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Direction-selective units in the frog's basal optic root nucleus

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Electrophysiological responses from 91 direction-selective (DS) units located in the basal optic root (nBOR) and the adjacent dorsomedial area have been recorded extracellularly in the frog (*Rana temporaria* L.). Based on characteristics of the recorded responses, 23 of the units are considered to be retinal ganglion cells' (RGC; axon terminals). The majority of the remaining 68 units were considered to be DS neurons of the nBOR. The results of our study suggest that in the nBOR area there might be four subtypes of the tegmental and retinal DS units that respond selectively to stimuli moving in the dorso-ventral, ventro-dorsal, caudo-rostral and rostro-caudal directions. The receptive field (RF) sizes of the nBOR DS neurons were estimated to be about 30–60°, while those for the retinal units were significantly smaller — just 6–8°. In response to abrupt darkening within the units' RFs, both the nBOR DS neurons and the RGC DS units respond by a weak discharge. Our results indicate that the frog nBOR DS neurons integrate the inputs from the retinal OFF-type DS units over relatively large segments of the visual field.

Keywords: Frog; vision; nucleus of basal optic root; retina; ganglion cells; direction-selective tegmental neurons; directional selectivity.

1. Introduction

In Anura, as well as in other studied vertebrate animals, tegmentum of the midbrain and pretectum (the stem part of the midbrain) receive direct inputs from the retina. Retinal ganglion cells that feed the tegmental system, send their axons to the basal optic root (nBOR) nucleus, which is located near the ventral brain surface close to the oculomotor nucleus (of the III cranial nerve). In frogs, the destruction of the basal optic tract or its nucleus leads to the partial or complete loss of the optokinetic nystagmus, i.e., the head movement following the movement of structured background (Lasar, 1973; Fite *et al.*, 1977, 1980). Later in the study of Montgomery *et al.* (1982) it was clarified that the complete loss of the horizontal optokinetic nystagmus in frog was evoked only by the destruction of tegmentum area located medially in respect to nBOR (in the peri-nBOR). On the other hand, destruction of the basal

optic tract and nBOR resulted in a reduction of the frequency of horizontal nystagmus only. Bilateral destruction of nBOR in turtle and pigeon resulted also in a reduction of horizontal nystagmus frequency (Fite & Scalia, 1976). The similar results were obtained in the chinchilla following bilateral lesion of the medial nucleus (Kimm *et al.*, 1979). It was also shown that after tectal ablation three modes of behavior disappeared in goldfish: optomotor response (swimming with the stripes in a rotating striped drum), food pellet localization and shadow-induced deceleration of respiration, but at the same time two modes of behavior were preserved: optokinetic nystagmus (movement of the eyes with the stripes in a rotating striped drum) and dorsal light reflex (Springer *et al.*, 1977).

The studied visual nBOR neurons and the proximate surrounding neurons are characterized by direction selectivity to moving visual stimuli as well as by spontaneous electrophysiological activity. The size of their receptive fields (RFs) can get as large as tens of angular degrees (Kondrashev & Orlov, 1976b; Gruberg & Grass, 1984). However, no clear classification of these cells either by type of response (ON, OFF or ON-OFF) or by preferred directions was made in those studies. In comparison to the nBOR direction-selective units, very little is known on the functional properties of the retinal ganglion cells sending their axons to the nBOR. Some initial information on direction-selectivity in the frog's retinal ganglion cells was obtained with electrophysiological recordings from an isolated frog eyecup (Bäckström *et al.*, 1978). In our earlier study, two types of responses (presumably preferring caudo-rostral and venttro-dorsal direction) from the axons of direction-selective retinal ganglion cells targeting the nBOR area were observed (Bastakov *et al.*, 1992). Functional properties of neurons of the accessory optic system (AOS) are of interest because of their relation to the optomotor responses and their possible role in the eye and head stabilization relative to environment (Lasar, 1973; Kondrashev & Orlov, 1976a). Here, we show that both, the nBOR DS neurons and their putative input-units direction-selective RGCs, are presumably represented in the AOS by four similar subtypes according to their preferred directions. All of the DS units are the OFF-type neurons. The only difference between the DS units of the tegmental and the retinal origin was found in the relative size of their RFs: large for the nBOR neurons and small for the RGCs. Our preliminary results could demonstrate the fundamental difference between the anuran and the well-studied mammalian AOS.

2. Materials and Methods

2.1. *Preparation and recordings*

Experiments were performed over a period of 1 year. A total of 58 frogs (*Rana temporaria L.*) were used in the experiments. The body length of the experimental animals was 5–7 cm. All surgical procedures were conducted under general anesthesia. After the injection of 0.15–0.20 mL of a 1% solution of MS222 (3-aminobenzoic acid ethyl ester) into the spinal lymphatic sac, the animals were immobilized with d-tubocurare and then placed on ice. Responses of all direction-selective units

were recorded from the nBOR. The position of the basal optic nucleus in the intact brain was located based on the previously published data (Kemali & Braitenberg, 1969; Gruberg & Grass, 1984; Cochran *et al.*, 1984; Montgomery *et al.*, 1981; Podugolnikova *et al.*, 1992). Generally, the neural structures were made available for the electrophysiological recordings through the opening in the skull that was made over the palate. However, in some cases the nBOR was reached with an electrode through the tectum from above. In both cases, the extracellular impulse activity was recorded with low-resistance (200–500 KΩ) metal-in-glass platinized microelectrodes (Gestesland *et al.*, 1959).

2.2. *Visual stimulation and data processing*

Computer generated visual stimuli, i.e., moving black stripes of various sizes were presented over the white stimulation area of the computer controlled CRT monitor to the right eye of the frog. The monitor was located at a distance of about 30–40 cm from the right eye of the animal. RFs of recorded DS units were approximately positioned in the center of the stimulation area. The speed of a stripe moving over the stimulation area on the monitor was about 11°/s. Once a single unit was recorded and the size of its RF was measured, the experiment on direction-selectivity was initiated. The start of stimulus movement within the frog's RF was synchronized with the pulse accumulation system of the neuron response. In the data analysis that followed the experiment only those spikes that exceeded the predetermined amplitude threshold were used. Experimental data were collected and processed in a system of three mutually connected and synchronized computer modules using special software package described in detail elsewhere (Damjanović *et al.*, 2009; Maximov *et al.*, 2005a, 2005b; Maximov & Maximov, 2010). In order to define the type ("ON", "OFF" or "ON-OFF") of each of the recorded DS units of both retinal and tegmental origin, they were stimulated by broad stripes that exceeded in size the stimulation area (Fig. 1). This stimulation procedure was as follows. Initially the leading edge of the broad black stripe moved into the white stimulation area located in the central part of the monitor (Fig. 1(a)). After the leading edge of stimulus crossed the area of stimulation, the central square remained darkened for a short time (Fig. 1(b)), and subsequently the trailing edge of the stimulus moved out of the stimulation area (Fig. 1(c)). Discharges of recorded units evoked by leading and trailing edges of the stimulus were determined as OFF-type and ON-type responses, respectively.

2.3. *Procedures*

After a single DS unit had been isolated and the approximate position of its RF had been found, we proceeded with measuring its directional tuning curve (polar diagram) with contrast edges moving in different directions across the unit's RF. In the course of the experiment, the monitor and the stimulation area on its screen were positioned in the visual field of the frog so that the stimulation area would cover the

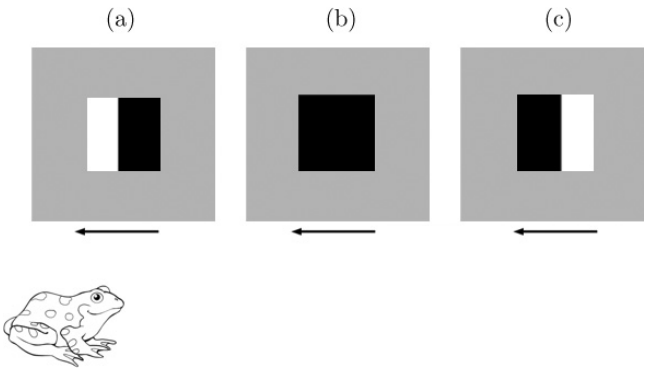

Fig. 1. Stimulation by the moving broad stripe exceeding stimulation area in width. White square stimulation area is located in the center of monitor. Initially the leading edge of the broad black stripe moves into the stimulation area (a). After the leading edge of stimulus leaves the area of stimulation the central square remains darkened for a short time (b), and subsequently the trailing edge of the stimulus moves out of the stimulation area (c). Discharges of recorded units evoked by leading and trailing edges of the stimulus were referred as OFF-type and ON-type responses, respectively. Direction of stimulus movement is marked by the arrow on the bottom. Orientation of the frog relative to direction of stimulus movement is demonstrated.

estimated RF for the unit. After that the values of the following stimulation parameters were specified: the velocity of the stimulus movement, the relative brightness of the stimulus (as a rule black), the background for the stimulation area (as a rule white), the initial direction of the stimulus movement, the total number of different directions of movement (usually 12), and, finally, the number of repetitive trials in each direction (usually 3). Mean number of spikes was calculated over the repeated trials for each of the directions of stimulus movement. After the responses of the unit to the stimulus moving in each of the 12 directions were recorded, an additional control trial was performed in which the stimulus moved along the first direction in the series, in order to test for the stability of the unit's response. The preferred directions of the stimulus movement was then determined according to the phase of the first harmonic of Fourier transform of the polar diagram.

The RF width along the preferred direction of the stimulus movement was evaluated on the basis of the duration of spike discharge, evoked by the movement of adequately oriented contrast stripes across the stimulation area. The duration of the response was determined as the time interval between the first and the last spikes in the discharge that was in turn measured using a special procedure based on the maximum likelihood method described elsewhere (Maximov *et al.*, 2005b). Figure 2 demonstrates the distribution of RF sizes, evaluated by likelihood method in 38 DS units recorded during the last three months. One can see that two main groups of units can be distinguished — those with relatively small RFs not larger than 10°, and those with significantly larger RFs exceeding 20° in diameter. Responses of DS units characterized by small RFs were attributed to RGCs, whereas the responses of units with larger RFs were referred to tegmental DS neurons.

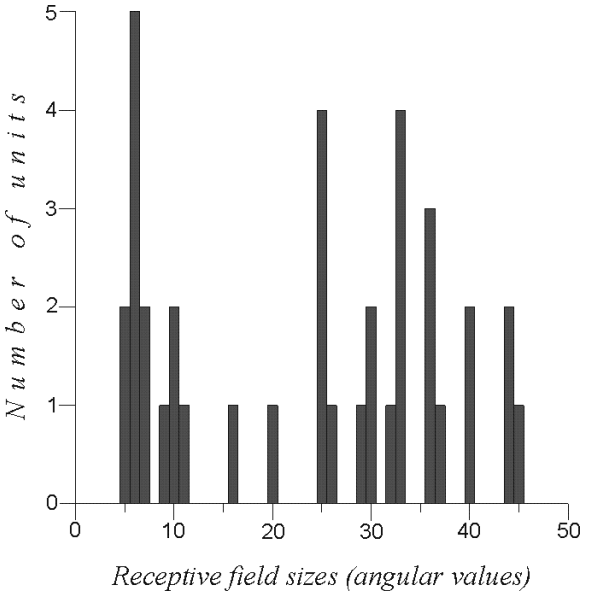

Fig. 2. Distribution of RF sizes (angular values) evaluated by the maximum likelihood method in 38 nBOR DS units of *R. temporaria* L. Detailed explanation in the text.

3. Results

In our experiments first the low-amplitude "group response" was recorded at the moment the electrode reached the ventral brain surface of the nBOR area. Apparently, such "group response" was recorded from several retinal ganglion cells' axon terminals. The "group responses" were recorded when both moving stripes and the overall darkening of the visual scene were used in the stimulation. As the electrode was guided some further into the brain tissue, single unit responses of the nBOR neurons as well as those from single RGC units (axon terminals) were recorded. These single responses are restricted to a depth of about 100 μm. We could distinguish the nBOR neurons' activity from that of the RGC units due to the fact the former cells were characterized by spontaneous spike activity, while the latter were not.

All above-mentioned units of the nBOR area, the nBOR neurons and the retinal GCs that send their inputs in the area are characterized by pronounced direction selectivity. An example of a polar diagram for one of the retinal DS units that is characterized by selective response to visual stimuli moving in the caudo-rostral direction is shown in Fig. 3. The unit was stimulated by broad black stripes consecutively moving in 12 different directions over the white background within RF of the unit. The two diagrams correspond to the responses of the unit to stimulation by the leading edge of the black stripe moving into the RF over the white background (Fig. 3(a)) and by the trailing edge of the same stimulus moving out of the RF (Fig. 3(b)). One can see that the leading edges of the moving stimuli evoked considerable excitation of the unit when the direction of the movement was close to the preferable (caudo-rostral). However, the same DS unit did not respond to the trailing

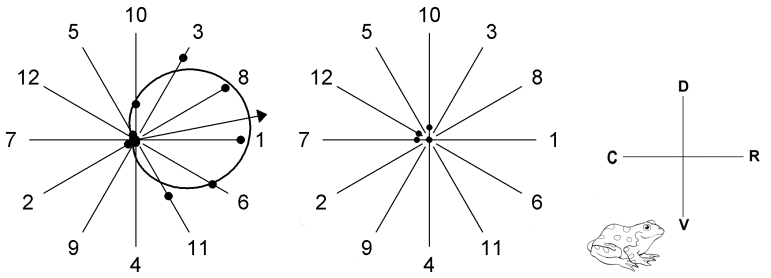

Fig. 3. Polar response patterns of a frog direction-selective unit of retinal origin selective to caudo-rostral direction of stimulus movement. Diagrams correspond to discharges to the leading (a) and the trailing (b) edges of stimuli. Responses to broad black stripes moving in 12 directions at a speed of 11°/s against a white background are shown. Stimuli were presented in three repeated runs for each direction. Numbers at the ends of radius-vectors in the polar plot indicate a sequence of presentations of different directions. Dots mark a mean number of spikes in responses recorded for each direction. Solid line is an approximation of experimental data by harmonic functions of first order. Preferred direction of the cell, determined according to the phase of first harmonic of the Fourier transform, is marked by the black arrow. (c) The coordinate directions in the visual field of the frog are designated on the right panel of the figure (R – rostral; C — caudal; D — dorsal; V — ventral).

edges of the same stimuli, no matter in which direction they moved. Thus, the unit responded only to the stimuli that corresponded to the relative darkening of its RF and can be considered to be an OFF-type DS unit. It should be noted here that all DS units studied (both of the retinal and tegmental origin) were exclusively OFF-type cells.

The nBOR area itself is very small and its retinotopical organization is still questionable not known in sufficient detail. Both the difficulties associated with the location of the required DS units of the nBOR area as well as the constraints associated with the selection of those units which RFs corresponded to the stimulation area on the computer monitor, lead to a very limited dataset of individual DS units. Thus, the limited number of DS units recorded in our experiments provide only preliminary results on the functional composition of the populations of direction-selective tegmental and retinal units of the nBOR area. Examples of characteristic polar response patterns of the tegmental and retinal DS units are shown in Figs. 4(a) and 4(b), respectively. As it can be seen from the picture, the patterns of direction selectivity were similar between the tegmental and RGC DS units of the nBOR area. Though for some of the units the preferred direction was evident in the experiments, the data analysis on the preferable directions performed for all of the 91 recorded units did not demonstrate any obvious clustering of the vectors corresponding to the preferable directions of the stimuli movement (Fig. 5). Thus, further research is required in order to unambiguously classify the preferred directions of stimulus movement for the DS units of the frog AOS.

Though the dataset acquired in our research was not enough to segregate DS units of the nBOR area according to the preferable directions of movement of visual stimuli, we were able to obtain some further data on both the tegmental and retinal

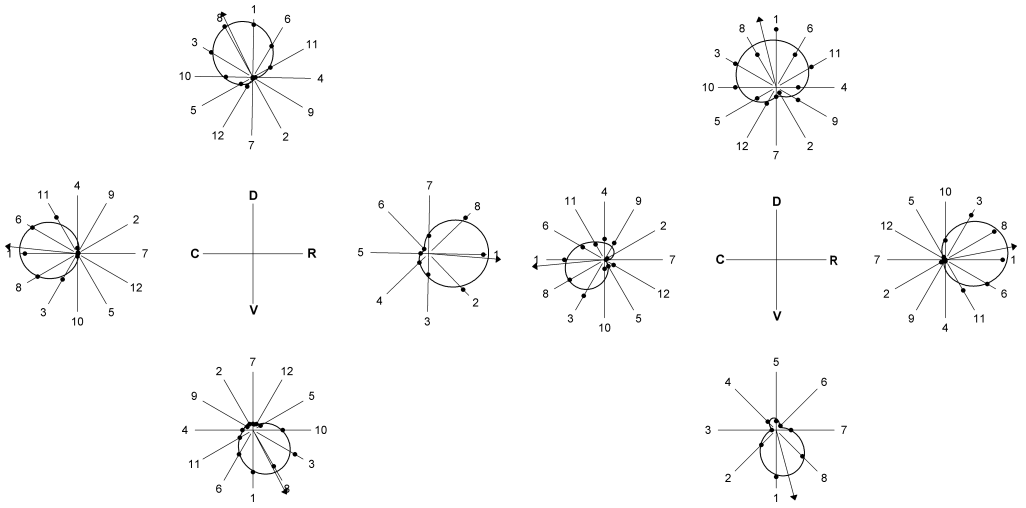

Fig. 4. Polar response patterns in four direction-selective neurons of the frog nBOR (a) and retinal DS units that send their inputs into the nBOR area (b). Four preferable directions were identified for the DS units: caudo-rostral, dorso-ventral, rostro-caudal and ventro-dorsal. Responses of the units to the leading edges of broad black stripes moving in either 8 or 12 directions at a speed of 11°/s against a white background are shown. The stimuli were presented in three consecutive runs for each of the direction. Other conventions are the same as in Fig. 3.

units of the area. These data provide some first insights into the functional role of basal optic system in the final integration of the visual afferent flow in the anuran visual system. The size of RF of the direction-selective retinal ganglion cells is approximately 6–8° (Fig. 2). These units (i.e., retinal ganglion cells) are characterized by the absence of any spontaneous electrophysiological activity. These two properties (small RF size and the lack of spontaneous activity) distinguish their responses to visual stimuli used in the experiment from those of the nBOR neurons. Contrary to

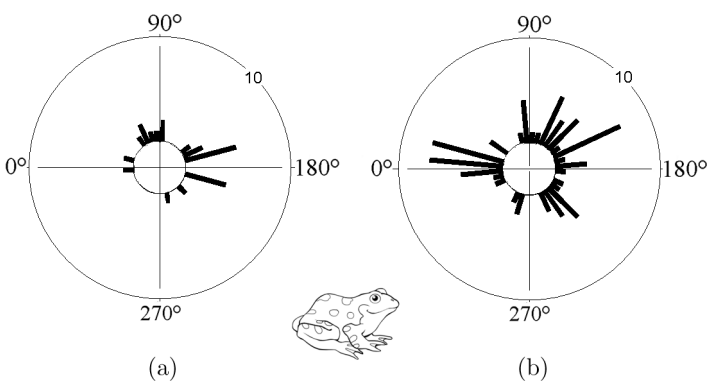

Fig. 5. Histograms of preferred directions for retinal DS GCs and nBOR DS neurons represented in polar coordinates. (a) Distribution of preferred directions calculated in 23 DS RGCs. (b) Distribution of preferred directions calculated in 68 nBOR DS neurons. Degree of clusterization was 10°. Orientation of the frog relative to directions of stimulus movement is demonstrated.

Fig. 6. (a) Firing pattern of one frog nBOR DS neuron selective to caudo-rostral direction of stimulus movement (OFF-type unit). Response to narrow black stripe (2.5° in diameter) moving in a preferred direction at a speed of 11°/s against a white background is shown. Direction of stimulus movement is marked by an arrow on the top. (b) Averaged spike form for the nBOR DS unit shown in expanded time scale (negativity upward).

the retinal DS units, DS neurons of nBOR have large RFs, as can be judged based on the durations of the spike trains (Fig. 6(a)). The waveform of individual spikes of the DS neurons' discharges was studied in detail. In extracellular recordings, made from the axons of the RGCs the spikes as a rule have a triphasic waveform with a positive deflection before the main negative wave, whereas the spikes that are recorded in the vicinity of the cell body of the DS neurons that receive inputs from the DS RGCs are biphasic and lack such a deflection (Maximova *et al.*, 2012). In our study the spikes recorded for the putative nBOR units were also characterized by the biphasic response, what confirms the tegmental origin of the neurons (Fig. 6(b)). Finally, it should be noted that in response to general illumination change both types of DS units showed weak discharge to the "light off".

The leading edge of broad dark stripes moving into the RFs of the DS units of the nBOR area in the preferred direction for the given unit evoked pronounced discharges. Thus, both the tegmental and RGC DS units can be described as the OFF-type neurons. Given that there is no pronounced difference between the preferred direction of visual stimuli between the tegmental and retinal DS units, the only obvious difference that we could reveal in our study apart of the spontaneous activity in the nBOR neurons, was in the size of their RFs: larger in case of the tegmental neurons (30° and larger) and smaller for the retinal DS cells (6–8°) (Fig. 2). The extralarge RF sizes of the tegmental DS neurons indicate that they might integrate inputs from the retinal OFF-type DS units over large segments of the visual scene.

4. Discussion

Our results are consistent with the data presented in other publications on the functional properties of the nBOR neurons (Kondrashev & Orlov, 1976b; Gruberg & Grass, 1984; Bastakov *et al.*, 1992). All DS units studied, both, the local tegmental neurons and the retinal ganglion cells that send their axonal inputs to the nBOR area were characterized as OFF-type direction-selective neurons: they did only respond to the relative darkening within their RFs.

The functional characteristics of the investigated direction-selective retinal cells and DS neurons of the nBOR area correspond to the general functional role of the

AOS, i.e., the detection of the global slip of the visual field as a result of the motion of the animal itself and fixing large dark objects within the visual scene. Direction-selective neurons of the AOS of different vertebrates have large RFs and are most sensitive to large moving stimuli, as it was shown in the goldfish (Masseck & Hoffmann, 2009), frog (Katte & Hoffmann, 1980; Bastakov *et al.*, 1992; Pushchin, 2013), pigeon (Winterson & Brauth, 1985), rabbit (Collewijn, 1975). The most thoroughly studied are the DS units of the mammalian AOS. Contrary to the AOS in the Anura species that has two nuclei (tegmental nucleus lentiformis mesencephali and the nBOR), the mammalian AOS consists of three nuclei (the medial terminal nucleus, the lateral terminal nucleus and the dorsal terminal nucleus) (Ebbeson, 1980). DS ganglion cells projecting to the mammalian AOS respond only to the leading edge of bright stimuli moving over a relatively dark background in the cell's RF, and are therefore referred to as the ON DS ganglion cells. ON DS neurons appeared to be divided into three distinct groups, characterized by the preferred movement directions of visual stimuli: the caudo-rostral, the ventro-dorsal, and the dorso-ventral directions that are separated by about 120° in polar coordinates (see review of Borst & Euler, 2011). The preferred directions correspond to the three axes of the semicircular canals in the inner ear (Simpson *et al.*, 1988). It is likely that the mammalian AOS are coactivated with the vestibular system in the process of the control of eye movement and gaze stabilization (reviewed in Berson, 2008; Vaney *et al.*, 2001). Contrary to DS units of the mammalian AOS mentioned above, the DS units of the frog AOS studied here generated excitatory responses exclusively to the leading edges of dark stimuli moving into their RFs over a white background. Thus, they were the OFF-type units. Our results highlight the functional differences of the OFF DS mechanism of the frog AOS and the ON DS mechanism described in mammalian AOS. Finally, it should be mentioned that our results are consistent with the morphological data testifying that the dendrites of the DS RGCs that project to the frog AOS branch exactly at the scleral OFF sublaminae of the inner synaptic layer (Bäckström *et al.*, 1978; Montgomery *et al.*, 1981). Further research is required to provide data on the structural and functional organization of the frog AOS.

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