

Suprathreshold excitation of network of frog tectal neurons by discharging of single retina moving-edge detector

Antanas Kuras, Armantas Baginskas, Vaida Batulevičienė

Institute for Biomedical Research, Kaunas University of Medicine, Lithuania

Key words: retinotectal transmission, neuronal network, suprathreshold excitation, frog retina, moving-edge detector, darkness detector.

Summary. *Objective.* It has been shown that discharge of single darkness detector in the frog retina can lead to suprathreshold excitation of the tectal neurons. The present study was designed to explore whether a suprathreshold excitation of frog tectal neurons can be elicited by the discharge of single moving-edge detector.

Material and methods. The discharge of a single retina ganglion cell was elicited by the electrical stimulation. The evoked electrical activity of the tectal neurons was recorded by the carbon-fiber microelectrode brought into the optic fiber layer F.

Results. The obtained data have suggested that a discharge of a single retinal moving-edge detector elicits a suprathreshold excitation of tectal neurons. The suprathreshold excitation of the tectal neurons is achieved due to the frequency facilitation of the fast retinotectal synaptic potentials.

Conclusions. Results of the present study suggest that activation of moving-edge detector gives rise to the same effects as the activation of the darkness one. However, the stronger excitation (the longer volleys of action potentials) for the moving-edge detector is needed to evoke suprathreshold excitation of tectal neurons compared to the darkness one. This difference could be caused by a lower quantal size of neurotransmitter release in synapses of the retinotectal input from the moving-edge detector than from the darkness one.

Introduction

It is considered that a coincident activation of several presynaptic axons is required for suprathreshold excitation of the most of central neurons (1–3). However, some reports indicate that a stimulation of single presynaptic axon may also lead to suprathreshold excitation of the neurons (4–9). For example, it was demonstrated that a discharge of single retina ganglion cell might evoke a suprathreshold excitation of neurons in the frog tectum (9).

In the frog, tectum is the main center for processing visual information (10, 11). It is formed of the uppermost layers of optic fibers as well as deeper layers of neuronal bodies alternating with layers of neural fibers, which exhibit structurally and functionally complicated connections (12). The layers of optic fibers in the frog tectum are named by the letters from A to G based on different retinal ganglion cell types sending their axons to those layers (13). H. R. Maturana *et al.* (10) have established that frog tectum layer F contains terminal arborizations of both moving-edge (also known as the 3rd) and darkness (also

known as the 5th) retinal detectors. Subsequently, A. V. Kuras and N. P. Chusainoviene (14) reported that two kinds of axons of ganglion cells can be distinguished in this layer of the frog tectum on the basis of amplitude and paired-pulse facilitation of retinotectal fast synaptic potentials (fSPs). The fSPs generated by synapses of terminal arborization of the first kind have modest amplitude and exhibit large paired-pulse facilitation whereas the fSPs from terminal arborization of the second kind have large amplitude and exhibit modest paired pulse facilitation (14). Recent report suggests that terminals of the axons of the first kind in the frog tectum layer F may be attributed to the axons of the moving edge detector, and of the second kind – to the axons of the darkness detector (9).

Previously we have described the responses of the frog tectum layer F neurons elicited by a discharge of single darkness detector (9). This study was designed to explore whether a discharge of a single moving-edge detector can evoke a suprathreshold excitation of frog tectum neurons.

Material and methods

Animal surgery

Experiments were done *in vivo* with ten adult frogs *Rana temporaria*. All experiments were carried out in accordance both to European Communities Council Directive (86/609/EEC) and regulations of Kaunas University of Medicine for the care and use of laboratory animals. The experiments were approved by the Animal Care and Use Committee of the State Food and Veterinary Service of Lithuania (permission No. 30). During the surgical manipulations, frogs were generally anesthetized using a high concentration of CO₂. Regions above the tectum and around the eye were additionally anesthetized locally by subcutaneous injection of procaine (Sanitas, Kaunas) and operated on. The dorsal tectum was exposed in the way described by A. V. Kuras *et al.* (9). In short, the skin above the tectum was cut off, the skull was trepanned and the meninges were removed. The retina contralateral to the investigative part of tectum was prepared according to the method of S. A. George and W. B. Marks (15). The upper eyelid, the nictitating membrane and the sclera were excised. The lens and the hyaloid were removed by suction. The eyeball cavity was filled with the Ringer's solution (in mM: 116 NaCl, 2.5 KCl, 1.8 CaCl₂, 1.0 MgCl₂, 1.2 NaHCO₃, 0.17 NaH₂PO₄ · 2H₂O; pH 7.3–7.4). During the experiment, the exposed tectum was perfused with the same solution. Following the surgical manipulations, the edges of wounds on the scalp and eye were anaesthetized by liniment lidocaine (Sanitas, Kaunas). Then, the frogs were immobilized by an intramuscular injection of 0.2–0.3 mg of d-tubocurarine (Sigma-Aldrich, USA), intubated and ventilated by a mechanical ventilator. Subsequent injections of 0.1 mg of d-tubocurarine were applied every 20–30 minutes to keep the frog immobilized during the experimental procedures. At the end of experiments the animals were euthanized by an ether overdose.

Stimulation and recording

All recordings were done in dark conditions at ambient temperature of 17–21°C following one hour of the artificial ventilation of frog's lungs allowing the general anesthesia of CO₂ to clear. The excitation of a single retina ganglion cell (or its axon) was achieved by the stimulation method described previously (9, 16, 17). In brief, a special stimulating block composed of two five-channel sub-blocks was placed on the nasoventral quadrant of the naked retina. The channel of the stimulating block consisted of a tungsten wire of 40 µm in diameter. Distances between the centers of different channels were in the range of 70–

250 µm and the resistance of a channel to a direct current was 180–190 kΩ. A single pulse of current (17–64 µA, 50 µs) or a train of two-five such pulses with interpulse intervals of 25 ms were applied to the retina through one pair of stimulating channels using stimulus isolator Iso-DAM8 (Precision Instruments, USA). The threshold current pulses were applied every two seconds, and the trains of pulses were delivered every ten seconds up to one minute.

The tectal responses were recorded as it has been described previously (9, 16, 17). The recordings were made in tectum areas four and one according to the map of retinotopic projections (18). The microelectrode was brought into tectum depth of 250 µm where layer F is located (14, 17, 19). Then, the best correspondence between the projection of excited optic fibers and the site of recording were set by switching over the channel pairs of stimulating electrode, searching for the largest evoked mass response. The evoked mass response usually consisted of short and long latency waves. The long latency wave was strongly diminished and disappeared completely with the gradual decrease of stimulation strength. Thereafter, a magnitude of stimulating current pulse was further decreased until the recording from terminal arborization of a single retinotectal fiber was achieved. We have thoroughly checked the generally accepted criteria for the response of single retinotectal fiber: 1) the “all-or-none” characteristic of the response; 2) occurrence of the response at a threshold stimulus intensity in half of stimulation trials and an abrupt disappearance of the response in all stimulation trials when stimulus intensity was gradually turned down below of a threshold; 3) an occurrence of the response in all stimulation trials when stimulus intensity is slightly increased above the threshold; 4) redoubling of amplitude of the response at still higher stimulus intensities (15–17, 20). Responses from an individual retinotectal fiber arborization were recorded by carbon-fiber microelectrode with an improved signal to noise ratio (21). The recoding tip of microelectrode was 35–75 µm in length. The level of background activity during recordings was 20 µV. The recording signals from the amplifier Iso-DAM8 (Precision Instruments, USA) were sampled at 10 kHz. The amplifier bandpass frequency was 0.001–3 kHz.

Application of drugs

Solution of nonspecific antagonist of ionotropic glutamate receptors kynurenic acid (4-hydroxyquinoline-2-carboxylic acid, Sigma-Aldrich, USA) was applied onto the tectum by perfusion with a rate of 0.4 ml/min. The 0.5 mM solution of kynurenic acid was freshly prepared before use by dilution in Ringer's

solution.

Data analysis

The response in the tectum elicited by a single threshold current pulse delivered to a frog retina consisted of a presynaptic action potential (AP) followed by a fast synaptic potential (Fig. 1A). Tectal responses to a train of three-five minimal current pulses with interpulse intervals of 25 ms contained, beside the APs and fSPs, a slow negative wave (sNW) and population responses, which followed the fSPs (Fig. 1B and 2). The latency of the APs with respect to the stimulus artefact, the amplitude of first AP from peak-to-peak (A_{AP1}), the amplitudes of first and second fSPs (A_{SP1} and A_{SP2}) and the half amplitude duration of first fSP ($T_{1/2}$) at the interpulse interval of 25 ms were measured. A paired-pulse facilitation of the fSPs was estimated as a ratio A_{SP2}/A_{SP1} . The investigated ganglion cell was regarded as a moving edge detector in a case ratio $f_{2/1}$ was above 1.8 (9, 14). If ratio $f_{2/1}$ of the investigated ganglion cell was below 1.8, this cell was not considered as a moving edge detector, and such ganglion cell was ignored in the present study. The recordings from 15 individual retinotectal axon terminals have met the above criterion of moving-edge detector. Averaged values in the text are given as mean \pm SD.

Results

Action potential and fast synaptic potential

The tectal responses to a threshold stimulus pulse consisted of a terminal action potential and individual fast synaptic potential generated by synchronously active synapses of an excited single retinotectal fiber (Fig. 1A). Decrease of threshold stimulation intensity by 0.4–0.7 μ A led to an abrupt disappearance of the responses in all trials. The size of the recorded APs and fSPs did not vary significantly until the stimulus intensity exceeded the threshold value by more than 3–6 μ A. This demonstrates sufficiently large margin of safety for the stimulation of a single retinal ganglion cell. The amplitudes of the fSPs have fluctuated from trial to trial slightly, indicating that large number of synapses participate in their generation (Fig. 1A).

The APs had a biphasic (+ –) or triphasic (+ – +) waveforms and occurred at latencies of 6.3–10.5 ms from the stimulus artefact (Fig. 1). All of the fSPs had a negative waveform indicating an excitatory nature of all investigated retinotectal synapses. In different ganglion cells, the amplitudes of the terminal action potentials A_{AP1} ranged from 52 μ V to 186 μ V, while the amplitudes of conditioning synaptic potentials, A_{SP1} , fell between 33–107 μ V (65 ± 27 μ V on average, $n=15$). A half maximum duration of the fSPs,

$T_{1/2}$, varied from 3.9 to 7.3 ms (5.6 ± 1.0 ms, $n=15$). The fSPs showed paired-pulse facilitation with $f_{2/1}$ ratio ranging from 1.8 to 2.3 (2.0 ± 0.1 , $n=15$).

Population responses

A train of three-five current pulses delivered to retina elicited a volley of action potentials of single moving-edge detector (Fig. 1B and 2). The tectal responses elicited by such train of action potentials of single moving-edge detector have consisted of the fSPs, population responses and sNW (Fig. 1B and 2). The fSPs exhibited frequency facilitation, however, there was no temporal summation of the fSPs (Fig. 1B and 2). The observed population responses were of two types. The population responses of the first type usually were negative spikes and occasionally – negative-positive spikes (Fig. 1B and 2). The population responses of the second type consisted of a diphasic (+ –) or triphasic (+ – +) presynaptic action potential followed by a negative postsynaptic potential with a latency of about 1 ms (Fig. 1B and 2). The action potentials of the second type population responses were not always clearly seen in the recordings while the associated individual postsynaptic potentials were.

The population responses were observed in all 15 recordings of the tectal activity elicited by a train of three-five action potentials of single moving-edge detector. A train of three APs was sufficient to elicit population responses (Fig. 2A) in five cases, while a train of four APs was needed (Fig. 1Ba) in seven cases. Even five consecutive APs were required to evoke population responses in three cases. However, no population responses were elicited by a train of two action potentials of single moving-edge detector (Fig. 1Bc). The frequency facilitation of the consecutive fSP is required to elicit population responses (Fig. 1B and 2). In 13 of the cases, the population responses of both types were observed together except two cases when the population responses of the second type were seen only. The population responses of both types occurred both on tops and on decreasing slopes of the fSPs (Fig. 1B and 2). Some population responses of the second type were also observed at some delay after the fSPs. In the latter case, they were usually situated on the sNW (Fig. 1B and 2A, C). The amplitudes of both types of population responses, recorded in the depth of the tectum where the corresponding fSPs had maximal amplitudes, ranged from 20 to 150 μ V.

The amplitudes of the fSPs have decreased gradually and the population responses of both types have disappeared suddenly by an application of solution of kynurenic acid in all four cases tested (Fig. 2 B). This effect of the kynurenic acid was reversible: the amplitudes of the fSPs have been restored and the

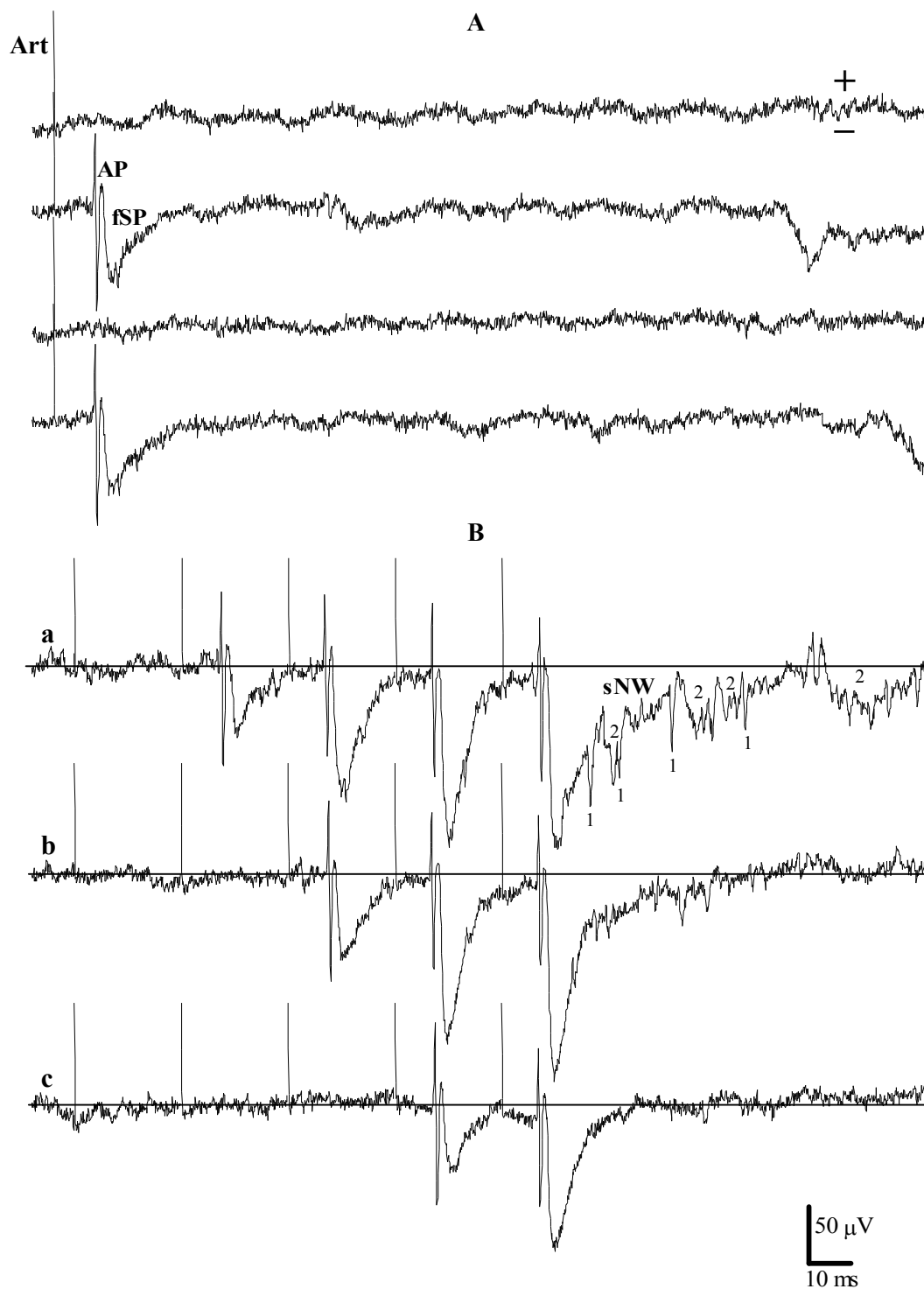


Fig. 1. Responses evoked in the frog tectum by the threshold stimulation of single retinal moving-edge detector

(A) The stimulus consists of a single current pulse applied every two seconds. The presynaptic terminal action potential (AP) and individual fast synaptic potential (fSP) comprise the response. Artifacts (Art) of the stimuli are seen at the beginning of the sweeps. (B) The stimulus consists of five current pulses with interpulse intervals of 25 ms delivered every ten seconds. The ganglion cell responds to stimulation by generation of a volley of four APs (a), three APs (b) or two APs (c). A volley of four action potentials (a) elicits, besides fSPs, many population responses and a slow negative wave (sNW). Population responses of the first type (marked by number 1) appear as negative spikes while population responses of the second type (marked by number 2) are seen as polyphasic spikes followed by synaptic potentials. Note that volleys of two APs (c) and three APs (b) fail to elicit population responses.

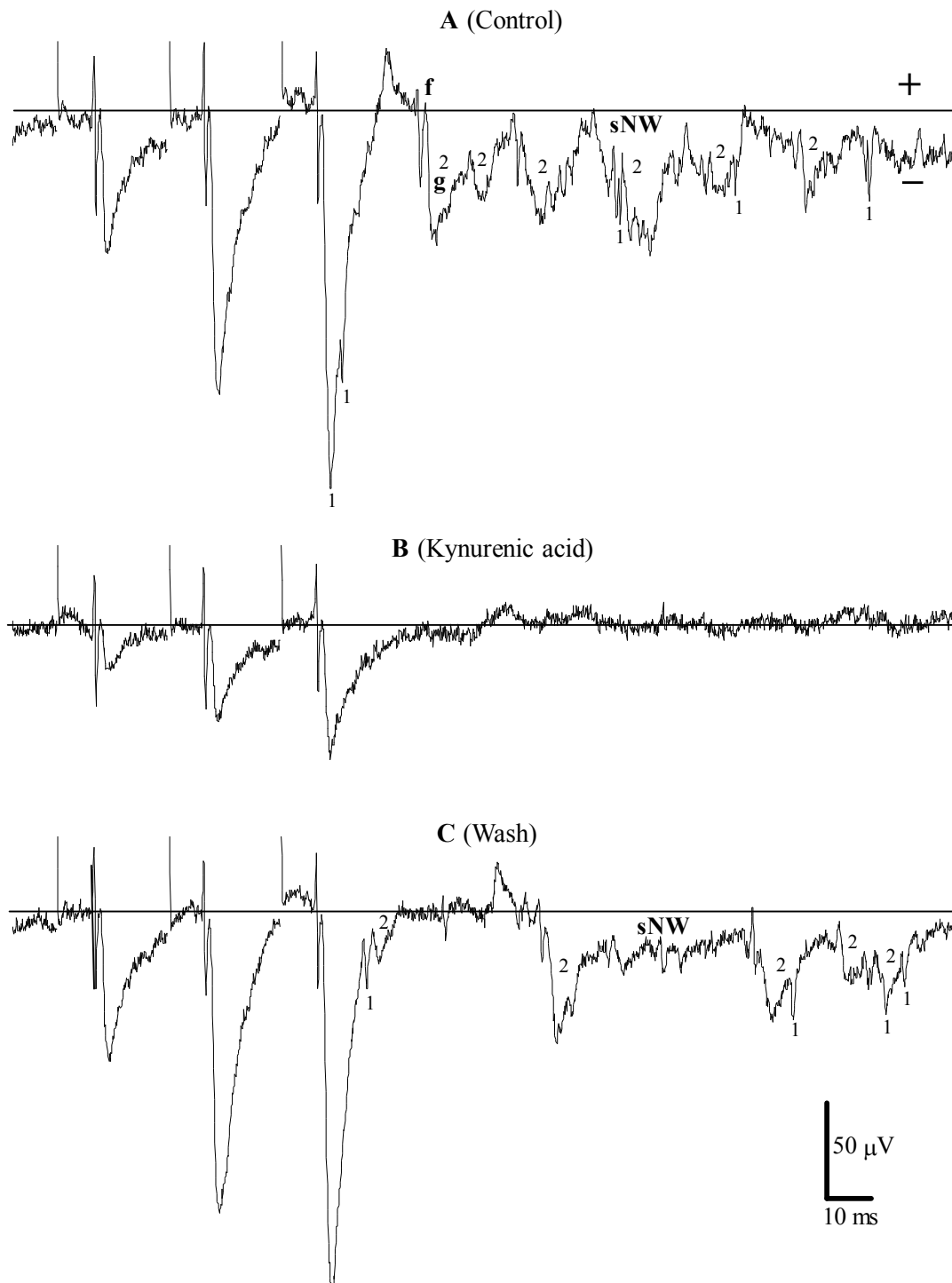


Fig. 2. Effect of kynurenic acid on tectal responses elicited by single moving-edge detector

(A) The response of the tectum to the stimulation of a single ganglion cell in the retina by a train of three current pulses with interpulse intervals of 25 ms. The population responses and a slow negative wave (sNW) are seen in the recording. Population responses of the first type (marked by number 1) appear as negative or negative-positive spikes while population responses of the second type (marked by number 2) are seen as polyphasic spikes (f) followed by synaptic potentials (g). (B) Weakening of the retinotectal transmission by application of 0.5 mM of kynurenic acid for eight minutes leads to disappearance of both the population responses and the slow negative wave. Note that the amplitudes of the fast synaptic potentials were significantly decreased by an application of kynurenic acid. (C) The wash of the kynurenic acid for 13 minutes with Ringer's solution restores both the population responses and sNW. Note that the amplitudes of the fast synaptic potentials were restored following the wash of kynurenic acid.

population responses reappeared after the perfusion of the tectum with Ringer solution for 8–15 minutes (Fig. 2C).

Discussion

The population responses of two types were observed in the recordings following the volley of action potentials of single moving-edge detector. The sudden disappearance of the population response with gradual decrees of the strength of retinotectal synaptic transmission shows that the observed population responses reflect a suprathreshold activation of frog tectal neurons (9). Such population responses were also observed in previous study of frog tectal neurons network excited by single darkness detector (9). In the present study we have showed that a volley of action potentials of a single moving edge detector also evokes a suprathreshold excitation of tectal neurons.

We suggest that the population responses of the first type, i.e. negative and negative-positive spikes, reflect a discharge of neurons situated in the frog tectum layers 8 and 6. It is known that axon of the pear-shaped neurons of the layer 6 originates from the dendrite far away from the cell body and goes back to the layers of terminal arborizations of optic fibers (12, 22, 23). Thus, the negative spikes most likely reflect a discharge in axon hillocks of the pear-shaped neurons of the frog tectum layer 6. It is also known that the large efferent ganglionic neurons are situated in the layer 8, which lies under optic fiber layer F (12). The negative-positive spikes may reflect the somatic discharge of those neurons in the frog tectum layer 8. The population responses of the second type, i.e. polyphasic spikes followed by excitatory synaptic potentials, reflect an activity of axon terminal arborizations of tectal neurons. Those neurons could be recurrent excitatory tectal neurons, for example pear-shaped ones of the tectum layer 6, or neurons from other nuclei of the frog brain that recurrently project back to the tectum, for example the neurons from nucleus isthmi (24).

The population responses in our recordings disappeared suddenly in a threshold manner when the strength of retinotectal transmission was weakened by an application of the kynurenic acid (it was established earlier that retinotectal transmission in lower vertebrates is glutamatergic (17, 25). We suggest that this observed threshold for appearance of the population responses reflects a threshold for firing of tectal postsynaptic neurons excited by a volley of action potentials in single retinotectal fiber.

Some delayed population responses of both types observed in the recordings were associated with the

slow negative wave. Those population responses may reflect delayed terminal activity of the excited pear-shaped neurons located in tectum layer 6 (12). Such delayed terminal activity could be evoked by a slow sustained neuronal soma suprathreshold depolarization. A slow inward dendritic current responsible for the dendritic bistability may cause such a depolarization (26, 27), therefore, a slow negative wave observed in our recordings could reflect the steady depolarization of multiple branchlets of the dendritic tree of tectal pear-shaped neurons. Such delayed population responses of the second type could also reflect an activity of isthmotectal terminals. It is known that the nucleus isthmi of the frog receive inputs from the ipsilateral tectum and projects bilaterally to the tectum, making up recurrent connections to the optic fiber layers (24). Interestingly, the reported delay of responses in isthmotectal recurrent connections 10–20 ms is consistent with the latency of some population responses observed in the present study (28).

In our resent study it was showed that a volley of two-three action potentials of a single retinal darkness detector reliable evokes a suprathreshold excitation of recurrent and efferent tectal neurons (9). Results of the present study indicate that longer volleys (three-five action potentials) are required for suprathreshold excitation of tectal neurons by single moving-edge detector. This difference could be caused by a lower quantal size of neurotransmitter release in synapses of the retinotectal input of moving-edge detector compared to the darkness detector (14).

Conclusions

1. The discharge of frog single retinal moving-edge detector can elicit a suprathreshold excitation of tectal neurons.
2. Recurrent connection circuits to the optic fiber layers of the tectum are activated by a discharge of single moving-edge detector.
3. The suprathreshold level of the single retinotectal input of moving-edge detector is achieved due to the frequency facilitation of the fast retinotectal synaptic potentials.
4. The longer volley of action potentials of moving-edge detector is required to elicit a suprathreshold excitation of tectal neurons compared to the darkness detector.

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Varlės akies tinklainės judančio krašto detektoriaus sukeltas tektumo neuronų tinklo viršslenkstinis sužadinimas

Antanas Kuras, Armantas Baginskas, Vaida Batulevičienė

Kauno medicinos universiteto Biomedicininii tyrimų institutas

Raktažodžiai: retinotektalinis perdavimas, neuronų tinklas, viršslenkstinis sužadinimas, varlės akies tinklainė, judančio krašto ir tamsos detektoriai.

Santrauka. Darbo tikslas. Ankstesni tyrimai rodo, kad varlės akies tinklainės vieno tamsos detektoriaus sužadinimas gali sukelti tektumo neuronų viršslenkstinį aktyvumą. Šio darbo tikslas – nustatyti, ar varlės akies tinklainės vieno judančio krašto detektoriaus sužadinimas gali sukelti tektumo neuronų viršslenkstinį aktyvumą.

Tyrimo medžiaga ir metodai. Viena varlės tinklainės nervinio mazgo ląstelė buvo sužadinama elektriniu stimuliavimu. Tektumo regos skaidulų F sluoksnyje angliniu elektrodu buvo registruojamas sukeltas tektumo neuronų elektrinis aktyvumas.

Rezultatai. Gautais duomenimis, varlės akies tinklainės vienas judančio krašto detektorius gali viršslenkstiškai sužadinti tektumo neuronus. Viršslenkstinis tektumo neuronų sužadinimas įvyksta dėl greitų retinotektalinių sinapsinių potencialų dažninės fasilitacijos.

Išvados. Šio tyrimo duomenys rodo, jog judančio krašto detektorius gali sukelti panašų tektumo neuronų sužadinimą kaip ir tamsos detektorius. Tačiau, lyginant su tamsos detektoriumi, stipresnis sužadinimas (ilgesnis veikimo potencialų pliūpsnis) yra reikalingas norint sukelti tektumo neuronų viršslenkstinį aktyvumą judančio krašto detektoriaus sužadinimu. Šis skirtumas gali būti sąlygotas judančio krašto detektoriaus retinotektalinėse sinapsėse išskiriamo mažesnio neurotransmiterio kiekio nei tamsos detektoriaus.

Adresas susirašinėti: A. Kuras, KMU Biomedicininii tyrimų institutas, Eivenių 4, 50009 Kaunas
El. paštas: kuras@trc.kmu.lt

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