PROPERTIES OF VISUALLY SENSITIVE NEURONS IN LATERAL SUPRASylvIAN AREA OF THE CAT

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Abstract. Functional properties of neurons in lateral suprasylvian area were investigated by single unit recordings in unanesthetized cats with the brain stem pretrigeminal transection. Majority of cells in the lateral suprasylvian area responded vigorously to moving visual stimuli. Many of them were responsive only to the movement of black objects, without any reaction to the light stimuli, 78% of the observed neurons revealed direction selective properties, the remainder being direction non-selective. Seventy eight percent of neurons revealed well defined responses to stationary flashes of light and 26% showed multimodal type of responses to moving and stationary visual stimuli. The vertical organization of neurons in the lateral suprasylvian area was investigated. The present results indicate that a regular vertical organization of neurons exists in the lateral suprasylvian cortex of the cat.

INTRODUCTION

Marshall et al. (27) were the first to describe the electrical activity in lateral suprasylvian (LS) area of the cat brain evoked by stimulation of the optic nerve. Observations of Marshall et al. (27) were confirmed by Clare and Bishop (9), thus a new visually responsive structure was outlined in the cat's cortex outside the well known visual areas 17, 18 and 19. Later the new visual region in the cortex became known as the Clare-Bishop area.
Numerous morphological investigations (11, 14, 16, 23, 30, 33) concerning the afferent and efferent pathways of the lateral suprasylvian (LS) area and electrophysiological data (15, 21, 24, 25, 31, 37, 40, 41) dealing with the studies of visually evoked responses of this area have established that the visually responsive suprasylvian area occupies a zone along the banks of the middle and posterior suprasylvian sulci. The main visual input from the retina to the LS area comes via the pathways from the posterior lateral nuclear complex of the thalamus (14, 26, 33) and dorsal lateral geniculate body (26, 33). The LS area also receives afferents from cortical areas 17, 18 and 19 and from the contralateral LS area (23, 34, 35).

The lateral suprasylvian area plays an important role in the processes of visual discrimination in the cat (1, 3, 39, 42). Recently Berlucchi et al. (4) presented results of the experiments with lesions of suprasylvian area in cats and analyzed the behavioral deficits resulting from the operation. They came to the conclusion that the LS area plays an essential role in the learning processes and in the interhemispheric transfer of visual information.

Hubel and Wiesel (21), Turlejski (40, 41), Spear and Baumann (37), Heath and Jones (16) have experimentally established that the neurons in the lateral suprasylvian area are responsive to several kinds of visual stimuli and emphasized their great sensitivity to moving objects.

Our earlier observations on the single unit activity of the cat's lateral suprasylvian cortex revealed some peculiarities of the properties of visually sensitive neurons in this area (15, 24, 25) as compared to neurons of the other cortical structures involved in the central visual processing (5, 6, 10, 12, 13, 18, 20, 32). The present study includes further investigations of the properties of LS area neurons responsive to stationary and moving visual stimuli. Some of our results have been briefly reported in an earlier communication (25).

METHODS

Fifty two cats between 2.5–3.5 kg were used in the experiments. They were anesthetized with ether for the initial surgical procedure. Tracheotomy and cannulation of the radial vein and the femoral artery were performed. To avoid the use of anesthetics the brain stem pretrigeminal transection was done (2, 44). The head of the animal was fixed in the stereotaxic apparatus of Horsley–Clarke modified for visual research. After trepanation, the hole in the scull above the suprasylvian cortex was filled with a 3% agar in 0.9% NaCl solution. The immobilization of the animal was achieved by the intravenous injection of ditilin
(diiodide dicholin ester of succinic acid) 7 mg/kg. Artificial respiration was administered (19 strokes/min, stroke volume 20 ml/kg). The body temperature was kept at 38°C by a heating pad. The pupils were dilated by topical application of 0.1% atropine sulfate solution and corneas were protected with zero power contact lenses. In addition spectacle lenses were commonly used to achieve optimal focus of the eyes on the perimeter screen and these lenses were mounted just in front of the cat's eyes. Arterial blood pressure was continuously measured and maintained at 90-100 mmHg. The heart activity and EEG were monitored continuously.

The single unit activity was recorded after 2–3 h from the cessation of the ether anesthesia. Tungsten microelectrodes (17) covered with vinyl varnish with the tip diameter of 2–3 μm were used. The neuronal spikes amplified with conventional amplifiers and transformed into standard pulses were fed to an interspike interval analyzer (8, 22). Each action potential was displayed on the oscilloscope screen as a light dot. Ordinates in all figures indicated the length of interspike intervals, abscissae — the time of stimulation. The averaging was achieved by the repetition of stimulation 15–30 times.

The receptive fields of neurons were plotted on a concave screen covering 90° of visual angle and situated in front of cat's head at a distance of 78 cm from the nodal points of the cat's eyes. Position of the area centralis on the screen was plotted with the reversible ophthalmoscope (7).

Stimulation was performed by moving light spots of different sizes (1–10°) with the speed of motion 120–180 deg/s. The same light spots were used as stationary stimuli with the flashing rate 1/s (500 ms — light, 500 ms — dark). The intensity of spot and background illumination was measured by a luxmeter and ranged within 2–230 lx on the screen for the light spots. The background illumination was generally kept within 0.1–1 lx.

At the end of experiment coagulations were performed at two points of the electrode track: on the surface of the cortex and at the depth of 2 mm. Perfusion of the brain was done routinely and the electrode track was reconstructed after the examination of histological sections.

RESULTS

Among the visually sensitive cells nearly 22% responded only to the movement of black objects and did not react at all to any stationary or dynamic light stimuli. In this study functional properties of light stimuli sensitive neurons only are presented. One hundred fifty eight
neurons responsive to different kinds of visual stimuli were investigated in the first series of experiments.

The majority of neurons (56%) displayed spontaneous activity with the frequency of 1–30 imp/s. Ocular dominance was investigated in 151 neurons, 104 of which were excited exclusively from the contralateral eye and 47 were binocularly driven.

Responses to stationary stimuli. Flashing light spots positioned in the center of receptive field were used as stationary stimuli. Appropriate size of stimulus was selected according to the optimal response of the cell. Six neurons out of 158 were driven only by the stationary stimuli and did not react to moving light spots.

Seventy two percent of all visually reactive neurons observed were responsive to the stationary spot flash stimulation of their receptive fields. Eleven percent of neurons showed “sustained” type of activity to the light “on” or “off” (Fig. 1, A, B). Sixty seven percent of neurons reacted with the “transient” type of response (Fig. 1C–H). Twenty two percent of neurons have mixed “transient and sustained” responses.

![Fig. 1. Responses of different neurons to the stationary flashing light spots. A, B, sustained type of responses; A, an “off” unit and B, an “on” unit. C, D, transient “on” responses. E, F, transient “off” responses, G, H, transient “on-off” responses. The numbers in the middle of each frame indicate the size of light spot in degrees. The ordinates show interspike intervals, abscissae — the time of stimulation. In all cases 15 repetitions of stimuli were performed. The above explanations hold for Figs. 2–4.](image)

All neurons were classified according to the character of their responses into three types: (i) “on” neurons (16%) responding to light “on”; (ii) “off” neurons (31%) responding to light “off”; (iii) “on-off” neurons (53%) responding to both light “on” and “off” (Fig. 1). The size of optimal stimulus is different for different cells and varies from 2 to 10° of visual angle.
Responses to moving stimuli. The vast majority of cells in the lateral suprasylvian area (152 out of 158) is sensitive to the moving stimuli. Twenty eight percent of neurons showed sensitivity to the moving stimuli only and did not react to stationary ones. All movement-sensitive neurons were classified as follows: (i) directionally non-selective neurons; (ii) directionally selective neurons and (iii) multimodal neurons.

Directionally non-selective neurons. Forty three percent of the investigated neurons were directionally non-selective. These neurons responded with equal number of spikes to any direction of stimulus movement through the receptive field. Almost all directionally non-selective neurons were responsive to the stationary light flashes. The change of stimulus contrast did not affect the character of response of this group of neurons. As a rule discharges were evoked during all the time when the stimulus was sweeping through the receptive field. Figure 2 shows directionally non-selective responses of three different neurons to the movement of light spot through their receptive field. The receptive field of the neuron presented in Fig. 2A was of the magnitude of $45 \times 20^\circ$, the one in Fig 2B — $10 \times 10^\circ$ and the one in Fig 2C — $7 \times 5$ deg. There is no correlation between the size of receptive field and the type of response to moving stimuli. All three neurons were directionally non-selective and produced equal number of discharges to the two opposite directions of stimulus movement. Generally these neurons had the homogeneous structure of the receptive field without any asymmetries in the distribution of sensitivity to light stimuli all over the receptive field surface.

Fig. 2. Responses of six different units to the movement of light spot through their receptive fields. A, B, C, directionally non-selective responses of three neurons with the different receptive field sizes. A, $45 \times 20$ deg; B, $10 \times 10$ deg; C, $7 \times 5$ deg; D, E, F, responses of three directionally selective neurons. Explanations in the text.
Directionally selective neurons. Thirty one percent of the investigated neurons showed directionally selective responses to stimulus movement i.e. responded vigorously to the movement in a preferred direction and inhibited discharges to the movement in the opposite (null) direction. Vertical, horizontal and oblique (45 deg) movements were tested for each neuron. The directional selectivity was observed at all orientations of movements, but most prominently at vertical and horizontal ones. To simplify the figures only horizontal movements are presented. Figure 2 illustrates the directionally selective responses of three neurons. The neuron presented in Fig. 2D prefers the movement from right to left and the one in Fig. 2E from left to right. Both neurons reveal negligible responses in the null direction. Thirty seven percent of all directionally selective neurons had preferential direction from right to left (centripetal) and 63% from left to right (centrifugal). In Fig. 2F responses of a different directionally selective neuron are presented. This neuron discharged to the movement of light spot in both directions, but the number of discharges in the preferred direction is almost 4 times greater as compared to that in the null direction.

When the orientation of axis of movement was changed the directionally selective type of response was preserved although occasionally a slight increase of the number of discharges in the null direction was observed. Most of the directionally selective cells gave weak "on", "off" or both responses to the stationary flashes. Their spontaneous activity was low and in nearly half of the cell it was absent.

Multimodal neurons. Twenty six percent of neurons were included in the group of multimodal neurons. These neurons are similar to the ones described by Pettigrew et al. (32) in the visual cortex of cat and named "the multimodal simple". It is necessary to clarify here, that the term "multimodality" used by us means the multimodal distribution of neuronal discharges and has nothing in common with the multimodality of sensory inputs to a neuron. During movement of a light spot through the receptive field of such a neuron two or more discharge peaks are elicited. Frequently these are two discharge peaks with an interval between them. The number of peaks (and not the length of the intervals between them) correlates with the size of stimulus presented. This is clearly seen on Fig. 3. When the moving stimulus is small (2°), only monomodal discharges are found (Fig. 3A). With the increasing dimensions of the moving light spot (5° and 6°) two peaks of discharges appear on each sweep of the stimulus through the receptive fields (Fig. 3B, C). Appearance of the two peaks in the response of this neuron could not be explained by the movement of leading and trailing edges of the stimulus through the receptive field. The length of the interval between
two peaks (250 ms) is almost twice longer than the time at which the stimulus crosses the receptive field (~100 ms), and the size of stimulus (5° or 6°) added little to these numbers. Trying to explain the multimodal responses, we postulated at first that the elements of its receptive field substructure have different latencies. To check this hypothesis responses of the same neuron to moving and stationary stimuli were compared. We assumed that if there are elements with different latencies of responses in the receptive field, then the stationary stimuli will reveal them. But we found that some neurons having multimodal responses to the moving stimulus (Fig. 4A), responded with one peak of discharges to the stationary flashing light spot (Fig. 4B). These neurons composed the most numerous group (44%). The next group of neurons

Fig. 3. The multimodal type of responses to the movement of the light spot. A, B, C, responses of the same neuron to three different sizes of the moving light spot.

Fig. 4. Responses of neurons to moving and stationary flashing lights. A, B, a neuron which responds with the bimodal distribution of discharges to the moving light spot (A) and the monomodal one to the stationary stimuli (B). The size of the receptive field of this neuron is 14 × 15", C, D, a neuron with the monomodal responses to the stimulus movement (C) and multimodal to light "on" (D). E, F, a neuron responding multimodally to the moving (E) as well as to a stationary light spot (F).
(40%) revealed multimodal responses to the stationary light spot and did not exhibit this property when the same light spot moved through the receptive field. Fig. 4C, D shows an example of responses of a neuron belonging to this group. Only small percent (16%) of neurons possess a multimodal pattern of responses both during movement and stationary flashing stimulation (Fig. 4E, F). So the hypothesis that the multimodality of responses could be explained by the existence of a substructure of elements with different latencies in the receptive fields of these neurons.

Fig. 5. Maps of the receptive field positions and pattern of responses of neurons in two microelectrode penetrations (A and B). Vertically oriented grouped organization of neurons is shown. The “O” point of coordinates corresponds to the “O” of H–C system. Numerals on right indicate consecutive neurons in one penetration. a, “on-off” response, directionally non-selective; b, “off” response, directionally non-selective; c, “on” response, directionally non-selective; d, “on” response, directionally selective. Explanations are the same for Figs. 6, 7 and 8.
was not confirmed. Further investigations are necessary to clarify this problem.

Columnar organization of neurons. The results of our earlier experiments (25) concerning the properties of responses of Clare–Bishop area neurons to visual stimulation have provided us with some observations on the vertical organization of neurons in that cortical area. The data collected in this series of experiments confirm the earlier observations and help to outline more definitely the modes of organization of neurons in the explored area.

In 55 penetrations more than two visually sensitive neurons were recorded and these tracks were fully examined. Three hundred and four visually sensitive neurons were investigated. This number is three times lower than the number of cells which did not react at all to visual stimulation. So the dispersion of visually sensitive elements in the lateral suprasylvian area is greater than in the visual areas 17, 18 and 19. Usually visually reactive neurons in a single penetration were intermingled with visually non-reactive cells.

All penetrations were classified into four groups. The largest group of penetrations (24 out of 55) showed a group type of vertical organization i.e. in one penetration a pair of neurons with identical characteristics

Fig. 6. Vertical columns of neurons with a spatial superposition of receptive fields (A, B) and without it (C, D).
was followed by the pairs of different types (Fig. 5A, B). On Fig. 5B one of such penetrations is presented. In this penetration the activity of eight neurons is recorded. The first two cells (starting from the surface of the brain) had "on-off" responses to the stationary flashing light spot and a directionally non-selective response to the movement of visual stimuli. The third and fourth cells had "on" response to the stationary stimuli and a directionally selective response to the motion. The fifth and sixth were "off" neurons and directionally non-selective, seventh and eighth — "on" neurons and directionally non-selective. So the whole column is organized by the groups of similar neurons.

In 18 penetrations the great degree of spatial superposition of the receptive fields were observed. Figure 6A, B illustrates examples of such columns. Such an organization could facilitate the perception of a rather wide sector of the visual field by neurons in a column, which could be especially important in the perception of moving objects. Figure 6C, D shows columns where spatial superposition of receptive fields was absent.

 Extremely regular organization i.e. vertical columns with neurons of similar characteristics, was observed only in eight penetrations. So this type of column could not be regarded as a common type of organization of neurons in the lateral suprasylvian cortex. As it is seen from Fig. 7A–E all neurons in such columns possessed similar properties.

In five penetrations no regularities were observed in the vertical organization of functional properties of neurons (Fig. 8A, B).

**Fig. 7.** Vertical penetrations where similar characteristics of neurons in one column were observed. e, response only to black stimuli, directionally non-selective; f, "on-off" response, directionally selective.
DISCUSSION

Our data indicate that the majority of visually driven neurons in the lateral suprasylvian area responded to the stationary visual stimuli. The data of Hubel and Wiesel (21) and Wright (43) showed somewhat different results. Above mentioned authors established that neurons of Clare–Bishop area did not react to the stationary visual stimuli. Spear and Baumann (37) observed that 5% of neurons give maximum response to the stationary flashing light and they did not rule out that many movement sensitive neurons also reacted to stationary flashing stimuli. Earlier Turlejski (40, 41) observed neurons in Clare–Bishop area sensitive to stationary light stimuli. Our data confirmed the observation of the
later authors. The discrepancies between their results could presumably be ascribed to the different methods used by the authors in their experiments.

Our data confirmed the observation of many authors (21, 36, 38, 40, 43) that the neurons of Clare–Bishop area are very sensitive to the stimulation of the retina by the moving objects. The multimodal type of responses evoked by moving stimuli was especially interesting for us. Our preliminary suggestion that the multimodality is the result of high excitability of border zones of the receptive field (15) was not fully confirmed. The organization of multimodal responses could not be explained either by the differences of latencies of various elements in the substructure of the receptive field. The data presented in this study rule out such a possibility. The fact that small stimuli evoked monomodal responses and the increasing size of the stimulus produced multimodal activity may support the assumption that neurons with this pattern of response participate in the analysis of sizes of moving objects.

Hubel and Wiesel (19) in their investigation of columnar organization of neurons in the visual cortex used consecutive microelectrode penetrations 100 μm apart from each other, which enabled them to observe the shape and size of each column. Unfortunately in our experiments we were not successful in performing this, our penetrations being at a distance of 0.5 mm. This was the minimal distance which gave us the certainty that the cortical tissue was not damaged and that the new track did not follow the old one. Unfortunately on the basis of our data it was impossible to make any assumption as to the shape and size of the vertical columns observed in the Clare–Bishop area. It was also difficult to accomplish penetration precisely perpendicular to the surface of the brain. To be sure of this, we had to select only the penetrations through the smooth surface of the lateral suprasylvian gyrus. The histological examination confirmed their perpendicularity. But these precautions narrowed substantially the region under investigation.

One of the difficulties of exploring the columnar organization of neurons in visual structures is the problem of correct definition of what to call the columnar organization. Visually sensitive neurons significantly differ from those described by Mountcastle (28, 29) in the somatosensory cortex. Hubel and Wiesel (19) in their experiments used only one property of the cortical neurons—the orientation selectivity which could not adequately characterize the visually driven neurons in the lateral suprasylvian cortex because of their weak orientation selectivity. In our investigations we tried to investigate the cells using various kinds of visual stimuli and only the real similarities between the cells are taken into account. As it was shown in our experiments only in 8 penetrations
cells showed enough similarity of their functional characteristics to postulate a column. The majority of penetrations showed grouped organization of neurons. We suppose that such an organization of neurons may be able to perform complicated functions in the integration of sensory inputs.

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