Thalamo-cortical connections and their correlation with receptive field properties in the cat’s lateral suprasylvian visual cortex

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Summary. Areas PMLS and PLLS of the cat’s lateral suprasylvian visual cortex display an interesting global organization of local features in their single unit response properties: direction preference is centrifugally organized and velocity preference increases with eccentricity. In addition it has previously been shown that binocular interactions are strongest around the visual field center. This characterizes the LS areas as apt for the analysis of optic flow fields and for visual processing in various kinds of visuomotor tasks (Rauschecker et al. 1987). In the present study we analysed the types of input to LS from the optic chiasm, the corpus callosum and from two thalamic relay nuclei (lateral posterior and lateral geniculate) that constitute important sources of afferent information to the LS areas. We were interested in learning how the afferent (and efferent) connections between LS and these structures relate to the response properties of LS neurons. Overlap of an RF into the ipsilateral hemifield was virtually always associated with callosal input. Latency differences between responses to electrical stimulation of the optic chiasm and the thalamic sites indicated almost exclusively fast-conducting Y-input to LS. Correlation of response latencies with receptive field properties revealed the following correspondences: A positive correlation was found between LP-latency and RF-size matching the dependence of RF size on laminar origin. The type of correlation found between LP-latency and directional tuning of LS cells suggests that an interaction between thalamic and other inputs may be responsible for direction selectivity in LS. Finally, correlation of LP-latencies with centrifugal direction preference suggests that this specific property is generated by intracortical wiring rather than by thalamic input.

Key words: Visual system – Lateral suprasylvian cortex – Electrical stimulation – Thalamo-cortical connections – Direction selectivity

Introduction

In a recent study (Rauschecker et al. 1987) we described a global organization for cells in the lateral suprasylvian visual cortex of the cat with respect to direction selectivity and velocity preference. In addition, our own data and those of previous studies (Spear and Baumann 1975; Hubel and Wiesel 1969) indicated that a similar global organization exists for binocularity. The tendencies were as follows: Direction preference depended on the location of the receptive field centers in such a way that cells possessed a centrifugal (foveofugal) bias for movement away from the point of fixation. Velocity preference increases with distance from the area centralis, especially for cells with a radial direction preference. Finally, binocular units were found more often in the central region.

All these properties taken together indicate strongly that LS cells are part of a visual subsystem suitable for the analysis of expanding visual flow fields, as they occur for example during forward locomotion (Gibson 1950, 1958, 1966; Regan and Beverley 1979, 1982). The information extracted from such flow fields can be used for various purposes, such as vergence eye movements, lens accommodation, and control of pupil size during vergence, for tracking of an object moving in three-dimensional space, and for visual control of stance and locomotion (Richards 1975; Lee and Lishman 1975; Lee 1976; Nakayama 1985). Interestingly, some of these functions have been associated with the activity of single neurons in the lateral suprasylvian cortex or...
related areas previously (Bando et al. 1981, 1984; Toyama and Kozasa 1982; Komatsu et al. 1983; Toyama et al. 1985; Shoumura et al. 1982; Sakata et al. 1983). In the present study we were interested to see how the connections to and from thalamic relay nuclei, as identified by electrical stimulation, were interrelated with the response properties of LS neurons in general and with their local and global directional properties in particular. The converse question of how the response properties of neurons in the lateral-posterior/pulvinar complex relate to their connections to and from LS will be dealt with in a future paper (Friederichs and Rauschecker, in prep.).

Some of the striking similarities in local and global visual response properties between LS and LP neurons have already been described in abstract form (Rauschecker et al. 1984).

Methods

Data were collected from ten electrode penetrations in six cats. All animals were of adult age and had been raised in a normal environment.

Single unit recording

Standard techniques for extracellular single unit recording were applied. The animal was initially anaesthetized with ketamine-hydrochloride (Ketanest, 25 mg/kg i.m.) and xylazine (Rompun, 2 mg/kg i.m.) after premedication with atropine sulfate (0.05 mg s.c.). Anaesthesia was maintained throughout the experiment by adding fluothane (Halothan) to the usual 70/30 mixture of N₂O/O₂ respiration gases. The concentration of fluorane was set at 1% initially and was then reduced stepwise to 0.4%. During the whole experiment the depth of anaesthesia was controlled by monitoring EEG and EKG. No responses were produced to noxious stimuli with a fluorane concentration of 0.4%. In preparation for artificial respiration, a tracheotomy was performed, and the animal was then fixed in a stereotaxic headholder. The skull was opened over the suprasylvian sulcus (L10-L16, A0-A8). After surgery was completed the animal was paralyzed with gallamine triethiodide (Flaxedil, 20 mg/kg h) and artificially respirated as noted above. Body temperature was kept at 38°C with an automatically controlled heating pad; endtidal CO₂ was measured with a Beckman monitor and kept at 3.8%. The animal's eyes were protected by contact lenses containing 3 mm pupils, treated with neosynephrine (to retract the nictitating membranes) and 1% atropine sulfate (to paralyze the ciliary and sphincter muscles), and focused on a tangent screen at 171 cm distance.

Extracellular recordings from single units in PMLS and PLLS between stereotaxic coordinates A2 and A7 were obtained with double-barrel micropipettes, one chamber of which was filled with 1.5 M K⁺ citrate, the other chamber with a 3% solution of horseradish peroxidase (HRP) in 0.2 M KCl and 0.05 M Tris buffer (pH 7.6), in order to mark the electrode tracks. Only single unit recordings were taken into account. Cells were usually isolated every 50–100 μm. It did not appear necessary to sample units in 100 μm intervals since with micropipettes (unlike low-impedance tungsten electrodes) it is always possible to identify successively recorded responses as coming from the same or different neurons. The electrode was pointed medially and deviated from vertical by an angle of 30–40 deg, thus following one bank of the sulcus from top to bottom. Some penetrations traversed the suprasylvian sulcus and contained recordings from both its banks. The right hemisphere was used in all but one animal, so that most cells had receptive fields in the left hemifield (Palmer et al. 1978). Responses were assessed by listening to an audio-monitor and by recording triggered spikes with a PDP 11/34, which delivered on-line raster displays and averaged peristimulus-time histograms (PSTHs).

Light stimulation

The positions of retinal landmarks (optic disk and area centralis) were projected onto the tangent screen with a Zeiss fundus camera. For specific testing of binocular interactions both areas centrales could be made to overlap, using Risley prisms. Visual stimuli consisted of spots and bars of various sizes with a luminance of 2.5 cd/m² that were projected onto a tangent screen of 0.1 cm² luminance. The position and size of the receptive field were determined for each isolated cell and marked on the screen. Among other parameters optimal spot size, optimal velocity, velocity tuning, ocular dominance, directional tuning and response quality were determined.

Special attention was given to assessment of preferred direction of a moving stimulus: analysis was usually started with a handheld projector and in most cases, especially unclear ones, followed by quantitative measurements with a computer-controlled optical bench system. PSTHs were produced for at least 8, sometimes 16 directions of movement from 10 or more runs in each direction. Runs in one direction were always interleaved with runs in the opposite direction. Directions (in degrees) were defined as follows: 0°-horizontal to the right, 90°-vertical up, 180°-horizontal to the left, 270°-vertical down, etc. Categories were separated by 22.5 deg. Preferred direction was designated as the direction of movement which gave the maximal number of spikes per sweep. Directional tuning borders were determined from those two directions of stimulus movement that just failed to elicit an increase in discharge rate. Cells for which such tuning borders could be determined, independent of their tuning width were called “directionally selective” (DS). If a cell responded to all directions, but did show one preferred direction, it was termed “directionally biased”. The combination of hand-plotting and quantitative analysis seems to us a fair compromise between purely quantitative data collection and the need for representative cell samples (see Rauschecker and Singer 1981).

Electrical stimulation

Pairs of bipolar concentric electrodes (Rhoades; resistance 100 kΩ) with a core-sleeve separation of 1 mm were stereotaxically positioned in the corpus callosum (CC) of one animal, optic chiasm (OX) of two animals, and the ipsilateral visual thalamus (LP-pulvinar complex [LP] and lateral geniculate nucleus [LGN]) of three animals (Fig. 1A). A linear array of four electrodes was lowered 15 mm deep from the cortical surface for thalamic stimulation in frontal plane A6 with a lateral spacing of 2 mm between them. LP electrodes situated medially at L5 and L7 and LGN electrodes laterally at L9 and L11 (Fig. 1B). Stimulation was possible either between the tips of each pair of electrodes or (as was usually the case) between core and sleeve of a single electrode, each pair being connected in parallel. The final placement of the electrodes was guided by functional criteria (cf. Singer et al. 1975). The placement of the OX electrode was judged from the charac-