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Spatial Modulations of Receptive Field Sizes in Extrastriate Area 21b of the Cat Brain Cortex

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Introduction

At present, it is well established, that the classic receptive field (CRF) of visually sensitive neuron play**s** a decisive role in the central processing of visual information. The extent of CRF is usually defined as a limited area in the visual field over which the activation of a cell may occur by applied stationary and moving visual stimuli [8, 11, 12]. The data presented by a group of authors [4, 5, 16, 18] have shown that in most cases the spatial dimensions of visually sensitive neuron RFs determined by stationary visual stimuli in primary visual cortex at the application of moving visual stimuli are not static and may undergo significant alterations, such as spatial expansions or shrinkage. Furthermore, as has been shown by a row of authors [1, 17, 19, 20], in the vicinity of RF under investigation the visual inputs of neighboring visually driven neurons elicited significant modulations of neuron response patterns to the applied moving visual stimuli. We have recently shown [2, 9, 10, 14], that at the application of moving visual stimuli the RF of visually driven neurons in extrastriate area 21a reveal significant spatial expansions and that of restructuring of the RF stationary organization. Thus, the neurophysiological mechanisms underlying the elaboration and central processing of visual information are evidently composed of an integrative activity of neuron groups to achieve the precise perception of moving visual images. The main goal of the present study was to find out whether the spatial parameters of visually driven neuron RFs in extrastriate area 21b are not stable and undergo certain alterations depending on the type of visual stimulus used. The results of experiments presented in this study showed that at application of moving visual stimuli there occur substantial alterations, mainly expansions of spatial dimensions of the neuron RF.

Material and Methods

Experiments were carried out on cats weighing 2.5 to 3.5 kg. Preliminary surgery, including tracheotomy, cannulation of the v. femoralis, and pretrigeminal sectioning of the brainstem, was performed under ether anesthesia [24]. In some cases, complete anesthesia was provided by additional injections of chloralose in doses (10 mg/kg). The animal's head was fixed in a stereotaxic device modified for the experiments on the visual system. A part of the cranial bone localized above the sulcus suprasilvius posterior was removed together with the dura mater; this allowed us to visually control the studied area. To decrease brain pulsation, the trepanation opening was filled with a 4% agar solution in physiological saline. The animals were immobilized with i.m. injections of ditilin (diodide dicholine ester of succinic acid, 7 mg/kg). The frequency of artificial respiration and inspiration volume were 19 strokes/min and 20-25 ml/kg, respectively; the body temperature was stabilized at 37.5 to 38°C by a heating pad. The pupils were dilated by 0.1% atropine dropped in the eyes. The cornea was protected from drying by contact lenses (dioptric power = 0). To provide focusing of the eyes on a perimeter screen, correcting lenses were used if necessary. Contraction of the nictitating membranes was provided by instilling 1% of neosynephrine into the conjunctival sac. The arterial pressure was maintained at the 90-100 mm Hg level. The state of the animal was periodically monitored by recording of EEG and ECG. The spike activity of single cortical neurons was recorded 2-3 h after termination of ether anesthesia. Tungsten microelectrodes (2 to 5 μm thick) were used. The activity was analyzed by plotting poststimulus time histograms (PSTH) mode. Averaging was achieved by repeating a stimulus 16 times. The parameters of RFs of the neurons and localization of the area centralis with respect to the visual coordinates were estimated on the perimeter screen positioned at 1.0 m distance from the nodal eye points; the screen could be moved, thus covering the entire vision field [3, 6]. Visual stimulation was realized by presentation of stationary and moving dark and light stimuli, in the neuron RF. Stimuli appeared as spots and strips of different contrasts, forms, and dimensions and as light/dark borders providing, when moved, illumination or darkening of the entire field of vision. Illumination of light and dark stimuli was 12 lux against a 2 lux background and 2 lux against a 12 lux background, respectively; thus, the contrast of the stimulus with respect to the background was constant in all experiments.

At the end of some experiment, successful recording points were coagulated. Then, the brain was perfused by a 10% formalin solution and fixed in this solution. Localization of the electrode tip was verified in 50 μm thick histological slices.

Results and Discussion

Extrastriate area 21b was outlined according to Tusa a. Palmer [23] and Tardiff et al. [22]. The response patterns of 73 visually sensitive neurons were recorded in extrastriate area 21b of the cat cortex. As a first step the neuron RF size and localizations in the visual coordinate system was performed by hand plotting. Afterwards the RF spatial structure was defined by stationary flashing light spot positioned side by side over the entire RF surface. This method allows to determine complete receptive field maps, their sizes, and locations in reference to the visual coordinate system. Neurons with small RF sizes defined by stationary flashing spots were chosen for further investigation, considering that dynamic modulations and expansions would be more salient in RFs of small sizes, and their detailed exploration will be more precise. Of 73 investigated neurons 25 units (34%) had comparatively small sizes not exceeding 6 deg² and these neurons were chosen for further investigation. According to Maffei a. Campbell [15], the vertical and horizontal orientations of visual stimulus motion are the most effective in visual perception, due to the lower thresholds compared with that of the oblique ones, so, in our experiments these orientations and two oblique 45° and 135° were chosen as the main tests. In Fig. 1, the response patterns of a neuron in area 21b to the stationary and

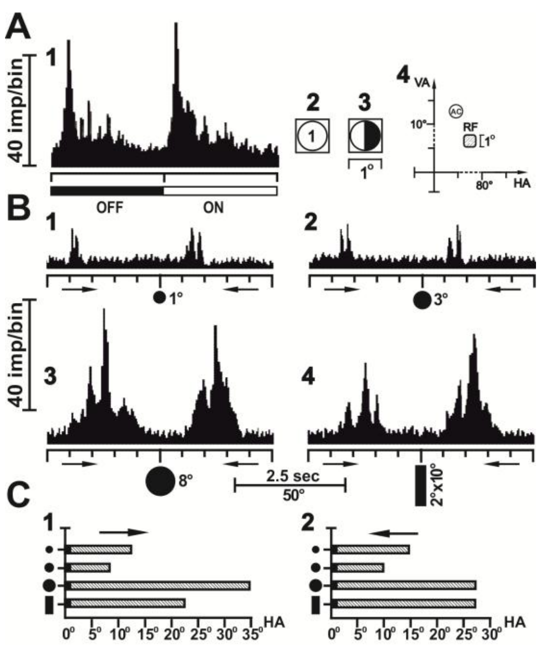

Fig. 1. Responses of a neuron in extrastriate area 21b to presentation of stationary and moving visual stimuli.
A1 – poststimulus time histogram (PSTH) of the neuron response to the stationary flashing bright spot (1°), positioned in the test zone (A2) of the RF. A3 - half-filled circle indicates On-Off responses of the neuron. A4 - the RF localization in the visual coordinate system. AC is the area centralis. B1-4 – PSTH of the same neuron responses to the moving dark spots and dark bar of different sizes, indicated under histograms, along the RF horizontal axis (HA). C 1-2 – graphical presentation of RF HA lengths measured for each applied stimuli at rightward (1) and leftward (2) directions of motion. Arrows indicate the directions of stimulus motion; black rectangles indicate the size of the stationary RF. Explanations are the same for all the figures.

moving visual stimuli are presented. As is seen in Fig. 1 A1, the neuron responded by On-Off pattern of responses to the stationary flashing light spot (1°) from a single test-field (Fig. 1 A2-4), and thus the lengths of horizontal and vertical axes of stationary RF did not exceed 1° magnitude. As a next step, we introduced moving visual stimuli of different shapes (spots and bar) moving along the RF horizontal axis. As is seen in Fig. 1 B1,2 the neuron reveals weaker responses to moving 1° and 3° dark spots compared to that evoked by 8° magnitude dark spot (Fig. 1 B3) and the dark bar of 2° x 10° magnitude (Fig. 1 B4). Precise measurements of neuron response patterns showed substantial differences in the lengthening of RF horizontal axis (HA) both in the leftward as well as in the rightward directions of stimulus motion depending on shapes and sizes of applied visual stimuli (Fig. 1 C1,2). The dark spots of 1° and 3° magnitudes evoked RF expansions of values 12,5° and 8,7° in the rightward and 15° and 10° in the leftward directions of stimulus motion, whereas the application of 8° dark spot provided an expansion of RF up to 35° in the rightward and 27,5° in the leftward directions of motion (Fig. 1 C1,2). The dark bar (2° x 10°) provided the RF expansions up to 22,5° in the rightward and 27,5° in the leftward directions of motion (Fig.1 C1,2). Thus, the neuron response patterns are distinctly diversified depending on the size and shape of the visual stimuli used. It is highly probable that simultaneous activation of the visual space of RF surrounding by moving stimuli has substantial modulatory influences on the neuron response patterns. In Fig. 2 the response patterns of the same neuron are presented to the moving stimuli of opposite contrast (bright) and moving edges covering the whole visual field. Although the neuron responded almost equally well to the stationary flashing spot both in On and Off phases of applied stationary visual stimulus (Fig. 1 A1), the neuron responses to the bright visual stimuli become more accentuated and diversified. In Fig. 2 A1-4 the response patterns of the neuron to moving bright spots (1°, 3°, 8°) and a bright bar (2° x 10°) along the HA of the RF are presented. As is seen in the figure, significant expansions of RF horizontal axis are the case especially in the preferred (rightward) direction of stimulus motion (Fig. 2 A 1-4, B1-2). The edge motion along RF HA also evoked extensive discharges of the neuron in the rightward direction of motion at the illumination of the visual space (Fig. 2 A5) and significant spatial expansion of RF HA (35°) was observed (Fig. 2 B1,2). Whereas, as a result of the leftward direction of edge motion (darkening of visual space), the elongation of RF HA is much less (10°). Changing the direction of the edge motion into the opposite one, when the rightward motion darkened the visual space, provided the change of preferred direction into the leftward one and RF HA expansion up to 25° (Fig. 2 A6, B2). It is highly probable that this effect may result from more pronounced influences of RF surrounding, contributing to substantial diversification of neuron response patterns to moving visual stimuli that ensures a precise perception of moving visual images. In the next neuron, which response pattern to the stationary

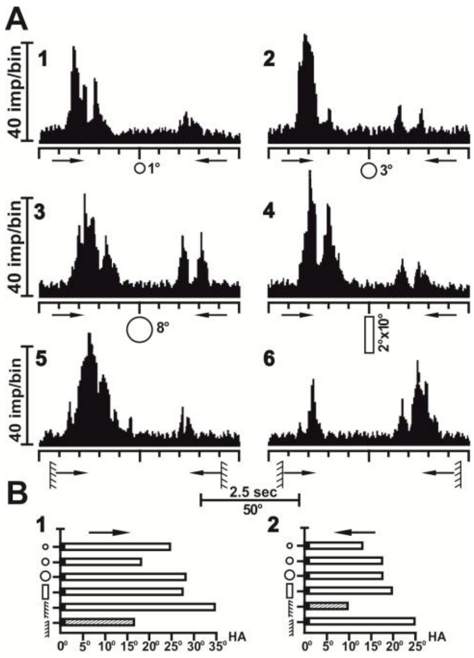

Fig. 2. Responses of the neuron presented in Fig. 1 to moving visual stimuli of different shapes and sizes.
A1-3 –PSTH of the neuron responses to the moving bright spots of different sizes, A4 - bright bar, A5,6 - moving edges, along the RF HA. B1-2 – lengths of the RF HA according to sizes, shapes and movement directions of the stimuli applied.

visual stimuli is illustrated in Fig. 3 A1, together with the measurements of the HA length, the length of the RF vertical axis (VA) was also estimated. As is seen in Fig. 3 B1, the dark spot (4°) moving along RF horizontal axis provided

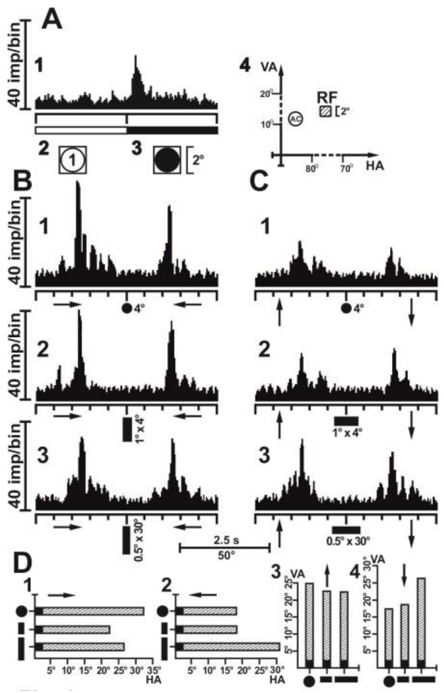

Fig. 3. Responses of a neuron to the stationary and moving visual stimuli along HA and vertical axis (VA) of the RF.
A1 – PSTH of neuron responses to stationary flashing 2° light spot, positioned in the RF test zone (A2), filled circle indicates “Off” response (A3), RF localization in visual coordinate system (A4). B1-3 – PSTH of neuron responses to dark spot and dark bars of different sizes moving along RF HA. C1-3 – PSTH of neuron responses to the same stimuli moving along VA of the RF. D1-4 – graphical presentation of RF HA and VA dimensions at application of corresponding visual stimuli.

significant elongation of RF HA up to 32,5° at rightward and 18,7° at leftward directions of motion (Fig. 3 D1,2). Whereas, the rightward and leftward movements of the dark bar (1° x 4°) brought to 22,5° and 18,7° elongations of RF HA (Fig. 3 B,2, D1,2). The dark bar of 0,5° x 30° magnitude elicited 26,2° elongation of RF HA at rightward and 31,2° at leftward motion of the visual stimulus along RF HA (Fig. 3 B3, D1,2). The most effective in this case were the rightward motion of 4° dark spot (32,5°) and the leftward motion of 0,5° x 30° dark bar (31,2°). When moving vertically along RF the same visual stimuli also provided substantial expansions of RF VA. The response patterns of the same neuron to the moving stimuli oriented vertically along RF VA are shown in Fig. 3 C 1-3. As is seen in Fig. 3 C3, the maximum RF VA expansion (26,2°) was observed at the application of dark bar of 0,5° x 30° magnitude, that moved downward along the VA of the neuron RF. The change of the stimulus contrast into the opposite one also leads to diversified expansions of RF HA, and VA depending on shapes and sizes of applied visual stimuli. The bright spot (4°) motion along RF HA evoked response patterns of the neuron and expansions of RF HA up to 11,2° at the rightward and 15° at leftward directions of motion (Fig. 4 A1, C1,2). When a bright bar of 1° x 4° magnitude was moved across

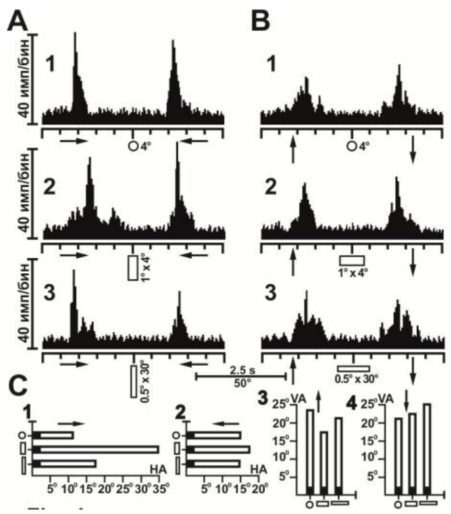

Fig. 4. Responses of the same neuron as in Fig. 3 to moving stimuli of the opposite contrast.
A1-3 – PSTH of neuron responses to moving bright spot and bars of different magnitudes along RF HA, B 1-3 – PSTH of neuron responses to the same stimuli moving along RF VA. C1-4 – graphical presentation of lengths of RF HA and VA at the application of moving visual stimuli.

RF HA, the expansions of HA became 35° at the rightward and 17,5° at the leftward direction of stimulus movement (Fig. 4 A2, C1,2), exceeding thus the magnitudes of expansions as compared to those evoked at the motion of bright spot. Meanwhile, at the presentation of the bar of 0,5° x 30° magnitude the maximum HA expansions were 17,5° and 15°, (Fig. 4. A3, C1,2) that are much lower compared to that evoked by 1° x 4° magnitude bar motion. As is seen in Fig. 4 B1-3, RF VA is elongated most effectively in the cases of upward motion of (4°) bright spot – 23,7° (Fig. 4 B1, C3,4) and downward motion of horizontally oriented (0,5° x 30°) bright bar - 25° (Fig. 4 B3, C3,4). Thus, substantial diversifications of RF HA and VA length were observed depending on the stimulus contrast and orientation of motion. So, it becomes necessary to explore the sizes of neuron RFs at application of visual stimuli also at oblique orientations of motion through RF center. The response patterns of another neuron to the flashing bright spot (1°) positioned consecutively in RF test-subfields (Fig. 5 B1) are presented in Fig. 5 A1-6. So, the dimensions of classic

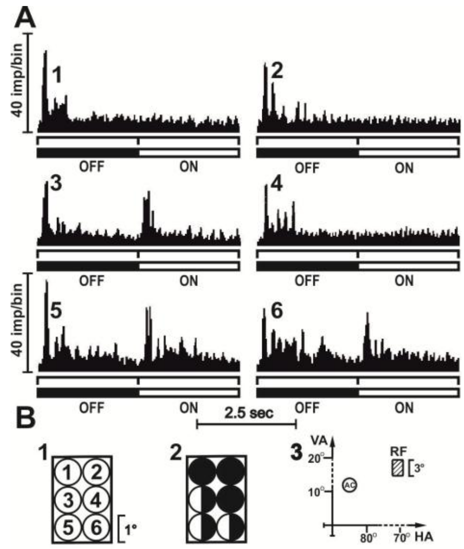

Fig. 5. Responses of a neuron to presentation of stationary visual stimuli and stationary organization of the RF.
A1-6 – PSTH of neuron responses to the stationary flashing light spot (1°) positioned in the test-zones of the RF. B1 - RF test-zones, B2 - RF functional organization, and RF position in the visual coordinate system (B3). Filled circles indicate "Off" responses, half-filled circles "On-Off" responses of the neuron.

RF were 2° of HA and 3° of VA lengths and the RF functional structure was composed of pure Off and On-Off zones (Fig. 5 B2). As a next step, moving visual stimuli (bars) of two opposite contrasts and sizes (1° x 4° and 2° x 11°) were applied moving through the neuron RF center at different orientations (horizontal, vertical, 45° and 135° oblique). As is seen in Fig. 6 A1, the horizontal motion of a bright bar (1° x 4°) elicited expansions of RF HA both in the leftward (12,5°) and in the rightward (16,2°) directions of motion (Fig. 6 A1, C1,2 white columns), much exceeding the RF HA measured by the stationary flashing spot (HA-2°). The introduction of the bright bar moving at 45° orientation through RF center also resulted in RF expansions both in the downward, and the upward directions of stimulus motion, being respectively 12,5° and 10° of RF axes lengths (Fig. 6 A2, C3,4). Meanwhile, the motion of the same visual stimulus at 135° orientation brought to more accentuated expansions of RF axis, up to 17,5° and 27,5° of lengths (Fig. 6 A3, C5,6). At the vertical orientation of motion of horizontally oriented bright bar 12,5° RF VA axis elongation at downward and 17,5° at upward directions of motion (Fig. 6 A4, C 7,8) were elicited. Next, the opposite contrast of moving stimulus (dark

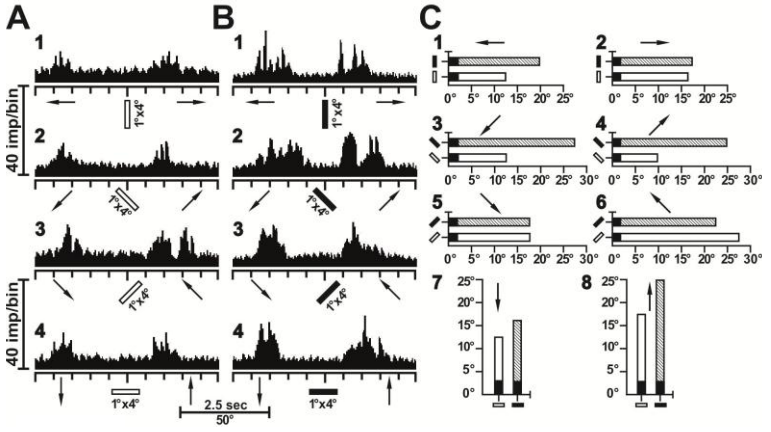

Fig. 6. Responses of the same neuron as in Fig. 5 to the bars of two opposite contrasts moving at different orientations through the RF center.
A1-4 – PSTH of the neuron responses to the moving bright bar (1° x 4°) in horizontal (1), oblique 45° (2) and 135° (3) and vertical (4) orientations (indicated by arrows) through RF center. B1-4 – PSTH of neuron responses to moving dark bar (1° x 4°) in horizontal (1), oblique (2,3) and vertical (4) orientations through the RF center. C1-8 – graphical presentation of neuron RF axes lengths at different orientations of applied moving visual stimuli.

bar) was tested. The response patterns of the same neuron to the moving dark bar at horizontal, vertical, 45° and 135° orientations through RF center are presented in Fig. 6 B 1-4. As is seen in the figure, there were also substantial

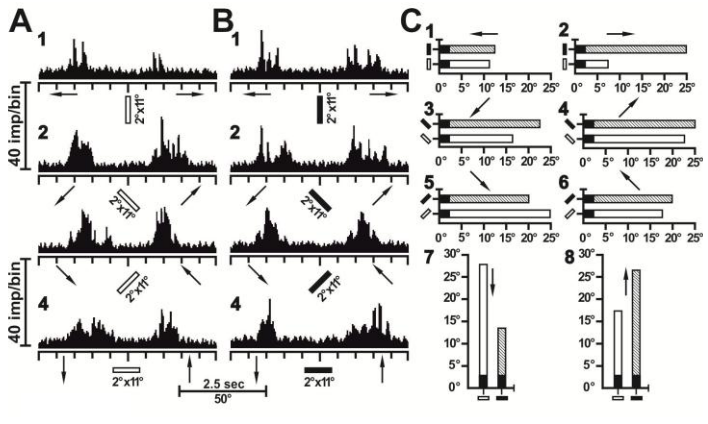

Fig. 7. Responses of the same neuron to the bright and dark bars moving at different orientations through the neuron RF center.
A1-4 – PSTH of neuron responses to the bright bar (2° x 11°) moving at horizontal (1), oblique 45°(2) and 135° (3), and vertical (4) orientations through the RF center. B1-4 – PSTH of neuron responses to the dark bar moving along different orientations through the RF center. C1-8 – graphical presentation of the lengths of RF axes according to the orientation of applied visual stimulus motion.

elongations of RF axes at the application of moving visual stimuli and generally RF expansions evoked by the dark moving stimuli exceeding that evoked by the bright moving stimulus (Fig. 6 C1-8, shaded columns). The same neuron was further investigated by the application of the moving bar of 2° x 11° magnitude, sufficient for excitation of more spatially distant RF surroundings. In Fig. 7 A, B response patterns of the same neuron are presented to the motion of bars (2° x 11°) of two opposite contrasts (Fig. 7 A1-4, B1-4). As is seen in the figure the RF axes elongations are the case (Fig. 7 C1-8). The moving bright bar evoked maximal elongations of RF axes at 135° and 90° orientations of motion (25°, and 27,5°) in comparison to that of horizontal (11,2° and 7,5°), and 45° (16,2° and 22,5°) orientations of motion. The moving dark bar (Fig. 7 B1-4) of the same magnitude also brought to RF spatial expansion exceeding in many cases those evoked by the bright bar (Fig. 7 C1-8). The results of the experiments indicate a diversified effect of the RF environment on the activity of neurons. Thus, the temporary activation of neighboring groups of neurons that have synaptic connections with the neuron under investigation, and the subsequent activation of certain neural networks, is very important in the central processing of incoming visual information by ensuring accurate perception of moving visual images.

The results of presented experiments show that at application of moving visual stimuli the RFs of visually sensitive neurons in extrastriate area 21b undergo significant spatial modulations, mainly expansions. According to our earlier presented data, the same phenomenon was observed in extrastriate area 21a [2]. Thus, it seems to be a general property of visually driven neurons in extrastriate visual cortex of the cat. The data presented in this study allow to suggest that the spatial expansions of neuron RFs are not merely due to the general increase of neuronal excitability but are the result of certain central processing of incoming visual information. As was reported by several groups of authors [7,13,21], the response patterns of striate cortical neurons to stimuli inside their classical RFs can be modulated by concurrent stimuli delivered outside the RF due presumably to the nonlinear summation of converging inputs to the neuron under investigation, as well as to the top-down feedback mechanisms. Furthermore, Das a. Gilbert [4] suggested earlier that RF expansion observed in visual cortex (area 17) is a result of activation of horizontal intracortical connections with their specificity of RF properties contributing to a formation of the major substrate for dynamic RF changes. According to our recently obtained data the response patterns of visually sensitive neuron in extrastriate cortical area 21a can be modulated (facilitated or suppressed) by parallel co-excitation of near surroundings of the neuron CRF [10]. So, it seems to be a general property of visually driven neurons in extrastriate visual cortex. Thus, mutual interactions among simultaneously activated neighboring neurons are of great importance to diversification and integration of incoming visual information. It is highly probable that such a central processing of visual

information may play a decisive role in precise perception of shapes, magnitudes and directions of motion of moving visual images.

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Пространственные модуляции размеров рецептивных полей в экстрастриарной области 21б коры мозга кошки

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Центральный анализ зрительной информации обеспечивается координированной работой множества корковых областей мозга. В ряде исследований установлено, что пространственная структура рецептивного поля (РП) зрительно-чувствительного нейрона лежит в основе анализа поступающей зрительной информации, обеспечивающей восприятие зрительного образа. Целью представляемой работы являлось изучение закономерностей динамики изменений пространственной структуры РП нейронов области 21б экстрастриарной коры мозга кошки. Результаты экспериментов показали, что пространственные параметры РП нейронов данной области претерпевают значительное увеличение в зависимости от величины, формы и контраста предъявляемого движущегося зрительного стимула. Становится очевидным, что одновременная активация множества взаимосвязанных нейронных сетей приводит к диверсифицированной вариабельности размеров РП, обеспечивая этим четкое восприятие движущегося зрительного образа.

Ընկալման դաշտերի չափերի տարածական փոփոխությունները կատվի ուղեղի կեղևի էքստրաստրիար 21բ շրջանում

Դ.Կ. Խաչվանքյան, Ա.Լ.Ղազարյան, Ա.Ա. Մելիքսեթյան, Վ.Է. Սարգսյան, Բ.Ա. Հարությունյան-Կոզակ

Տեսողական տեղեկատվության կենտրոնական մշակման գործընթացում ընդգրկված են գլխուղեղի բազմաթիվ կեղևային շրջաններ: Մի շարք ուսումնասիրություններում հաստատվել է, որ տեսազգայուն նեյրոնի ընկալման դաշտի (ԸԴ) տարածական կառուցվածքը կանխորոշում է մուտքային տեսողական տեղեկատվության վերլուծությունը, որն ապահովում է տեսողական պատկերի ընկալումը: Ներկայացվող աշխատանքի նպատակը գլխուղեղի կեղևի էքստրաստրիար 21բ դաշտի նեյրոնների տարածական կառուցվածքի փոփոխությունների օրինաչափությունների ուսումնասիրությունն է: Փորձերի ար-

դյունքները ցույց են տվել, որ տվյալ դաշտում նեյրոնների ԸԴ-երի տարածական պարամետրերը զգալիորեն աճում են՝ կախված ներկայացված շարժվող տեսողական խթանիչների չափից, ձևից և կոնտրաստից: Պարզ է դառնում, որ շրջապատող նեյրոնային ցանցերի միաժամանակյա ակտիվացումը հանգեցնում է ԸԴ-երի չափերի համակարգված փոփոխության՝ այդ եղանակով ապահովելով շարժվող տեսողական պատկերի հստակ ընկալումը:

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