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MOVEMENT-DEPENDENT SPATIAL EXPANSION OF VISUAL RECEPTIVE FIELDS OF NEURONS OF THE EXTRASTRIATE CORTEX

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The spatial structure of the receptive field (RF) of a visually sensitive neuron, as defined by presentation of stationary visual stimuli, predetermines in most cases central processing of visual information concerning moving visual images. In our study properties of a group of neurons in the extrastriate cortical area 21a (≈18% of the examined sampling) with extremely small RF sizes (≈1.5 deg²) determined by stationary visual stimuli were investigated. It was found spatial dimensions of each neuronal RFs may undergo manifold expansions; the neuronal response profiles depended strongly on the size, shape, and contrast of the applied moving stimuli. As a result, a high degree of diversification of neuronal response patterns depending of the shapes and contrasts of applied moving stimuli was observed. These data confirm the suggestion that the RFs of neurons in the extrastriate area 21a undergo temporary dynamic changes due to activation of surrounding neuronal groups (networks) by moving visual stimuli. Thus, it is evident that processing of visual information in the course of visual image recognition is realized by integrated activity of a complex of the corresponding cortical networks of visually sensitive neurons.

KEYWORDS: receptive field (RF), visually sensitive neuron, moving stimulus, RF dimension, extrastriate cortex, area 21a.

INTRODUCTION

Basing on modeling experiments, Xing and Gerstein proposed that central processing of sensory information is carried out by clusters of neurons organized in functional groups; the latter are dynamic and could be changed by incoming stimuli [1–3]. Later investigations confirmed this interpretation [4–7]. Substantial modulations of the response patterns of neurons in the primary visual cortex were observed as a result of application of visual stimuli outside their classical receptive fields (RF) [8–10]. Thus, as was emphasized by Angelucchi et al. [11], coordinated integrated activity of the surrounding neuronal groups, including feedback influences, plays, most probably, a decisive role in central processing of visual information concerning visual image recognition. Furthermore, it has been shown by a group of authors [12–15] that the RF sizes of visually sensitive neurons, defined by presentation of stationary visual stimuli, may undergo dynamic changes (usually expansions) upon introduction of moving visual stimuli. Recently, we presented data, according to which a part of visually sensitive cortical neurons (5.3%), lacking stationary RFs and displaying no responses to a stationary flashing light spot positioned within the hand-plotted RF borders, generated intense discharges to presentation of moving visual stimuli [16].

In this our study, another group of cortical neurons was investigated; these units also revealed certain preferences in movement perception. These were neurons of the area 21a with small RF sizes, the length of which along the horizontal and vertical axes determined by stationary flashing light spots (HA and VA, respectively) did not exceed 1.5 deg. These cells showed significant expansions of the RFs along HA and VA when moving visual stimuli were applied. Results of our experiments demonstrated a high level of discrimination and diversification of the contrasts,

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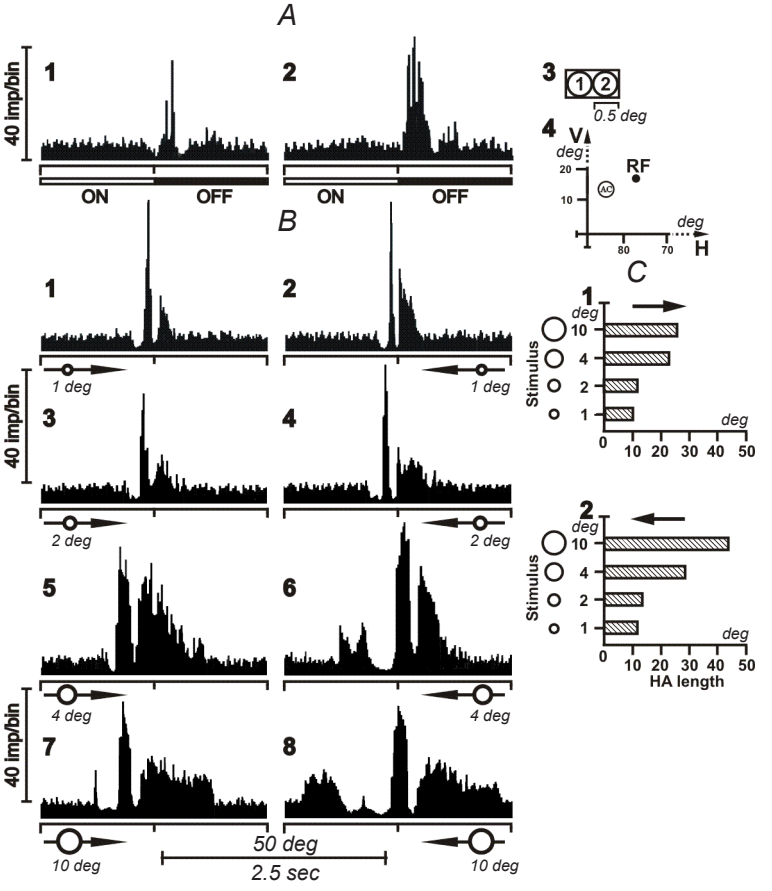
shapes and sizes of applied moving stimuli by corresponding modulations of the neuronal response patterns. Averaged response profiles of these neurons were investigated in detail, with special attention to the dynamics of RF spatial modulations in response to moving visual images. A preliminary report has been presented [17].

METHODS

Experiments were performed on 23 cats weighting 2.5-3.5 kg. Animals were initially anaesthetized with alfa-chloralose (60 mg/kg, i. m.). Tracheostomy and cannulation of the femoral artery were performed. Throughout the experiment, the anaesthesia level was maintained by chloralose given i.v. (10-20 mg/kg per hour). The animal's head was fixed in a stereotaxic apparatus (Horsley-Clark, modified for visual research). A bone piece (6 × 10 mm) was removed from the skull above the posterior suprasylvian cortex according to the Horsley-Clark coordinates: lateral 8-16 mm and posterior 0-8 mm [18, 19]. The opening was covered with 3% agar in 0.9% NaCl solution, to prevent brain pulsations and allow the experimenter to visually control electrode penetrations into the cortical area 21a. The immobility of the animal was achieved by intramuscular injection of the myorelaxant Ditilin (diiodide dicholine ester of succinic acid, at 7 mg/kg). Artificial respiration was administered at 19 min^{-1}, with the stroke volume of 20 ml/kg body mass. The body temperature was kept constant at 38°C with a heating pad. The pupils were dilated by topical application of 0.1% atropine solution, and the corneas were protected from drying with contact lenses of a zero power. Nictitating membranes were retracted by instilling Neosynephrine (1%) into the conjunctival sac. The arterial blood pressure was continuously monitored and stabilized at 90-100 mm Hg. Electrocardiograms and electroencephalograms were continuously acquired throughout the experiment. In some cases, coagulation was performed at the end of the experiment, in successful recording points; this was followed by perfusion of the animal with a 10% formalin solution. The electrode tracks were reconstructed after examination of 50-μm-thick histological sections. Extracellular recording of single-unit activity was performed by tungsten microelectrodes coated with vinyl varnish (exposed tip 1-3 μm); the impedance of the electrodes was 10-15 $M\Omega$. Action potentials were conventionally amplified, triggered, and passed to a digital analyzer for on-line analysis and data storage, using the post-stimulus/peristimulus time histogram (PSTH) mode. Averaging was performed for 16 realizations. The receptive field spatial borders for each visually responsive cell were defined by hand-held stimuli, and plotted on a perimeter screen. The optic discs and *area centrals* (AC) were plotted on the screen, and the RF position in the visual field was referenced to the AC location [20, 21]. As an initial characterization, the RF borders of a visually sensitive single cell were outlined in detail by stationary flashing light spots (0.5-1 deg test-zones) positioned consecutively across the hand-plotted area of the RF. Subsequently, moving visual stimuli (spots, bars, edges, and slits of different sizes and contrasts) were applied with the speed of motion 20 deg/sec. The contrast values for light and dark stimuli against the background were kept constant with the contrast defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} are the maximum and minimum luminances, respectively. Bright stimuli were 15 lx against the 2 lx background, and dark stimuli were, conversely, 2 lx luminance against 15 lx of the background.

RESULTS

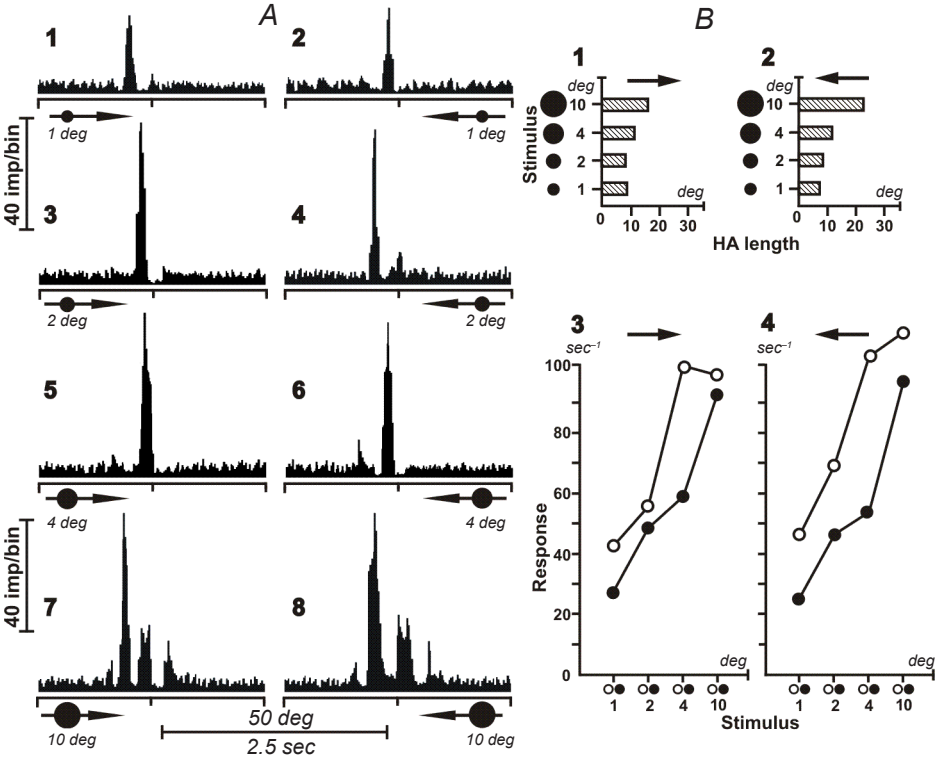
Response patterns of 147 visually sensitive neurons in the extrastriate associative area 21a were studied. As a first step in determination of the RF sizes of recorded neurons and their localization in the visual coordinate system was performed by hand-plotting. Neurons with small RFs (≈1.5 deg^2) defined by stationary flashing spots were chosen for further investigation, considering that dynamic modulations and expansions would be more salient in the RFs of small sizes, and their detailed exploration will be easier. Of 147 investigated neurons, 27 units (18.3%) had comparatively small RF sizes not exceeding 1-2 deg^2, and these cells were chosen for further exploration. The majority of these neurons were excited monocularly, while four of them were driven binocularly. All the neurons with small RF sizes had the homogenous spatial structure of the receptive fields and responded with the same response profiles, when tested by a stationary flashing light spot positioned in the test subregions of the RF. Twelve neurons responded by an "*off*" reaction to the flashing spot, eight neurons revealed "*on*" response patterns, and seven neurons responded to both flash



F i g. 1. Response patterns of an area 21a neuron to presentation of stationary and moving visual stimuli. A1, 2) Peristimulus histograms (PSTHs) of the responses to the stationary flashing spot (0.5 deg), positioned in the test-zones of the receptive field (RF) (A3). A4) RF localization in the visual coordinate system; AC is the *area centralis*. White bar under the histograms indicates the "*on*" phase, while, the black bar shows the "*off*" phase. B1-8) Response patterns of the same neuron to the moving bright spot of different sizes (indicated under the histograms) along the RF horizontal axis (HA). C1, 2) Graphical presentation of the RF HA length measured for each applied stimuli at the rightward (1) and leftward (2) movements. Arrows indicate the directions of stimulus motion. The respective explanations are the same for all figures.

Р и с. 1. Патерни відповідей нейрона поля 21а на пред'явлення стаціонарних та рухомих зорових стимулів.

"*on*" and flash "*off*". In Fig. 1, the response patterns of a neuron to the stationary flashing light spot (0.5 deg) positioned in the test-zones of the hand-plotted RF are shown (A1-A3). The neuron responded by "*off*" responses from two test-zones (Fig. 1A1,2), thus the RF HA defined by the stationary flashing spot was 1 deg long, while its VA was 0.5 deg. As is seen from Fig. 1B,1,2, the response pattern of the neuron to the moving 1 deg bright spot is clearly bimodal, with complete inhibition of background activity before the bursts of spikes. The second period of inhibition was followed by a second period of excitation, which indicated, with a great probability, that the neuron has a double-peaked RF center [22]. Thus, the response pattern in the rightward direction covered 10 deg distance in the visual space, and that in the leftward direction of stimulus motion was 11.2 deg (Fig. 1C,1,2). It was obvious that a moving visual stimulus provides excitation and arrival of subsequent influences from the surrounding neighbor neurons. Thus, it is logical to expect that changing the stimulus size may exert a certain influence on that of the response profile of the neuron under investigation. In Fig. 1B,3-8, the response patterns of the same neuron to the moving bright spots of different sizes are presented. As is seen from this figure (Fig. 1B,3,4) a 2-deg bright spot moving along the RF horizontal axis evoked extensive bursts of spikes intermingled with inhibitory periods, and the RF HA lengths became 11.2 deg at the rightward and 13 deg at the leftward directions of stimulus motion (Fig. 1C,1,2). So, the RF sizes many times exceeded those measured by stationary flashing bright spots. Further increase in the size of the moving stimulus (4 deg), along with the substantial increase in the number of spikes, led to modulation of the response profile by the appearance of additional bursts in the leftward direction before the first inhibitory period of the response pattern (Fig. 1B,6). In this case, the movement direction was discriminated too (because of the absence of initial excitation of the neuron at stimulus motion in the opposite (rightward) direction (Fig. 1B,5). The maximal elongation of the RF HA was observed at the movement of a 10 deg bright spot (Fig. 1B,7,8). It was equal to 26.2 deg at the rightward



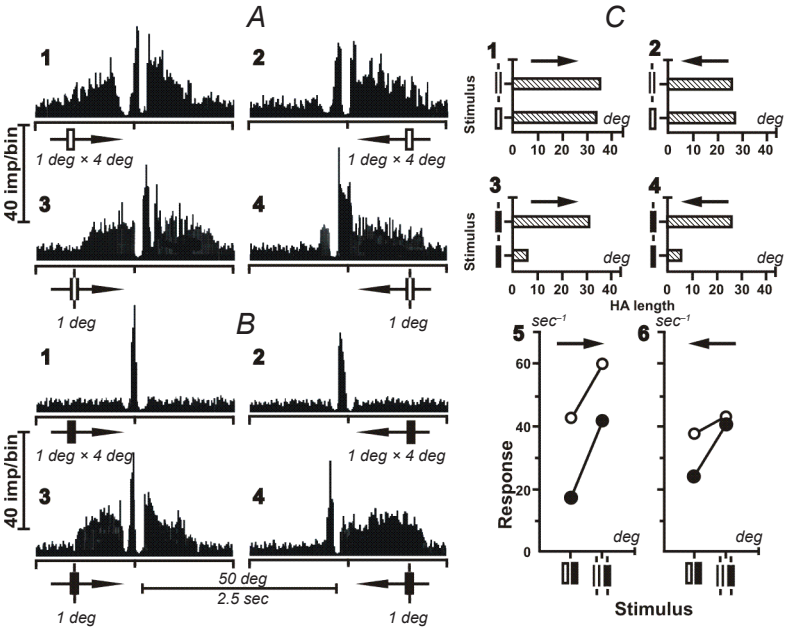
F i g. 2. Response patterns of the neuron to moving dark spots of different sizes. A1-8) Response patterns of the same neuron as in Fig. 1 to moving dark spots of different sizes. B1, 2) Lengths of the RF HA according to the sizes and movement direction of the stimuli applied. B3, 4) Distribution of numbers of spikes evoked by moving bright and dark spots of different sizes.

Р и с. 2. Патерни відповідей нейрона на пред'явлення рухомих темних плям різного розміру.

and 43.7 deg at the leftward directions of the stimulus movement (Fig. 1C,1,2).

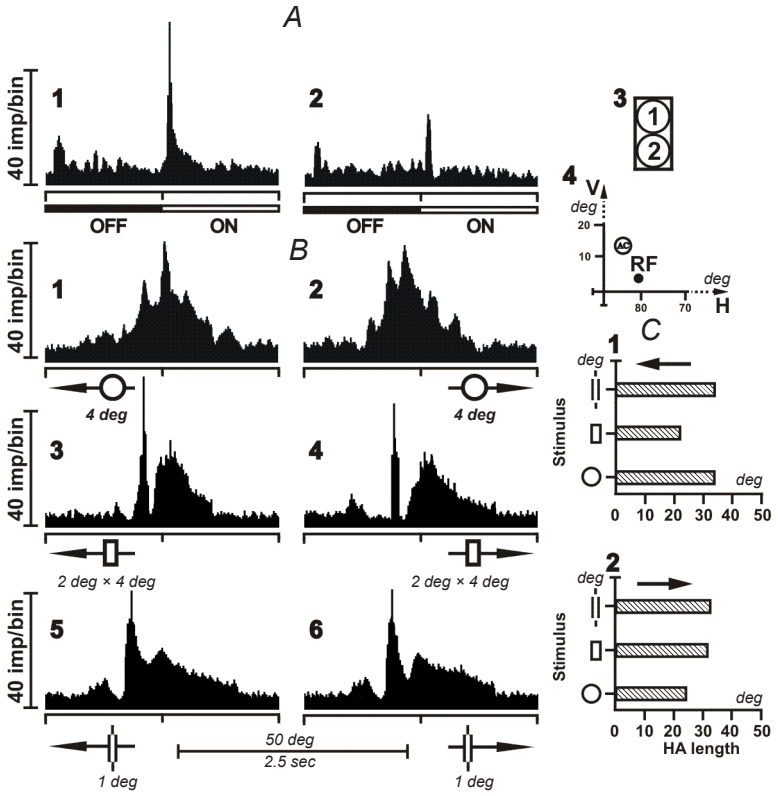
Then, the opposite contrast of the moving stimuli (dark spots) was tested. The response patterns of the same neuron to presentation of moving dark spots across the RF HA are shown in Fig. 2A,1-8. As is seen, substantial elongations of the RF HA were obvious (Fig. 2B,1,2), but those did not exceed the values observed at the movements of bright spots. Comparing the values for the HA lengths measured at the movement of bright and dark spots having the same diameter (10 deg) showed that the bright spot rightward movement led to the mean elongation of the HA of 26.2 deg (Fig. 1), whereas the dark spot the respective value was 17.1 deg. The leftward movement of the bright spot resulted in the mean HA elongation of 43.7 deg, while the dark spot showed 22.5 deg. The corresponding differences were observed also in the spike numbers of neuronal responses in relation to the contrasts and magnitudes of the applied moving stimuli (Fig. 2B,3,4). Thus, it is obvious that, visually sensitive neurons in the extrastriate area 21a with small homogenous-structure RFs were able to perform discrimination and diversification of incoming visual information by modulations of their response patterns relative to the applied stimulus contrast and size.

In Fig. 3, the response patterns of the same neuron to bright and dark moving stimuli of different shapes and sizes are shown. There were significant differences in the response profiles depending on the shape of the stimulus used. A moving bright rectangle (1 deg × × 4 deg) elicited bursts of spikes interspersed between inhibitory periods at stimulus motions in the leftward and rightward directions (Fig. 3A,1,2), with expansions of the discharge field to 33.5 deg in the rightward and 27.5 deg in the leftward directions (Fig. 3A,1,2, C,1,2). A moving bright 1-deg-wide strip covering the entire length of the vertical meridian elicited mixed inhibitory and long-lasting excitatory discharges of the neuron. The receptive field HA lengths in this case were 35 deg at the rightward and 26.2 deg at the leftward directions of movement (Fig. 3A,3,4, C,1,2). A moving dark rectangle (1 deg × 4 deg) led to moderate HA expansions of 6.8 deg at the rightward and 6.2 deg at the leftward directions of stimulus motion (Fig. 3B,1,2, C,3,4). Strong expansions of the RF HA were observed upon application of a 1-deg-wide dark strip at both rightward and leftward directions (Fig. 3B,3,4), producing the RF expansions up to 30.6 and 26.2 deg (Fig. 3C,3,4). Significant differences in the discharge numbers depending on the stimulus used were



F i g. 3. Response patterns of the neuron to moving bright and dark rectangles and strips. A1-4) PSTHs of the responses to the movement of the bright rectangle (1,2) and bright strip (1 deg wide) covering the whole length of the vertical meridian (3,4) at the rightward (1,3) and leftward (2,4) directions of stimulus motion. B1-4) PSTHs of the responses to the movement of the dark rectangle (1,2) and dark strip (1 deg wide) (3,4) at the rightward (1,3) and leftward (2,4) directions of stimulus motion. C1-4) Graphical presentation of the RF HA length for each applied stimuli at the leftward (1,3) and rightward (2,4) movements. C5, 6) distribution of spike numbers evoked by moving stimuli.

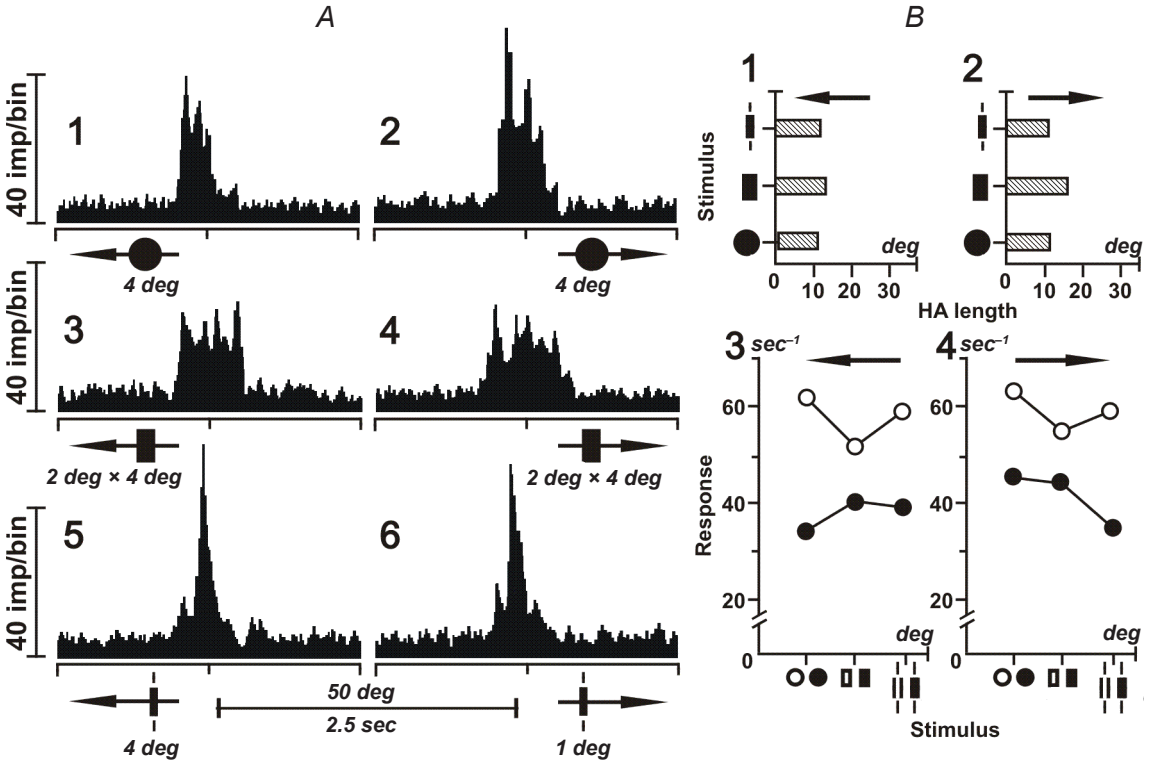
Р и с. 3. Патерни відповідей нейрона на пред'явлення рухомих яскравих та темних прямокутників і смуг.



F i g. 4. Responses of another area 21a neuron to stationary and moving visual stimuli. A1, 2) PSTHs of the responses of the neuron to the stationary flashing spot positioned in the RF test-zones (A3). A4) Localization of the RF in the visual coordinate system. B1-6) PSTHs of the responses to moving visual stimuli of different shapes and sizes. C1, 2) Graphical presentation of the HA length distribution in relation to the shapes, sizes, and motion direction of the applied moving stimuli.

Р и с. 4. Відповіді іншого нейрона поля 21а на пред'явлення стаціонарних та рухомих зорових стимулів.

observed too (shown in Fig. 3C,5,6). The properties of the next neuron of this group are illustrated in Fig. 4. This cell responded by an "*on-off*" pattern to the stationary flashing bright spot (0.5 deg) positioned consequently in the test-zones of the hand-plotted RF (Fig. 4A,1-4). The RF size measured by this way was 0.5 deg × 1 deg, the HA being 0.5 deg long. In Fig. 4B,1-6, the response patterns of this neuron are shown when bright moving stimuli of different shapes and sizes were applied. As is seen in Fig. 4, there were

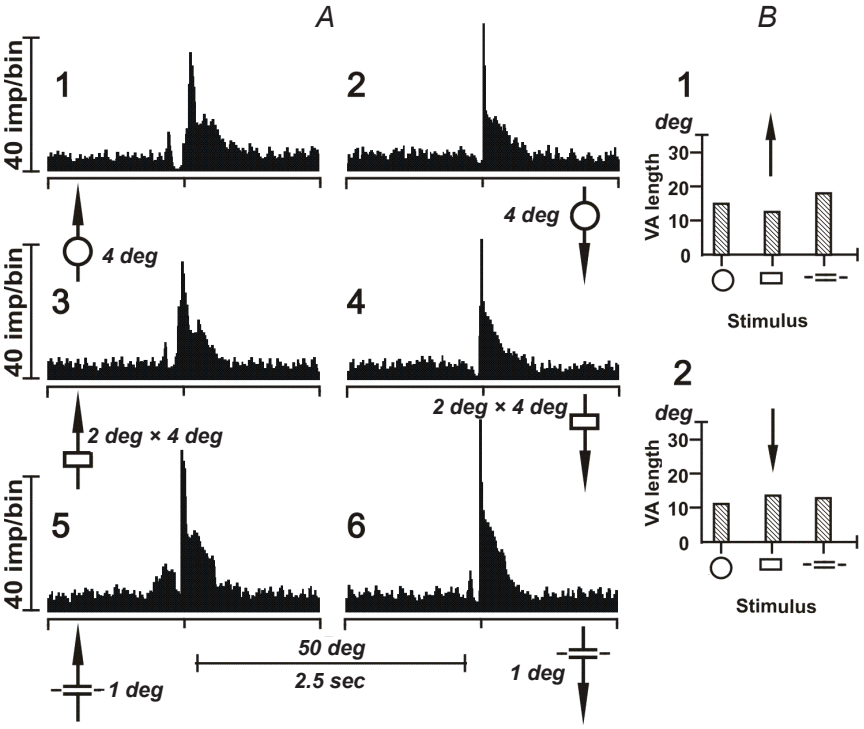


F i g. 5. Response patterns of the same neuron as in Fig. 4 to moving stimuli of the opposite contrast. A1-6) Averaged PSTHa of responses the dark moving stimuli of different shapes along the RF HA. B1, 2) Length of RF HA calculated with respect to the type of moving stimulus used. B3, 4) Spike numbers in the responses calculated for the applied stimuli of two opposite contrasts.

Р и с. 5. Патерни відповідей того самого нейрона, що й на рис. 4, на пред'явлення рухомих стимулів протилежних контрастів.

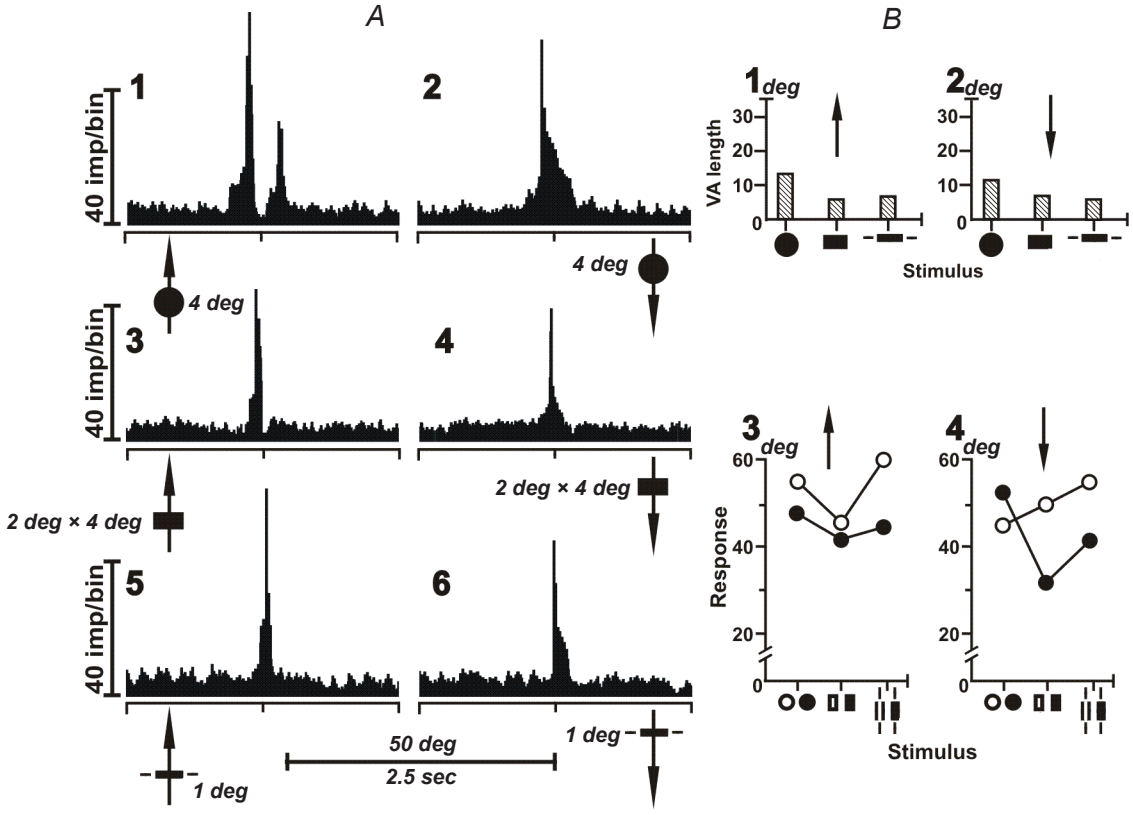
differences in the response profiles depending on the shape and magnitude of the stimulus used. A moving bright spot (4 deg) elicited long-lasting vigorous bursts of spikes without inhibitory periods at both leftward and rightward movement directions (Fig. 4B,1,2). The RF HA was 34.3 deg long at the leftward and 24.3 deg at the rightward direction of the stimulus movement (Fig. 4C,1,2). The moving bright rectangle (2 deg × × 4 deg) and 1-deg-wide bright strip covering the entire vertical meridian elicited somewhat different response patterns with intermingled inhibitory and excitatory short- and long-lasting periods (Fig. 4B,3-6). The RF HA value measured on the base of the response duration was, in this case, 21.8 deg in the leftward and 31.3 deg in the rightward directions of movement for the 2 deg × 4 deg rectangle and, correspondingly, 33.1 deg and 32.6 deg for the 1-deg-wide strip (Fig. 4B,3-6, C,1,2). Taking into account that the spatial stationary structure of the RF was homogenous "*on-off*", it is rather difficult to explain the origin of such a response profile.

Changing the stimulus contrast into opposite one (dark) also provided to a clear-cut diversification of the responses of the same neuron, depending on the shapes and sizes of moving stimuli (Fig. 5A,1-6). The moving dark spot (4 deg) led to the RFs expansion up to 11.2 deg at the leftward and 12.2 deg at the rightward movement direction (Fig. 5A1,2, B,1,2). Dramatic expansions of the neuronal RF were observed at application of the 2 deg ×4 deg dark rectangle; these were 12.5 deg at the leftward and 16.2 deg at the rightward stimulus movement directions (Fig. 5A,3,4, B,1,2). For the dark strip (1 deg wide), these values were 12.1 and 11.8 deg, correspondingly (Fig. 5A,5,6, B,1,2). Besides this, discharge numbers became smaller at application of the moving 1 deg strip covering the whole vertical meridian, comparing to those at the 2 deg × 4 deg moving rectangle, which may be indicative of the development of surround suppression (Fig. 5B,3,4). Thus, diversification at changes of the shapes and magnitudes of the applied stimuli was quite obvious. Substantial elongations of the RF axes were observed also when the movement orientation of the applied stimuli was changed into a vertical one.



F i g. 6. Response patterns of the neuron to presentation of bright moving stimuli of different shapes and sizes in the vertical orientation. A1-6) PSTHs of the responses to the moving bright stimuli of different shapes along the RF vertical axis (VA) upward and downward. B1, 2) The VA lengths measured for each type of moving stimuli.

Р и с. 6. Патерни відповідей нейрона на пред'явлення яскравих стимулів різної форми та розмірів, що рухалися вздовж вертикальної осі.



F i g. 7. Responses of the neuron to presentation of dark moving stimuli in the vertical orientation. A1-6) PSTHs of the responses to the moving dark stimuli along the RF VA. B1, 2) Graphical presentation of the VA values measured according to the responses to the moving stimuli. B3, 4) Spike numbers in the responses in relation to the type of the moving stimuli applied.

Р и с. 7. Відповіді нейрона на пред'явлення темних стимулів, що рухаються у вертикальному напрямку.

As is shown in Fig. 6, the bright spot (4 deg) moving along the RF vertical axis evoked elongation of the VA up to 15.2 deg at the upward and 11.3 deg at the downward direction of motion (Fig. 6A,1,2, B,1,2). The vertically oriented moving bright rectangle (2 deg × 4 deg) revealed VA elongations of about 12.2 deg at the upward and 13.5 deg at the downward motion directions (Fig. 6A,3,4, B,1,2). Even greater elongation (18.7 deg) was observed at the upward movement of the 1-deg-wide bright strip (Fig. 6A,5,6, B,1,2). The same neuron demonstrated elongations of the RF VA and more changes in the response profiles when moving dark stimuli were presented. As is shown in Fig. 7A,1,2, the dark spot (4 deg) evoked bimodal responses of the neuron at the upward movement along the RF vertical axis with VA at 13.1 deg (Fig. 7A,1, B,1) and a monomodal response profile is the case at the downward motion of the dark spot with the VA of 10.8 deg (Fig. 7A,2, B,2). Significant decreases in the VA values, compared to that at moving bright stimuli, were observed for the vertical movement of dark the rectangle (2 deg × 4 deg) for upward and downward motions (5.6 and 7.7 deg of the VA lengths, respectively) (Fig. 7A,3,4, B,1,2). The moving dark strip (1 deg wide) evoked elongations of the RF VA length of, correspondingly, 6 deg at the upward and 5.7 deg at the downward directions of stimulus motion (Fig. 7A,5,6, B,1,2). On Fig. 7B,3,4, changes in the spike numbers in neuronal responses are shown at two opposite contrasts of the applied moving stimuli. The maximal numbers of spikes were observed in neuron responses to the upward and downward movements of the 1-deg-wide dark and bright strips (Fig. 7B,3,4). All 27 investigated neurons with small RF dimensions stably showed elongations of the RF axes and qualitative and quantitative modifications of the response patterns described above, with mild differences.

DISCUSSION

The results of our experiments allowed us to suggest that during perception of moving visual images, the spatial structures of the RFs undergo significant dynamic changes in both size and qualitative characteristics of the response pattern, and, due to this, discrimination and diversification of visual image shapes, sizes, and motion directions became much more accurate. As a first step, a suggestion was put forward on the probable temporary reorganization of the RF stationary structure due to activation of surrounding (neighboring) groups of neurons and subsequent triggering of the networks exerting synaptic influences on the neuron under investigation.

The results of described experiments demonstrated that a group of neurons (≈18%) with small RF sizes measured by stationary flashing light spots (mean 1.5 deg²) localized in the extrastriate area 21a undergoes significant expansions of the RF horizontal and vertical axes at application of moving visual stimuli. These data allowed us to suggest that RF expansions are not merely due to a general increase in the neuronal excitability, but these effects are results of certain central processing of incoming visual information. As was earlier reported by several groups of authors [15, 23-25], the responses of the neuron to the stimuli applied inside its classical RF can be modulated by concurrent stimulation coming from the RF surrounding, which may be due to nonlinear summation of converging inputs to the neuron under investigation and also to the action of intracortical top-down feedback mechanisms [26]. Furthermore, Das and Gilbert [14] suggested that RF expansion observed in the visual cortex (area 17) results from activation of horizontal intracortical connections with their specificity for the RF properties, which contributes to the formation of the major reason for dynamic RF changes. The results of our experiments point to a high degree of diversification of incoming information concerning processing of the motion direction, contrast, and shape of a visual stimulus by the neurons in visually sensitive extrastriate area 21a. Furthermore, these authors confirmed the data presented in the previous report [7] that the stationary spatial RF structure undergo significant modifications depending on the magnitude and contrast of the applied moving stimuli. It is very likely that feedback synaptic connections exert a decisive influence too on final elaboration and central processing of visual information.

All experimental procedures involving animals were approved by the Ethical Commission at the Yerevan State Medical University and corresponded to the international standards.

The authors of this study, H. R. Aslanian, A. P. Antonian, B. A. Harutiunian-Kozak, A. V. Khachatryan, A. L. Ghazaryan, J. A. Kozak, and D. K. Khachvankian, confirm that the research and publication of the results were not associated with any conflicts regarding commercial or financial relations, relations with organizations and/or individuals who may have been related to the study, and interrelations of co-authors of the article.

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ЗАЛЕЖНЕ ВІД РУХУ ПРОСТОРОВЕ РОЗШИРЕННЯ ЗОРОВИХ РЕЦЕПТИВНИХ ПОЛІВ НЕЙРОНІВ ЕКСТРАСТРІАТНОЇ КОРИ

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Р е з ю м е

Просторова структура рецептивного поля (РП) зоровочутливого нейрона, визначена при пред'явленні стаціонарних зорових стимулів, передбачає у більшості випадків процес центральної обробки інформації щодо зорових зображень, котрі рухаються. Ми досліджували групу нейронів екстрастріатного кортикального поля 21а (приблизно 18 % обстеженої вибірки) з дуже маленькими РП (близько 1.5 град²), визначеними за допомогою пред'явлення стаціонарних зорових стимулів. Виявилося, що просторові розміри таких нейронних РП можуть зазнавати багаторазового розширення; профілі відповідей нейрона істотно залежали від величини, форми та контрасту пред'явлених рухливих стимулів. В результаті цього спостерігалася висока ступінь диверсифікації патернів відповідей нейрона залежно від вказаних властивостей рухливих стимулів. Отримані дані підтверджують гіпотезу про те, що РП нейронів екстрастріатного поля 21а піддаються тимчасовим динамічним модифікаціям через активацію нейронних груп/мереж, оточуючих вказаний нейрон, під дією рухливих зорових стимулів. Таким чином, очевидно, що обробка візуальної інформації в перебігу розпізнавання зорових образів реалізується за участі інтегративної активності певного комплексу кортикальних мереж зоровочутливих нейронів.

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