ACTA NEUROBIOL. EXP. 1983, 43: 251-262

RETINOTOPIC ORGANIZATION OF THE LATERAL SUPRASYLVIAN AREA OF THE CAT

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Key words: retinotopic organization, receptive field, lateral suprasylvian area

Abstract. The retinotopic organization of the lateral suprasylvian area (L.S.A.) was investigated by microelectrode recording from single neurons. 560 penetrations were made on the medial and lateral banks of the middle suprasylvian sulcus (M.S.S.). The receptive field positions of single neurons were mapped in relation to the retinal landmarks. A striking variability of the visuotopic organization from one animal to another was observed. The most persistent organization was the representation of the lower contralateral quadrant of the visual field in the rostral and middle parts of the L.S.A. and a slight shift to the upper contralateral quadrant of the visual field in the posterior regions of the L.S.A.

INTRODUCTION

Hubel and Wiesel (5) in earlier investigations of the functional significance of the Clare-Bishop area have demonstrated that this area has a retinotopic organization of the visual field with the representation of mainly the lower quadrant of the contralateral hemifield. Later Palmer et al. (6) have shown that the lateral suprasylvian area (L.S.A.) of the cat's cortex posseses a precise representation of the visual space. On the basis of these investigations the entire L.S.A. was divided into six parts, i.e., three symmetrical pairs on the lateral and three on the medial bank of the middle suprasylvian sulcus (M.S.S.).

Turlejski and Michalski (9) and Spear and Baumann (8) who also investigated the visuotopic organization of the L.S.A., have observed a great variability of results. We have also come across this problem in our preliminary experiments. Thus, the retinotopic organization of the L.S.A. as a functional unit of the cortical structure, evidently needs further investigations with a special attention to the variability of results.

The present investigation was designed to obtain additional information on the retinotopic organization of the L.S.A.

METHODS

The experiments were conducted on 35 adult cats with body weight ranging between 2.5 and 3.5 kg. Tracheotomy, cannulation of the femoral artery and fixation of the animal's head in the stereotaxic apparatus (Horsley-Clarke, modified for visual research) were performed under ether anesthesia. Pretrigeminal brain stem sections were made (11) and after an application of the myorelaxant Ditilin (diiodide dicholine ester of succinic acid) 7 mg/kg, artificial respiration was administered (stroke volume 20 ml/kg, 19 strokes/min). The skull bone above the left M.S.S. and adjacent cortex was removed and the window thus obtained was filled with a 3% Agar solution in physiological saline. The body temperature was kept at 37.5°C by a heating pad. EEG and ECG were monitored continuously and the mean blood pressure was sporadically measured at 80–100 mm Hg. The eyelids were removed and corneas, after an administration of 0.1% atropine sulfate for pupillary dilation were covered by "0" power contact lenses. Throughout the experiment additional lenses of a suitable power were placed in front of the eyes to focus them on the perimeter screen.

The screen was situated in front of the eyes at a distance of 78 cm from the nodal points. It was a 90° section of a concave hemisphere with a mechanical system allowing the position of the screen to be shifted in the horizontal and vertical planes over 180° so that the whole visual field be available for exploration. Retinal landmarks were plotted on the screen by the method of Fernald and Chase (1).

Tungsten microelectrodes (4) covered with vinyl varnish were used. Their tip diameter was 2–5 μm. The L.S.A. was explored with a series of microelectrode penetrations at 1–2 mm intervals, with the longitudinal electrode shift tilted laterally 30–45° from the vertical. The medial and lateral banks of the M.S.S. were explored within the limits of A-14 and P-2 (left hemisphere). The positions of receptive fields of single neurons were determined in each penetration. All receptive fields were defined for the contralateral eye only. Multineuronal responses were investigated in a special series of experiments.

In each penetration the first and last points of recording were electrically coagulated (0.6 μA, 30 s.). After each experiment the brain was perfused initially with physiological saline followed by 10% formalin solution. After a proper fixation of the brain, histological verification and reconstruction of microelectrode tracks were made. The 30–40 μm (frozen cut) histological sections were subsequently stained with Cresyl Violet and photographed.

RESULTS

560 penetrations were performed along the whole length of the M.S.S. symmetrically on its medial and lateral banks. Positions of the receptive fields of 3 or 4 neurons in each penetration were defined by hand-held black figures with an accuracy of ±1°. Despite of numerous experiments we could not find two cats with identical retinotopic organization of their visual fields in the L.S.A. cortex. Thus special attention was paid to the variability of the results and this was the reason why we exclude the combined figures with data taken from different experiments. Furthermore, our results show that it is extremely difficult to outline a precise topography of the L.S.A. and one could speak only about trends in its retinotopic organization.

The neurons of the frontalmost parts of the L.S.A., between A-14 and A-11 generally displayed unstable reactions to the visual stimuli and often no visually-driven neuron could be recorded from the entire penetration track. Therefore, the figures presented in this paper show only the data collected within the limits of A-10 to P-2.

The positions of the receptive fields of neurons picked up in penetrations of the anterior portion of the L.S.A. (A-10 to A-6) are shown in Fig. 1. Three coronal sections of the cortex are presented together with the reconstructed tracks of electrodes. In one penetration on the lateral bank (A-6) no visually sensitive neurons were found. It is clearly seen from the Figure that a majority of receptive fields are located close to the horizontal meridian and the deeper is a neuron situated in the sulcus, the lower is the position of its receptive field (Fig. 1 *A–E*). The receptive fields of neurons located in the rostral M.S.S. were shifted slightly towards the upper quadrant of the visual field near the level of the horizontal meridian (Fig. 1 *A*, *B*). In the same penetrations the receptive fields of neurons situated deeper in the sulcus were still

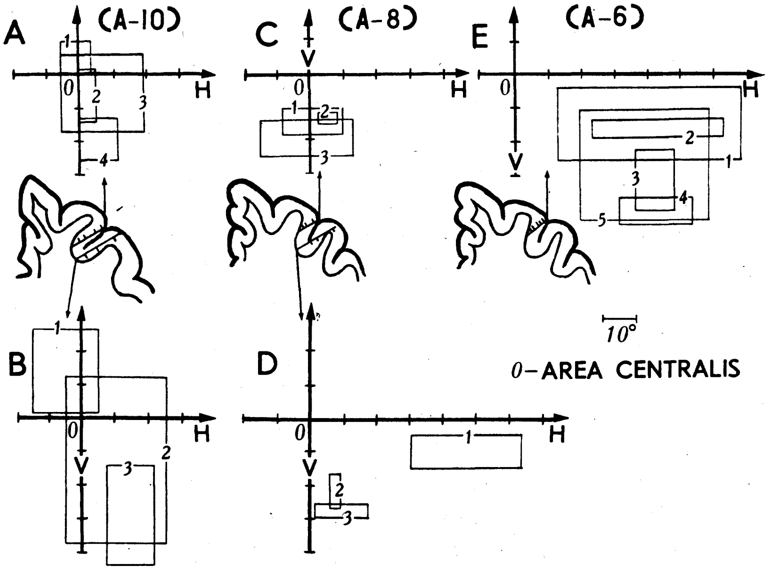

Fig. 1. Three coronal sections through the cat cortex showing reconstructed microelectrode penetrations through the anterior L.S.A. Sections proceed from rostral A-10 to caudal A-6. The receptive field plots are associated each section, those above the sections show receptive fields for points on the medial bank (*A*, *C*, *E*), those below the sections show receptive fields for points on the lateral bank (*B*, *D*). The central point "0" of the coordinates indicates the position of the "area centralis". H, horizontal meridian; V, vertical meridian. The numbers on the receptive fields correspond to the successive numbers of neurons recorded during the microelectrode penetration through the cortex. All indications are the same for the subsequent figures.

located lower than the horizontal meridian. Such a tendency of retinotopic organization is most commonly observed in the L.S.A. In other experiments, however, a different situation could be observed. For example, results of another experiment are presented in Fig. 2. The *H–C* coordinates of penetrations were the same as in Fig. 1 but, as seen from the Figure, almost all the receptive fields were located below the horizontal meridian except one (Fig. 2*A*). A penetration of the lateral bank at A-6, unlike those of the previous experiment, revealed visually-driven reactions of neurons. Besides, there is a rather bizarre distribution of the receptive fields independently of the positions of neurons throughout the cortex along the penetration track of the microelectrode. The neurons situated at the fundus of the sulcus could have their receptive fields positioned at the more peripheral region of the visual field than the superficial cells (Fig. 2 *A*, *D*).

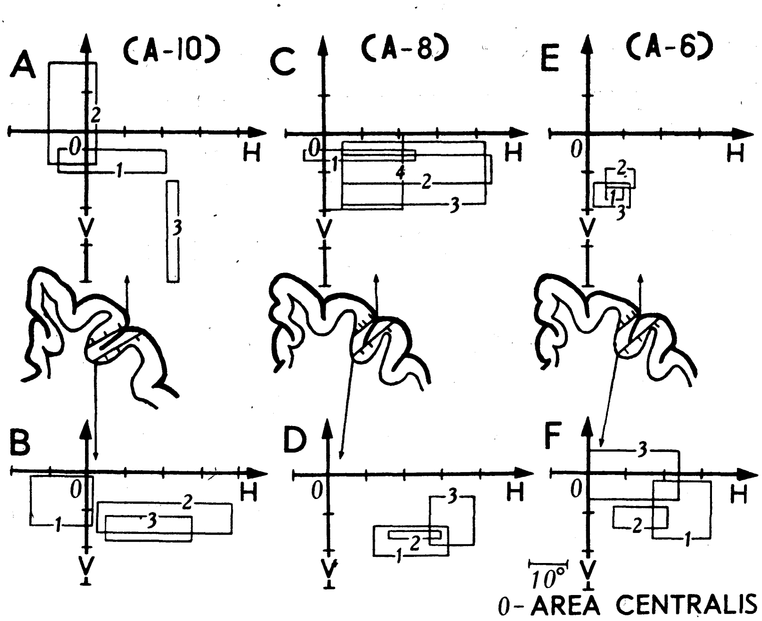

Fig. 2. Three coronal sections through another cat's cortex showing reconstructed electrode penetrations through the anterior L.S.A. Sections proceed from rostral A-10 to caudal A-6.

Figures 3 and 4 present the results of two different experiments showing the positions of the receptive fields in the medial and lateral banks of the M.S.S. (from A-5 to A-2). Penetrations were made at the same *H–C* coordinates in both cases. As seen from Fig. 3 all the receptive fields of the medial bank of the M.S.S. were situated in the lower quadrant of the visual field below the horizontal meridian whereas in the lateral bank, the third penetration (Fig. 3*F*) shows a receptive field situated at its level. In another experiment (Fig. 4) the same coordinates of penetrations revealed a somewhat different picture. The receptive fields are located below the horizontal meridian in all penetrations, without any exception. Thus, in this region of L.S.A. (from A-5 to A-2) the most stable organization in the visual field representation seems to exist.

The caudal part of the L.S.A. was investigated in four symmetrical penetrations from P-1 to P-2. The most characteristic organization of this part of L.S.A. was the position of receptive fields near, or on, the level of horizontal meridian and their slight shift to the vertical meridian caudally. Figure 5 presented four penetrations of the PLLS and PMLS areas (posterolateral and posteromedial L.S.A.) in two different experiments (Fig. 5*A*, *B*) which represent the most typical visuotopic organization

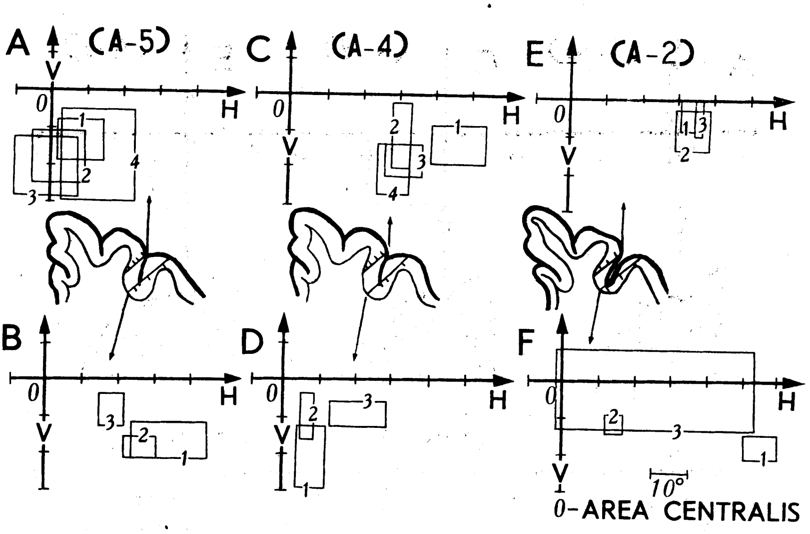

Fig. 3. Three coronal sections through the cat cortex showing reconstructed microelectrode penetrations in the middle part of L.S.A. Sections proceed from rostral A-5 to caudal A-2.

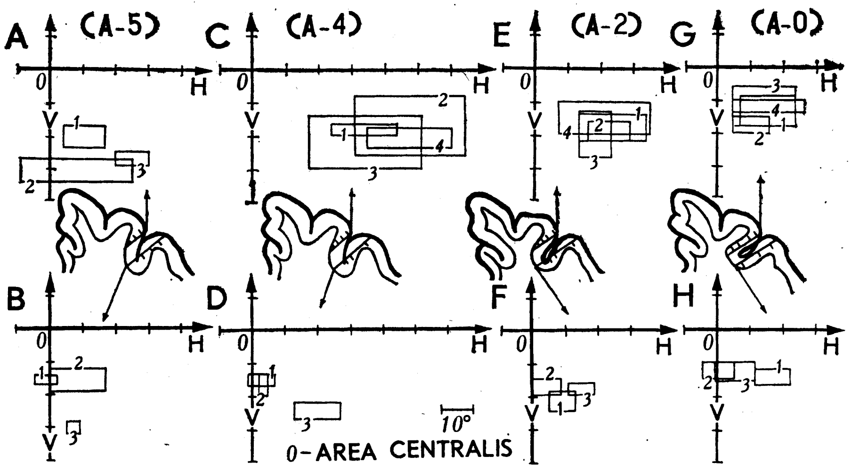

Fig. 4. Four coronal sections through another cat's cortex with the reconstructed tracks of electrode penetrations in the middle part of L.S.A. Sections proceed from rostral A–5 to caudal A-0.

of this part of the L.S.A. Some differences between the two experiments could still be observed. In Fig. 5*A* the first penetration (*H–C* P-1) shows the receptive fields to be located below the horizontal meridian,

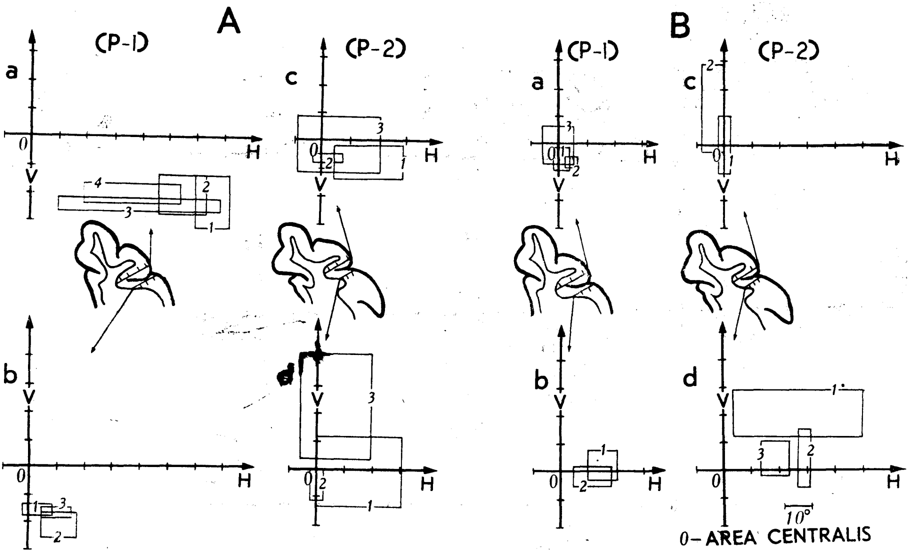

Fig. 5. Four coronal sections through the cat cortex showing reconstructed microelectrode penetrations through the posterior L.S.A. in two different experiments (*A* and *B*). Sections proceed from rostral P-1 to caudal P-2.

both in the medial and in the lateral banks of the M.S.S. In contrast, the receptive fields found in penetrations performed according to the same coordinates in the next experiment (Fig. 5*B*) are located at the level of the horizontal meridian close to the Area centralis.

Figure 6 shows the results of an experiment where the penetrations along the entire L.S.A. (from A-10 to P-2) were performed. This type of retinotopic organization is the most characteristic for the L.S.A. As seen from Fig. 6 all neurons of the medial bank of the M.S.S. have their receptive fields located below the horizontal meridian, and close to the vertical meridian. On the contrary, symmetrical penetrations of the lateral bank in the rostro-caudal direction show the displacement of the receptive fields from the lower portion of the visual field to its upper part. The distribution of the receptive field centers (Fig. 6*a–g*) reveals such an organization more clearly. In all experiments the only tendency seen in the retinotopic organization of the L.S.A. is that its anterior part is mainly devoted to the lower quadrant of the visual field and posteriorly a slight tendency exists for the upper quadrant of the visual field to be represented.

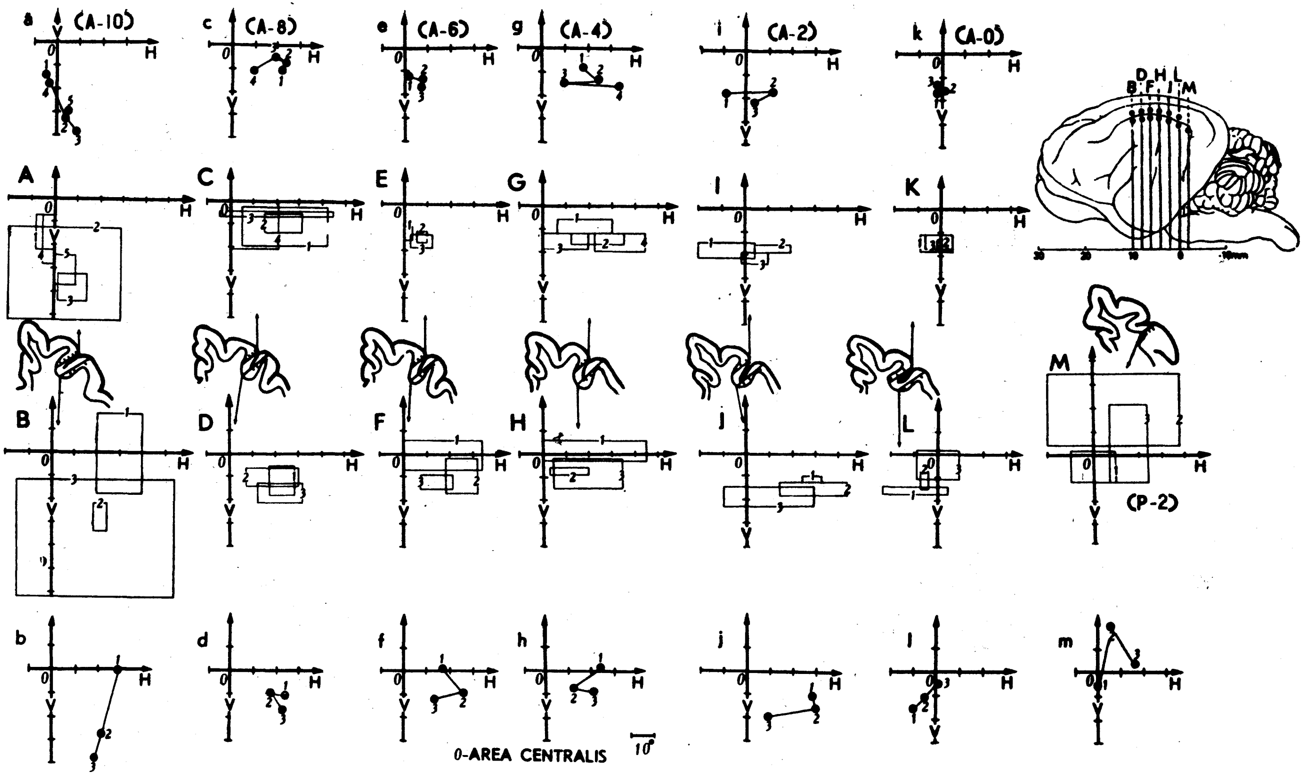

Fig. 6. Seven coronal sections through the cat cortex showing the reconstructed tracks of electrode penetrations successively from rostral A-10 to caudal P-2. The distribution of the receptive field centers are presented alongside the receptive field plots corresponding to each penetration and indicated by small letters (*a*–*k* and *b*–*m*).

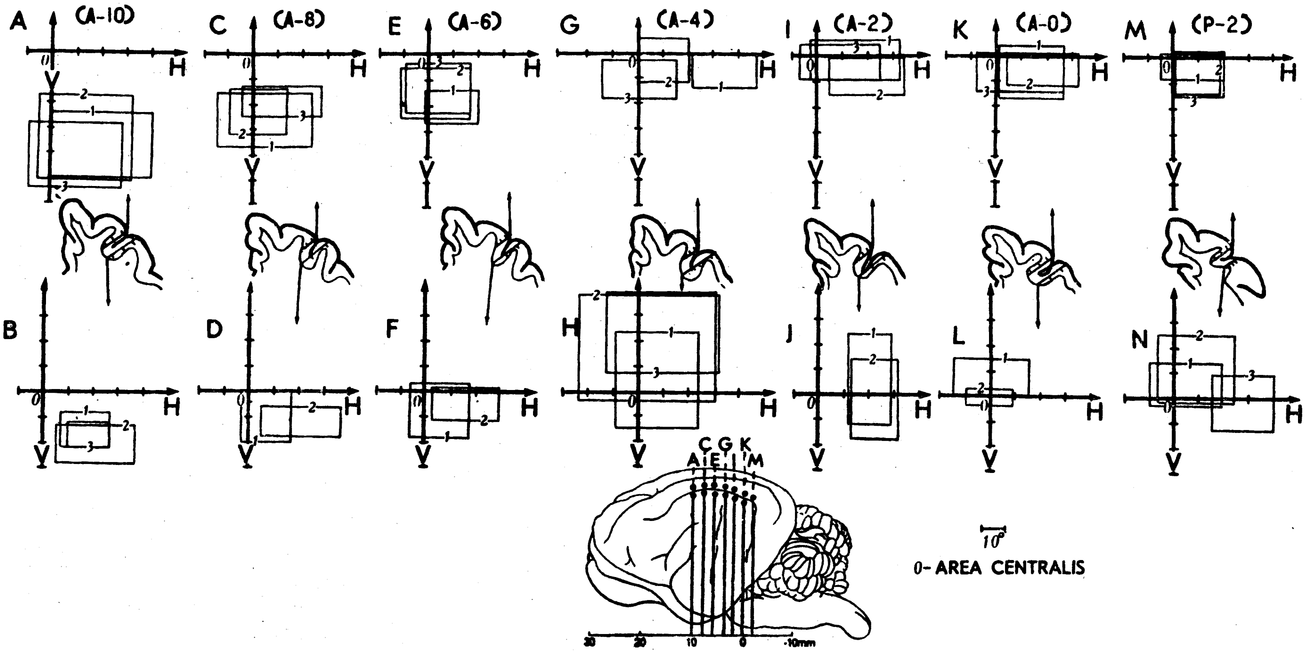

Fig. 7. The "swish-fields" (see Results) recorded at different levels of the electrode penetration through the cortex. Seven coronal sections through the cat cortex show the reconstructed tracks of the electrode penetrations. Sections proceed from rostral A-10 to caudal P-2.

In another series of experiments we analyzed the multineuronal (multiunit) receptive fields. In each penetration the area on the screen was defined from where the multiunit responses, the so-called "swish" reaction, could be elicited. The "swish" consists of light-modulated spike responses of numerous cells with the receptive fields located in a certain part of the visual field near each other. We called them "swish-fields". The estimations of boundaries of the "swish-fields" were made at three points along the cortical microelectrode track. The first recording was made at the beginning of the electrode track, the second one — half-way to the bottom of the M.S.S. and the last one was generally the lowermost point of recording. Such an approach allowed one to obtain a more integrated profile of the visual space representation in the entire L.S.A. Figure 7 illustrates the results of one such experiment. The penetrations were conducted along the medial (A-M) and lateral (B-N) banks of the M.S.S. A regularity in representation of the visual field in the L.S.A. is more pronounced in the results shown in Fig. 7. The lower quadrant of the visual field is represented in the medial bank of the anterior part of the M.S.S. (from A-10 to A-6). Beginning from A-4 up to P-2 where the L.S.A. almost ends, the visual field around the horizontal meridian is represented. The changes on the lateral bank are more dynamic. Only in the two anteriormost (A-10 and A-8) penetrations the lower quadrant of the visual field is represented. At the level of A-6 the "swish-fields" shift to the level of the horizontal meridian and from A-4 to A-2 the upper quadrant of the visual fields is represented. In penetrations at A-0 the "swish-fields" again shifted slightly down to the level of the horizontal meridian (Fig. 7*L*).

DISCUSSION

Turlejski and Michalski (9) in their paper on the visuotopic organization of the L.S.A. have emphasized the differences of the visual field representation in this part of the visual cortex from animal to animal. This fact has complicated the attempts of the investigators to find out any regularities in the representation of the visual field in the L.S.A. Spear and Baumann (8) and Palmer et al. (6) mention the variability of their results. Nevertheless, a sketch of visuotopic organization was outlined by the authors. According to the data of Palmer et al. (6), the anterior part of L.S.A. cortex represents mainly the visual field around the peripheral parts of the horizontal meridian, disal from Area centralis. The vertical meridian is represented mainly in the middle portion of the L.S.A. More caudally, the receptive fields are located at the level of the horizontal meridian within ±10° to 20° from the Area centralis.

The same authors observed that on the whole length of the M.S.S. the neurons situated deep at the bottom had their receptive fields close to the Area centralis. Thus, it was concluded that the bottom of suprasylvian sulcus represents the central vision (6).

It was very difficult to establish such a precise visuotopic organization in our experiments because of a great scatter in the receptive field sizes and their prominent overlap in space. We could not differentiate between the peripheral positions of the receptive fields in the rostral L.S.A. We have found that the visual sensitivity of neurons of the anterior L.S.A. within A-14 to A-12 is very unstable. Next, in the bottom of the M.S.S. we found not only neurons with the receptive fields close to the vertical meridian positioned deep in the sulcus. However, a retinotopic organization could be traced in the L.S.A. in our experiments. Thus, generally, the lower contralateral quadrant of the visual field is represented in anterior L.S.A. with the tendency of shifting to the upper one in the caudal part of the area. In the middle part of L.S.A. the receptive fields are positioned mainly at the level of the horizontal meridian. It was striking to find that the lateral bank of the M.S.S. appears to be organized in a more stable manner than the medial bank.

Thus, despite of the complicated afferent system of the L.S.A., which receives afferents from the lateral geniculate nucleus (10), from the primary visual cortex (7) as well as from the midbrain tectum (2) and the posterior lateral nuclei of thalamus (3), it appears to be organized in a more or less determined manner. This fact confirms its role as a functional unit in the central processing of visual information.

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