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Visual, Auditory and Bimodal Activity in the Banks of the Lateral Suprasylvian Sulcus in the Cat*

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In addition to visually driven cells we found within the lateral suprasylvian visual cortex of cats a considerable number of auditory and/or bimodal cells. Most of the visually driven cells were direction and orientation selective with responses that were neither highly stimulus time locked nor very stable. Most of the auditory responses were also not very stable, had relatively high thresholds, and were readily habituated. Previous studies have suggested that populations of cells within the lateral suprasylvian area are specialized for the analysis of optic flow fields (Rauscheker et al., 1987; Sherk et al., 1995). Given that a remarkable proportion of cells within this area can be also driven by auditory stimuli, we hypothesize that the 'optic flow' model may be extended to the bimodal domain rather than restricted to visual clues only. This, however, remains to be corroborated experimentally.

KEYWORDS: Cortex, suprasylvian area, visual, auditory.

INTRODUCTION

Several investigators have described regions in the posterior medial bank of the suprasylvian sulcus of the cat extrastriate cortex as being responsive to visual stimulation (e.g., Clare and Bishop, 1954). These areas have been divided into six separate regions, roughly arranged in space as three symmetrical mirror pairs, separated by the fundus of the middle or posterior sulcus (Palmer et al., 1978): a posteromedial and posterolateral (PMLS and PLLS) pair (the largest); an anteromedial and anterolateral (AMLS and ALLS) pair; and the dorsal and ventral lateral suprasylvian areas (DLS and VLS). The mutual connection of these areas to the thalamus and to other cortical areas has been comprehensively explored (see review by Scannell et al., 1995). However, studies of their response properties to visual stimuli are scarce and limited mainly to the PMLS and PLLS. It has been shown that cells in these areas have relatively large receptive fields and strong direction selectivity to moving light stimuli (Hubel and Wiesel, 1969; Wright, 1969; Spear and Baumann, 1975; Camarda and Rizzolatti, 1976; von Grünau et al., 1987; Zumbroich and Blakemore, 1987; Sherk and Mulligan 1993, 1995; Kim et al., 1997; Mulligan et al., 1997; Brenner and Rauscheker, 1990). Cells in these two areas also tend to respond best to light stimuli that retreat centrifugally from the area centralis (Rauscheker et al., 1987).

Recently we found that visual receptive fields in the ALLS and AMLS too are large, and their boundaries are hard to define. Many of the responding cells habituated quite readily through repeated visual stimuli (Yaka et al., 1999). Since all three pairs receive afferents from the anterior ectosylvian cortex (AE) (Scannell et al., 1995), where

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different sensory modalities are known to coexist (Reinoso-Suárez and Roda, 1985), we hypothesized that these visually considered areas receive input from other sensory modalities as well. Indeed, in this study we provide electrophysiological evidence that the PLLS, PMLS, ALLS and AMLS are not exclusively visual areas, but can also be activated by auditory stimuli.

MATERIALS AND METHODS

A total of 14 adult cats were used in this study. Deeply anesthetized cats (Ketamine HCl 25 mg/kg, Rompun 10 mg/kg, i.m.), held in a stereotaxic apparatus by means of hollow ear bars, were tracheotomized, and a craniotomy was performed over the suprasylvian area (Fig 1A). Subsequently the animals were slightly anesthetized by a continuous i.m. administration of thiopentone sodium (3 mg/hr), and iv infused with a mixture containing gallamine triethiodide (7.5 mg/kg/hr, in order to avoid eye movements while mapping visual receptive fields), atropine (1.25 μg/kg/hr), potassium chloride (4.0 mg/kg/hr), isoproterenol HCl (Isuprel 6 μg/kg/hr), and dextrose-saline solution (2 ml/kg/hr). Cats were artificially respirated and body temperature, ECG rate, urine volume, and expiratory CO_2 levels were constantly monitored and kept within the physiological range.

Single unit activity was extracellularly recorded by means of epoxylite coated tungsten microelectrodes (impedance: 4–5 MΩ at 1.0 kHz) that were advanced perpendicularly to the cortical surface by a calibrated hydraulic microdrive. Action potentials were monitored audiovisually, amplified, discriminated from background activity, digitized, and stored for off-line analyses on a PC.

Visual stimuli consisted of light spots and bars (410 lumens/m^2) that were produced by a computerized optical stimulation system, projected on a tangent opaque glass screen placed 1 m in front of the cat. Stimuli, of various angles, directions, velocities, and duration were presented binocularly and to each eye separately on a homogeneous background luminance of 0.7 lumens/m^2. Auditory stimuli consisted of clicks generated by 0.1 ms square pulses, broad band (0.5–20 kHz) white noise, pure tones (0.1–35 kHz) presented in sequential steps of 0.2–1 kHz, and frequency modulated (FM) tones swept from 0.1 to 20 kHz and backwards at a constant rate of 199 kHz/sec. The noise, pure tones, and FM tones were shaped into 200 ms bursts by a trapezoidal wave form with 15 ms rise and fall time. Stimuli were power amplified and delivered binaurally through calibrated earphones. The latter were located at the outer apertures of the hollow ear bars and attached to them by means of a short plastic tube. Calibration of the sound delivery system was accomplished by simulating the experimental conditions.

Determination of recording sites was based on electrolytic lesions made along the last penetration track. At the end of the experiment the animals were deeply anesthetized with an overdose of pentobarbital sodium and perfused through the carotid artery first with 0.9% saline/heparin followed by 10% neutral buffered formalin. Cresyl violet stained coronal sections (frozen or paraffin) were used to assign recording sites. For detailed procedures see Yaka et al., 1999.

All surgical and experimental procedures were performed in accordance with the guidelines issued by the Tel Aviv University Animal Care and Use Committee.

RESULTS

The borders between dorsal aspects of the four areas under investigation and the adjacent overlying cortical areas have not been distinctly defined. Our own attempts to determine these borders by cytoarchitectonic criteria, using Nissl stain, also yielded ambiguous results. Thus, we defined these boundaries electrophysiologically by the appearance of the first visually driven cell. On the basis of this criterion, our total neuronal sample consisted of 831 cells: 235 in the ALLS, 259 in the PLLS, 179 in the AMLS, and 158 in the PMLS. Figure 1A is a schematic overview of a cat's right hemisphere illustrating all our electrode penetration sites. A single penetration track is illustrated in Fig. 1B.

Strikingly, although these four areas are commonly considered to be strictly visual, all of them also possessed cells that responded to auditory stimuli, or to both auditory and visual stimuli (bimodal cells). The responsiveness profiles of all the cells in the four areas are summarized in Table 1. It is evident that about half of the cells, in all four areas, responded to at least one of the stimuli we used, with the AMLS being the most responsive area. Had we used a larger repertoire of stimuli, it is probable that responsiveness would have been even greater. The relative number of auditory cells was quite considerable in all four areas, with the ALLS being the most auditorily activated area and the PMLS being the least activated. No distinction was made, in this analysis, with respect to the location of the cells in the different cortical layers. However, their depth from the upper cortical surface was determined and the results of this analysis are depicted in Fig. 1C.

It is apparent that the relative number of strictly visual cells in the ALLS and PLLS increased systematically towards the fundus, whereas the distribution of auditory cells showed an opposite pattern. In the AMLS and PMLS this pattern was less pronounced. In all four areas only a very small proportion of bimodal cells was found, with a somewhat larger representation of such cells in the AMLS and PMLS. It seems, therefore, that regarding these prop-

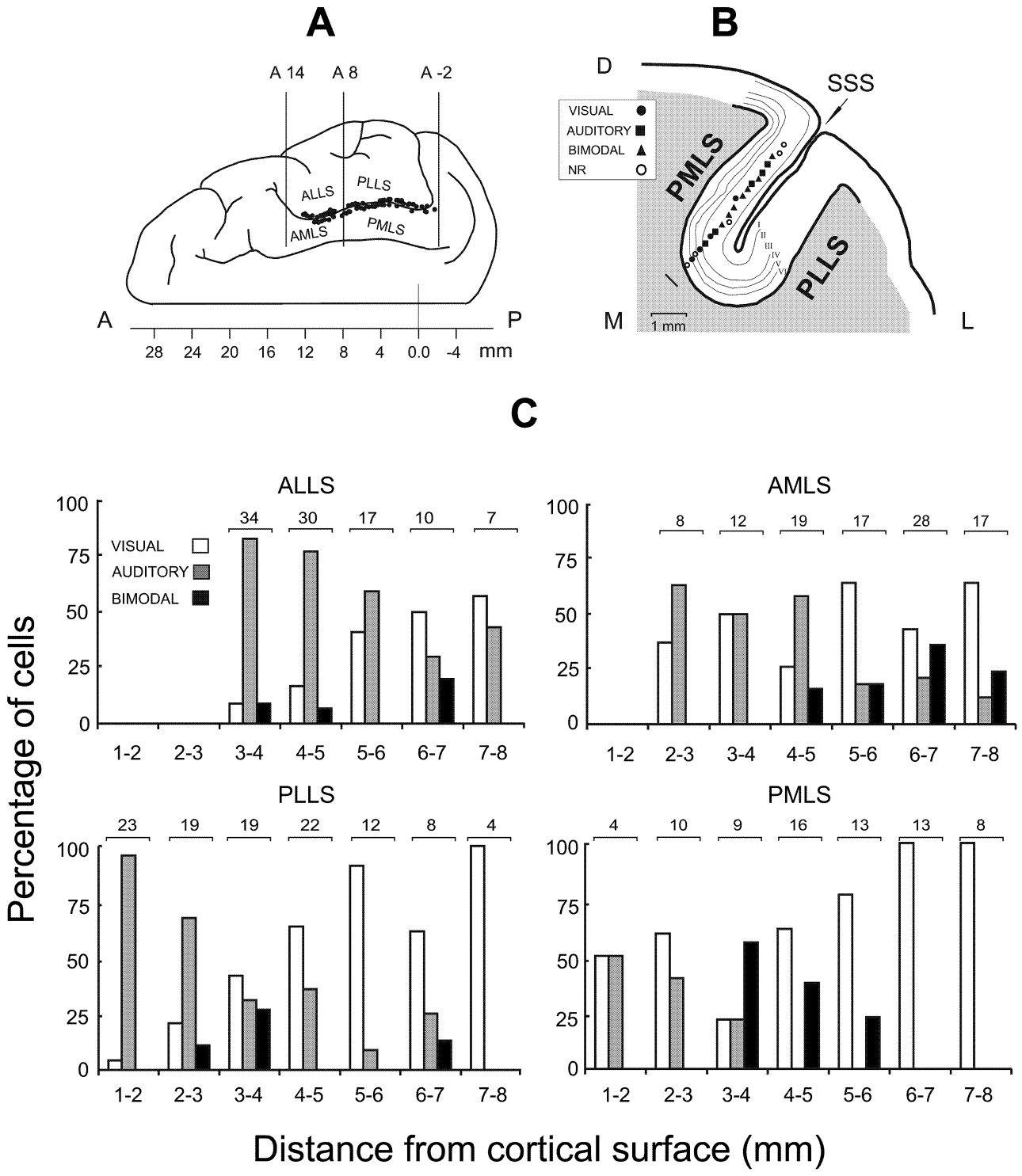

Fig. 1. Responsiveness of cells to visual and auditory stimuli according to their depth from the cortical surface. *A*) a dorsal view of the cat's brain indicating electrode penetration sites (referred to Horsley–Clarke coordinates). A – anterior; P – posterior. *B*) a coronal section through the posterior suprasylvian area (at A4) illustrating a reconstructed electrode penetration and responding cells locations. M – medial; L – lateral. Roman numerals refer to the various cortical layers. NR – no response. SSS – suprasylvian sulcus. *C*) bargraphs depicting distribution of responding cells, in the four explored areas, according to their response and depth from the cortical surface. Numbers above each group of bars designate the total number of cells within each depth. Responsiveness to each stimulus is expressed relative to the total number of responding cells at each depth. PMLS – posteromedial lateral suprasylvian area; PLLS – posterolateral lateral suprasylvian area; AMLS – anteromedial lateral suprasylvian area; ALLS – anterolateral lateral suprasylvian area.

TABLE 1. Responsiveness of Cells to Visual and Auditory Stimuli in the Four Explored Areas

Area	No. of cell	Responding cells	Visual cells*	Auditory cells*	Bimodal cells*
Anterolateral lateral suprasylvian area	235	98	25	68	7
Posterolateral lateral suprasylvian area	259	107	44	49	7
Anteromedial lateral suprasylvian area	179	101	47	33	20
Posteromedial lateral suprasylvian area	158	73	70	11	19

* Values are expressed as percentage of the total number of responding cells in each area, rounded to the nearest whole number.

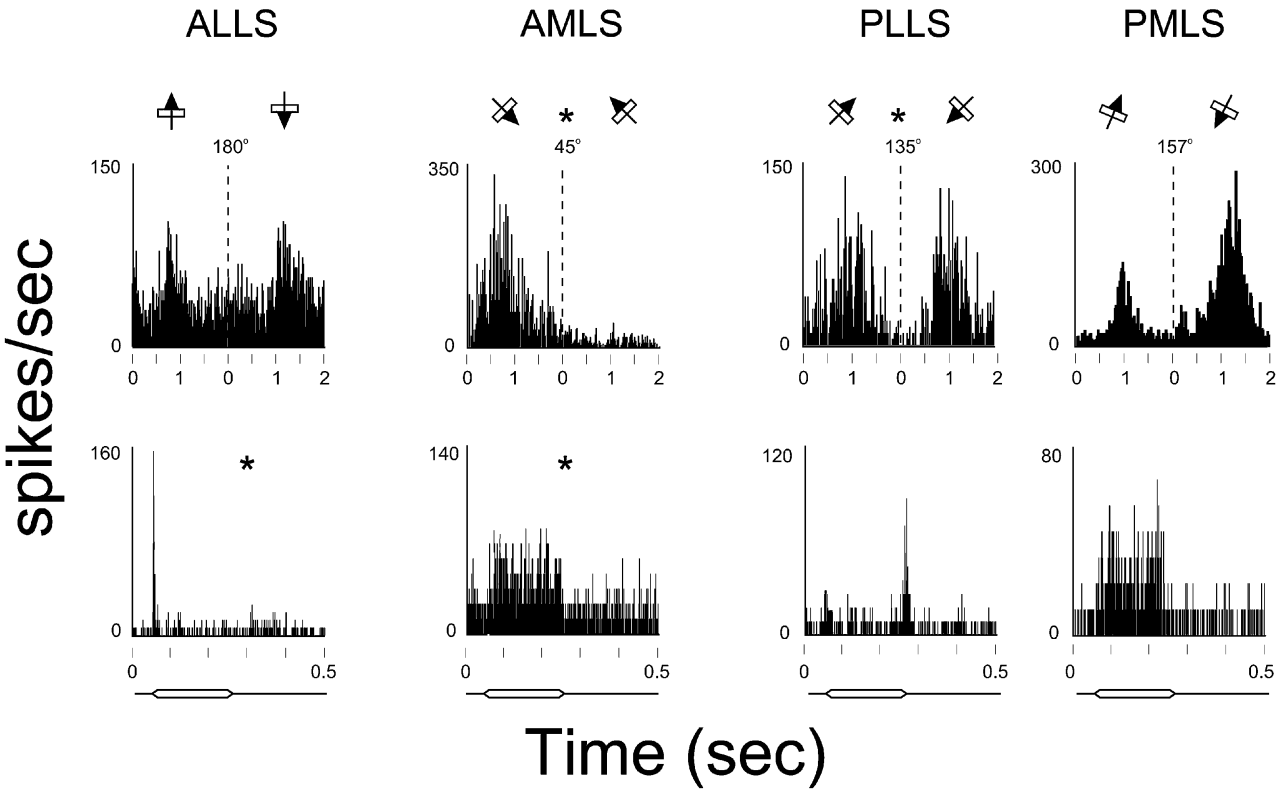

Fig. 2. Peristimulus time histograms (PSTHs) illustrating responses of cells to visual (upper row) and auditory (lower row) stimuli. Visual stimuli consisted of moving light bars, and auditory stimuli were pure tone bursts at the best frequency of the cell. Rectangular boxes and arrows at the top of the visual responses indicate preferred orientation of the cell and direction of the moving bars, respectively. The timing of auditory stimulus is indicated by the envelope of the stimulus at the bottom of the PSTHs. Asterisks designate bimodal cells. PMLS – posteromedial lateral suprasylvian area; PLLS – posterolateral lateral suprasylvian area; AMLS – anteromedial lateral suprasylvian area; ALLS – anterolateral lateral suprasylvian area.

erties, the anterior and posterior areas on one side of the suprasylvian sulcus show greater resemblance than their 'partners' on the other side of the sulcus.

Figure 2 illustrates visual and auditory responses of exclusively visual, exclusively auditory, and bimodal cells. Most visually driven cells, in all four areas, were direction and orientation selective (see also Palmer et al., 1978). However, the responses were less stimulus time locked as compared to area 17 and not always very stable. In many cases this caused some difficulty in delineating the exact borders of visual receptive fields, which typically were much larger than those characteristic of A17 cells (Yinon et al., 1994). The mean RFs areas (±SD) in degrees^2 were: ALLS – 249.4 ± 157.3; PLLS – 148.2 ± 98.4; AMLS – 89.0 ± 68.5; PMLS – 124.2 ± 92.9.

Many of the responses to auditory stimuli, as evaluated by eye inspection, were also not very stable and were readily habituated. Of the various auditory stimuli that we applied, pure tones were the least effective and tuning curves were usually quite flat with relatively high thresholds. Frequency modulated tone bursts and white noise bursts were the most effective.

DISCUSSION

Although some multisensory neurons have been found previously in the most rostral aspect of the lateral suprasylvian (LS) cortex (Stein et al., 1993), the banks of LS are generally considered to be strictly extrastriatal visual areas. In this study we demonstrated that in addition to exclusively visual cells, the ALLS, AMLS, PLLS and PMLS also contain a remarkable proportion of auditory and auditory/visual bimodal cells. We did not examine whether these areas could also be activated by somatosensory stimuli. However, since they receive afferents from polysensory areas such as the anterior ectosylvian sulcus (AES) (Scannell et al., 1995), it would not be too surprising if these sensory modality were also to be found there.

The function of the lateral suprasylvian cortex in the processing of sensory information is still obscure. It has been shown that the information that LS neurons convey to the superior colliculus is primarily visual. However, in the light of our findings the possibility that other sensory modalities are also conveyed cannot be ruled out (Wallace et al., 1992). Hence, it is reasonable to assume that auditory information in addition to visual information probably plays a role in modulating the activity of the superior colliculus cells.

It has been suggested that there are two distinct cell populations within the LS, both located on the medial bank of the suprasylvian sulcus and separated by a gap of about 2 mm: one located anterior to Horsley-Clarke A2 level (within the PMLS area) and the other posterior to it (Sherk and Mulligan, 1993, 1995; Kim et al., 1997; Mulligan et al., 1997; Brenner and Rauscheker, 1990). The first population comprises cells with radial-outward preferred directions and is apparently engaged in the visual analysis of moving scenes or objects (defined as "optic flow" cells). The second population consists of cells that prefer directions orthogonal to radial. Neurons, which most probably play a major role in the processing of visual motion, have also been recently isolated in the medial superior temporal area (MST) – an extrastriate visual cortex, of the macaque monkey (Wurtz 1998; Eifuku and Wurtz 1998).

We did not conduct similar experiments in the ALLS and AMLS. However, the similarity in the cellular response properties in these areas to those of the PLLS and PMLS, in their connectivity patterns and in their close spatial vicinity, argues for the possibility that the ALLS and AMLS too are somehow involved in the visual detection of a relative movement of an object towards or away from an observer. If indeed this is so, it is not unlikely that cells in these areas use both modalities for that purpose.

The ability of an observer to detect moving subjects has an extremely high survival value especially when considering interaction with conspecifics, predators, or prey. Using auditory clues in addition to visual ones while performing such a task would thus have an obvious advantage. Some analogy, in this respect, can be made with long-standing but generally neglected findings (Morrell et al., 1972; Fishman and Michael, 1973), showing that some neurons in cortical visual areas in the cat respond to both visual and auditory stimuli. Moreover, it has been shown that visual and auditory spatial receptive fields for many of these cells match, suggesting a synergistic effect of the two sensory modalities in the spatial localization of an object. However, in order to prove this working assumption, specifically designed experiments remain to be performed.

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