540 nm) on the cortical surface and the orientation map by shining a red light (640 nm) with a CCD camera (Dalsa, Canada) focused at 500 μm below the pial surface. The differential functional map was constructed to increase the signal to noise ratio as reported previously [24,1,26,6]. This map was used to guide the WGA-HRP injections into single columns as described earlier [25].

As previously reported [25], the contours of a highlighted orientation column in an optical imaging map elicited by a drifting grating of 0.58 cycles/degree (Fig. 2A) in the given cortical region at Horsley–Clarke coordinates P1.5–P7.5, L1-P2.5 in area 17, where most neurons prefer to respond to gratings of spatial frequencies higher than 0.3 cycles/degree while those of area 18 prefer to lower than 0.3 [17], was superimposed onto the vessel map of the same cortical area (Fig. 2B). Using these blood vessels as landmarks, injections were made in the center of the region of activation defining a single orientation column (black dots). A glass micro-pipette with a tip diameter of 20–40 μm filled with 4% WGA-HRP in saline was inserted perpendicular to the cortical surface and lowered to a depth of 600–1000 μm. Then, a micro-electrophoresis injection was made into area 17 (positive impulse current of 3 μA, 1 s on and 0.5 s off, for 20 min). The micro-pipette was routinely kept in the brain for 10 min after the injection to avoid pulling the label back up the pipette track. In most cases, the diffusion size of the WGA-HRP electrophoretic injections were confirmed to be about 300–500 μm in diameter (Fig. 2C).

In area 7, and in some cases area 17, large pressure injections of 3.0 μl (4% WGA-HRP saline) were made using a micro-syringe. We defined area 7 as the area occupying Horsley–Clarke coordinates A0–A8, L6–L12, as originally defined by Gurewitsch and Chatschaturian [10] and others [19,20].

Animals survived for 36–48 h after the WGA-HRP injections. Under deep anesthesia animals were perfused conventionally using a saline rinse and aldehyde fixative. The parts of brain containing areas 7 and 17 were removed for frozen sectioning. The 60 μm-thick coronal or sagittal sections were cut and reacted using the Hanker–Yates's method. Conventional Nissl staining was employed for differentiating cortical layers.

The main finding of this work is that feedback projections from area 7 to area 17 exist in the cat's visual cortex. The labeled large pyramidal neurons were located in a fairly large area covering almost all of area 7 in the four animals studied after one or two neighboring iso-orientation columns were injected in area 17, as shown in Fig. 3. Notably, almost all of these labeled cells were arranged in a single row in layer 5 of area 7 just underneath the granule cell layer (i.e. layer 4). Since the mean number of