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# Mechanisms of Achromatic Vision in Invertebrates and Vertebrates: A Comparative Study

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Intracellular recording in the retina of the snail, Helix pomatia L., reveals the existence of two types of cell responsive to diffuse flashes of achromatic or monochromatic light: B-type cells, which respond with sustained depolarization that is sometimes accompanied by spikes, and D-type cells, which respond with sustained hyperpolarization. The peak of spectral sensitivity for both B- and D-cells falls in the 450-500 nm range and coincides with range of maximal sensitivity for the rhodopsin family of photopigments. Within a proposed two-channel model of snail achromatic vision, responses of the B- and D-cells are represented by a two-dimensional 'excitation vector'. The length of the 'excitation vector' is approximately constant, and its direction correlates with light intensity. The vector model of light encoding in the snail is discussed in relation to models of achromatic vision in vertebrates (fish, frog, monkey, and humans) based on psychophysical, behavioral and neurophysiological data. Intracellular data in the snail taken together with data from vertebrate animals support the hypothesis that a 2-dimensional model of brightness and darkness encoding utilizes a universal mechanism of 'vector encoding' for light intensity in neuronal vision networks.
*Keywords: achromatic vision, retina, mollusk, brightness and darkness neurons, vector encoding.*

El registro intracelular en la retina del caracol, Heliz pomatia, L., muestra la existencia de dos tipos de células que reaccionan a destellos difusos de luz acromática o monocromática: las células tipo B responden con una depolarización constante con picos de actividad ocasionales; y las células tipo D responden con una hiperpolarización constante. El pico de sensibilidad espectral de las células B y C se centra en un rango de entre 450-500 nm y coincide con los rangos de máxima sensibilidad de las rodopsinas, de la familia de los fotopigmentos. Desde el modelo de dos-canales de visión acromática del caracol, las respuestas a las células B y D están representadas por un vector de excitación de dos-canales. La extensión de este vector de excitación es más o menos constante, y su dirección correlaciona con la intensidad de la luz. El procesamiento de la luz de los caracoles se discute en términos del modelo del vector en relación con modelos de visión acromática en vertebrados (peces, ranas, monos, y humanos) basados en datos psicofisiológicos, conductuales y neurofisiológicos. Tomados en conjunto, los datos intracelulares del caracol y los de animales vertebrados se sostiene la hipótesis de que el modelo de 2-dimensiones para el procesamiento del brillo y la oscuridad se basa en un mecanismo universal de codificación vectorial para la intensidad de la luz en las redes neuronales de visión.
*Palabras clave: visión acromática, retina, molusco, brillo y oscuridad, neuronas, codificación vectorial.*

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Professor Y.N. Sokolov passed away on May 14, 2008.

There is a convention in color science to consider the ability of humans and animals to differentiate 'color tones' as 'chromatic vision' and the ability to differentiate gradations of light intensity', the intensity of colors and of colorless light as well, as 'achromatic vision' (Judd & Wyszecki, 1975). Color scientists refer to the intensity of radiant light as "brightness" and the intensity of light reflected from a surface as 'lightness'. This article concentrates on the sensation of brightness.

Neurophysiological studies of light and color brightness perception in vertebrate animals show that there are two types of neuron that have opposite responses to brightness gradations (Chernorizov, 1999; Chernorizov, & Sokolov, 2001; Clarke, & Ikeda, 1985; DeValois & DeValois, 1975; Izmailov, Zimachev, Sokolov, & Chernorizov, 2006; Jung, 1973; Kusunoki, Moutoussis, & Zeki, 2006; Latanov, Leonova, Evtikhin, & Sokolov, 1997; Sokolov, 2000, 2003; Zeki, 1983; Zrenner, 1983). Neurons of first type increase their firing rate with increased light intensity and decrease their responses when intensity is reduced. These cells are called 'Br-type cells' and are thought to encode brightness (= 'brightness or luminance neurons'). Neurons of the second type respond to changes of brightness in the opposite way to Br-type cells and are known as 'Da-type cells' (= 'darkness neurons'). These neurons are thought to encode darkness. Br- and Da-neurons are found in the retina, superior colliculi, lateral geniculate nucleus and visual cortex of mouse, cat, rabbit and monkey (Clarke & Ikeda, 1985; De Valois & De Valois, 1975; Evtikhin, Polianskii, Alymkulov, & Sokolov, 2008; Jung, 1973; Pang, Gao, & Wu, 2003; Poggio, Baker, Lamarre & Sanseverino, 1969; Polianskii, Evtikhin, & Sokolov, 2005; Polianskii, Evtikhin, Sokolov, & Alymkulov, 2006; Polianskii, Alymkulov, Evtikhin, & Sokolov, 2008; Sokolov, 2003; Valberg & Seim, 2008) (See figure 1).

In lower vertebrates (fish, amphibians) there are neurons analogous to Br- and Da-neurons, known as ON- and OFF-cells according to the widely accepted classification of visual neurons offered by Hartline (1940). These cells are found in the retina at the level of bipolar cells and in the ganglion cell layer (Chalupa & Gunhan, 2004; Chernorizov, 1999; Chernorizov & Sokolov, 2001; Kolb, Fernandez & Nelson, 2008; Manookin, Beaudoin, Ernst, Flagel, & Demb, 2008; Pang et al., 2003).

According to the theory of "vector encoding", proposed by Sokolov (2000), the characteristics of Br- and Da-neurons correspond to *predetectors* forming a *"2-dimensional neuronal module for brightness encoding"* (Sokolov, 2000, 2003). The coding of brightness in such a model is represented by a 2-dimensional *'vector of excitation'*. The components of this vector are the responses of Br- and Da-neurons. One can consider this kind of excitation vector as an encoding vector of brightness at the level of predetector neurons. The term 'predetector neurons' means that these neurons perform a preliminary analysis of brightness, the results of which constitute inputs to 'brightness detectors' for the final identification of light intensity (see Figure 2).

The 2-dimensional model responsible for achromatic vision along with also two-dimensional color-opponent chromatic module provides separate inputs to the visual system. In accord with vector theory, the perception of pure brightness (colorless black-white lights) is two-dimensional because it can operate alone. Color perception, on the other hand, is four-dimensional, because it cannot perform without activation of the brightness-coding system. These consequences of vector theory have been successfully demonstrated in human psychophysical experiments (Sokolov, 2003), as well as in behavioral (monkey, rabbit, fish) and neurophysiological (fish, frog, rabbit) experiments on vertebrate animals (Chernorizov, 1999; Chernorizov & Sokolov, 2001; Evtikhin et al., 2008; Izmailov, Isaichev, & Shekhter, 1998; Izmailov et al., 2006; Latanov, Polianskii, & Sokolov, 1991; Latanov et al., 1997; Leonova, Latanov, Polianskii, & Sokolov, 1994; Polianskii et al., 2008; Sokolov, 2003; Zimachev, & Chernorizov, 2001). In particular, the multidimensional scaling procedure applied to matrices of differences between color stimuli measured in these experiments has shown that color stimuli of different hue, brightness (or lightness) and saturation are located on a hypersphere in four-dimensional space (for review see: Izmailova, Sokolov, Izmailov, & Livshits, 1988; Izmailov, Sokolov, & Chernorizov, 1989; Izmailov & Sokolov, 1991; Leonov & Sokolov, 2006, 2008; Sokolov, 2000, 2003.). Figure 3 demonstrates some principal features of this color space obtained in experiments with humans.

The *Cartesian coordinates* of color points in four-dimensional color space reconstructed by the method of multidimensional scaling closely correspond to excitations of four types of visual neurons: RG, BY, Br and Da. *The spherical coordinates* (angles) in this model correspond to the subjective aspect of colors: hue, lightness and saturation. The chord distances between points representing colors on the hypersphere closely match the differences between stimuli obtained in perceptual experiments. To clarify the representation of colors on a hypersphere, the color-points may be projected onto two planes. The *color tone plane* is composed of two axes. One axis (Z1, Figure 3 A) consists of R+G- and R-G+ parts and the other (Z2, Figure 3 A) has B+Y- and B-Y+ parts. Two parts of axis Z1 closely correspond to the responses of color-opponent R+G- and R-G+ cells and the parts of axis Z2 - to the responses of color-opponent B+Y- and B-Y+ cells. Monochromatic light stimuli are located along a circle corresponding to their hue tone (wavelength). On the *brightness (achromatic) plane* composed of a brightness axis, Z3, and darkness axis, Z4, saturated colors are located near the center, while

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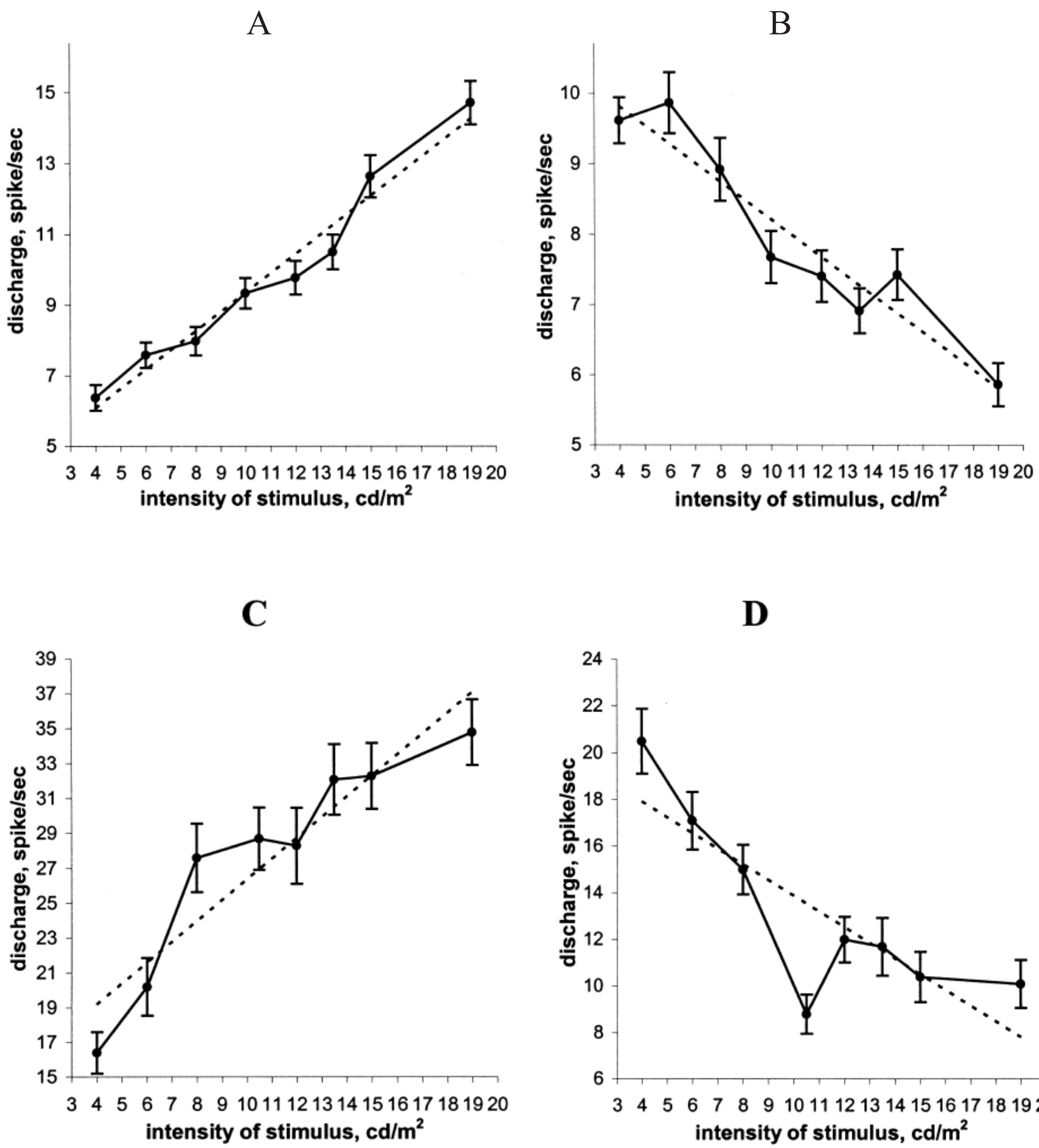


*Figure 1*. Opponent characteristics of Br- and Da-neurons in the lateral geniculate nucleus (LGN) and in superior colliculi (SC) of rabbit (From Evtikhin, Polianskii, Alymkulov, & Sokolov, 2008). Abscissa: intensity of black-white stimuli (cd/m$^2$). Ordinate: average frequency of spike discharge per sec.

A, B: Tonic responses of neurons in LGN as a function of black-white light intensity. Br-neurons (panel A) increase their firing rate with increased light intensity and decrease their responses with reduced intensity. Da-neurons (panel B) respond oppositely to brightness changes.

C, D: Opponent responses to black-white stimuli of Br-neurons (panel C) and Da-neurons (panel D) in SC.

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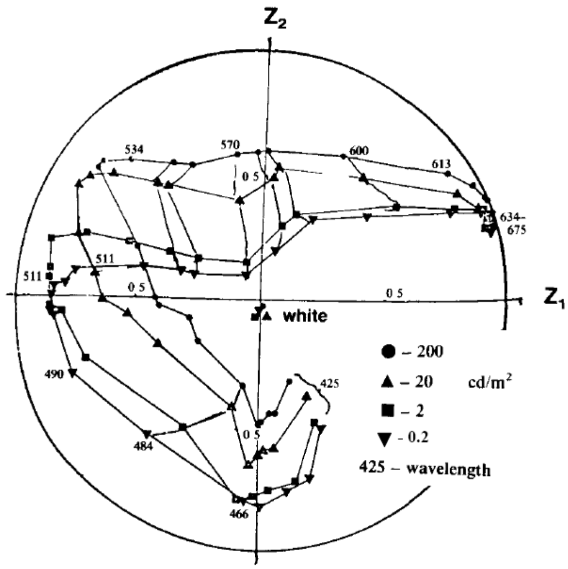


Figure 3 A

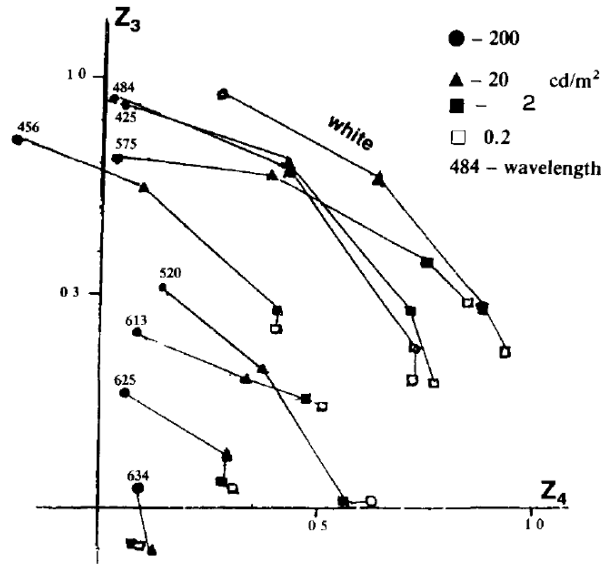


Figure 3 B

less saturated colors area close to the periphery (Figures 3 B, C). The brightness plane of the four-dimensional model is slightly modified under high-contrast light stimulation but remains two-dimensional in structure (Figure 3 D). Thus, color stimuli are encoded by specific locations on the map represented by the hypersphere in four-dimensional space. A peculiarity of the model is that

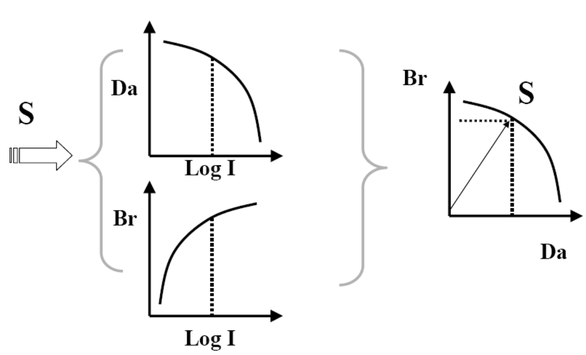


*Figure 2.* Hypothesis of vector encoding of light intensity in the visual system by the combined excitation of neurons of Br- and Da-types (Chernorizov & Sokolov, 2001; Sokolov, 2003). According to the vector encoding hypothesis, the characteristics of Br- and Da-neurons correspond to those of predetectors, which constitute a 2-dimensional neuronal module for encoding of brightness. The coding of brightness of a stimulus ‘S’ of fixed intensity (log I) in such a module is represented by a 2-dimensional vector of excitation. Components of the vector are the response values of Br- and Da-neurons to the log intensity (log I) of the stimulus.

so called ‘brightness’ is encoded by a two-dimensional excitation vector of constant length to which excitation of both brightness (Br) and darkness (Da) neurons contribute (Izmailov & Sokolov, 1991). Analogous color spaces have been obtained in behavioral experiments with monkeys (Latanov et al., 1991) and carp (Leonova et al., 1994) and in electrophysiological experiments on frog and carp retinae (Chernorizov, 1999; Chernorizov & Sokolov, 2001; Izmailov et al., 2006; Zimachev & Chernorizov, 2001).

Following from the above we can ask the following questions:

1. What are the neural mechanisms of achromatic vision in the invertebrate visual system and how do they correspond to the neural mechanisms of brightness perception in vertebrates?
2. Is the principle of vector encoding true for invertebrate vision and does it constitute a universal principle of encoding of light intensity in neural nets of animals?

To answer these questions we chose to study the visual system of the mollusk *Helix pomatia L.* (Roman’s or grape snail) (Nordsieck, 2008; Zaitseva, 1994). Mollusks represent one of the most ancient branches of the ‘evolutionary tree’. The retina of Helix pomatia eye contains only one photopigment – rhodopsin (Chernorizov, Shekhter, Arakelov, & Zimachev, 1994; Von Berg & Shneider, 1972). For this reason the snail can distinguish gradations of light intensity but not color. Thus, the achromatic visual system of snail is very convenient for the study of neural mechanisms involved in the encoding of brightness in the invertebrate.

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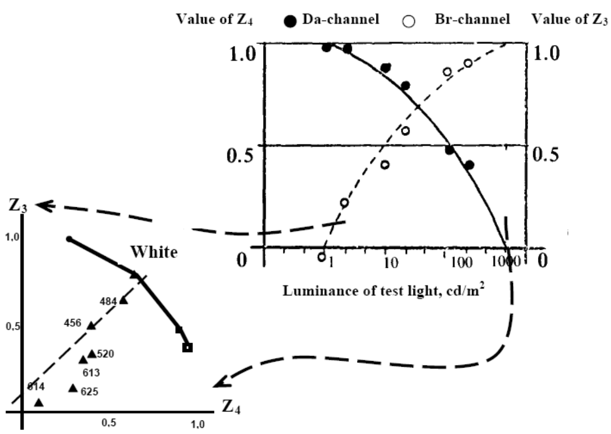


Figure 3 C

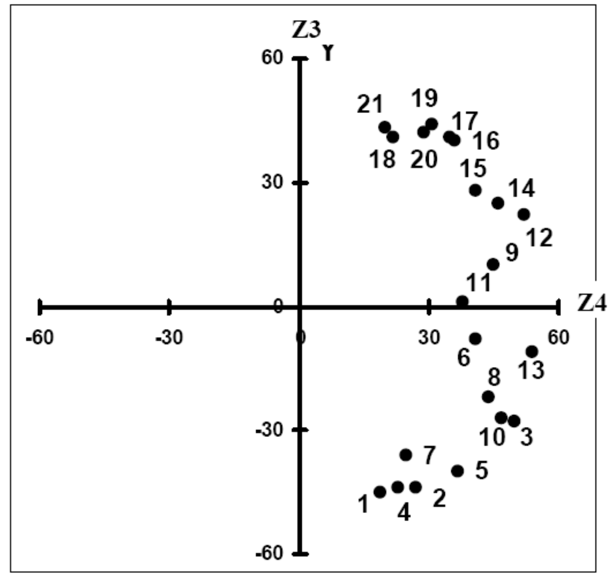


Figure 3 D

*Figure 3.* Four-dimensional color space in the human modified from Fig. 5 of Izmailov & Sokolov (1991) by kind permission of authors; based on research reported by Izmailova, Sokolov, Izmailov, & Livshits (1988); Izmailov, Sokolov, & Chernorizov (1989); Izmailov & Sokolov (1991).

Monochromatic color stimuli and achromatic lights stimuli of different intensity are represented on a spherical surface in four-dimensional space defined by multidimensional scaling. Cartesian coordinates correspond to the excitation of four types of color-sensitive neurons. Three angular coordinates of the hypersphere correspond to three subjective aspects of color perception: hue, brightness, and saturation.

A: A projection of color points on a plane constructed from red-green (Z1) and blue-yellow (Z2) axes demonstrates circular locations of wavelengths (numbers near points, nm) in accordance with hue (nm) and intensity (.2, 2, 20 and 200 cd/m2). Achromatic stimuli (white) are positioned in the center.

B: The plane through four-dimensional color space constructed from brightness Z3 and darkness Z4 axes shows that achromatic (white) lights are located along the periphery in accord with their intensity (.2, 2, 20 and 200 cd/m2). Similar traces demonstrate monochromatic stimuli (nm) being, however, located closer to the center (wavelengths (nm) are indicated by numbers near corresponding traces: 425 nm, 456 nm and so on).

C: The plane illustrates the interpretation of axes Z3 and Z4 as 'brightness'- and 'darkness'- neuronal channels (parameters of stimuli and designations are the same as in Figs. 3 A, B). From figures 3 A, B, C it is apparent that for saturated monochromatic colors (614 nm, 625 nm) red-green and blue-yellow axes predominate over brightness and darkness ones. On the contrary, for achromatic (white) and less saturated colors (456 nm, 484 nm) brightness and darkness axes predominate over red-green and blue-yellow ones. But for all stimuli the length of the four-dimensional excitation vector remains constant.

One can make sure that coordinate functions of test stimuli (values of Z3 and Z4) are well approximated by sine and cosine functions.

D: Brightness plane through the four-dimensional model of color vision in human is slightly modified under high-contrast stimulation but remains two-dimensional in structure (Izmailov, & Sokolov, 1991). As compared with Fig. 3 B, one quadrant of the model transforms into a semicircle that is accompanied by the subjective perception of 'black'. Points numbered 1-21 represent achromatic lights of discs observed by human against the ring background on the computer screen. The disc-ring configurations were formed by combining 7 intensities of disc (.2; 1; 2; 10; 20; 100 or 200 cd/m2) with 3 intensities of ring (1; 10 or 100 cd/m2) (for a total of 21 combinations). Distances between points represent perceived subjective differences between disc fields, independently from ring fields. Points at the bottom of the configuration (1, 2, 3, 4, 5, and 7) represent black colors against surrounding rings of highest luminance, and the lowest luminance of the disc field. Intermediate points (6, 11, and 13) represent white colors, which are characterized by the equivalence of disc and ring luminance. Points at the high part of the configuration (18, 19, 20, and 21) represent bright colors, which are characterized by the lowest luminance of the ring field. Two Cartesian axes are interpreted as dark (Z4) and bright (Z3) neuronal channels of achromatic vision. (The figure 3 D is modified Fig. 5 from Izmailov & Sokolov (1991) by kind permission of authors).

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In this paper we analyze the intracellular responses of photosensitive cells in the snail's eye to test the following hypotheses:

– *Hypothesis 1*. There are 'brightness-'and 'darkness-coding' cells in the invertebrate visual system analogous to Br- and Da-neurons in vertebrate visual system.
– *Hypothesis 2*. The encoding of brightness in the invertebrate visual system is represented by a 2-dimensional vector composed of responses of 'brightness-'and 'darkness-coding' cells analogous to Br- and Da-neurons in vertebrate visual system. The direction of the vector varies as a function of the level of light intensity (brightness) while the length of the vector remains constant.

## Methods

The experiments were conducted in accordance with international legislation on the use of experimental animals. The researchers were guided by recommendations of the code of ethics adopted by the Council for International Organizations of Medical Sciences and by Russian legislation regulating biomedical research on animals.

### *Preparation*

The experiments were conducted on a dark-adapted partial preparation that included the eye ball, optical nerve, and cerebral ganglion. Access to the retina was achieved by opening the eye and removing the crystalline lens. The preparation was kept in a special light-isolated dish with a standard physiological solution for cold-blooded animals (Sokolov & Palikhova, 1999).

### *Stimulus Parameters*

For light stimulation we used (1) diffuse flashes of white light and (2) 13 equiquantum monochromatic wavelengths between 400 - 700 nanometers (*nm*) generated by interference filters each with the full width half maximum 7÷15 nm. Stimulus duration was 1 second and the inter-stimulus interval was 3 to 5 minutes. Stimulus intensity was varied in .1 - .2 log unit steps within the limits of 1.5 log units from – 1.5 log units (minimum) to .0 log units (maximum). Maximal intensity of white light measured at the eye of the mollusk was $5.0 \cdot 10^5$ erg$\cdot$sm$^{-2}$ $\cdot$s$^{-1}$ (= .0 log units). Calibration of the photostimulator was performed using a computerized spectrophotometer S-2000 (WPI, Sarasota, USA).

### *Electrophysiological Recording*

The experimental set-up for intracellular recording included an intracellular amplifier MEZ-8201 (Nihon Kohden), a two-beam Oscilloscope VC-10 (Nihon Kohden) (0 ÷ 1000 Hz) and a personal IBM computer with a 16-channel analogue-digital converter (digitizing frequency = 400 Hz). The microelectrodes were ultra thin glass tubes with tip diameter less than 2 microns and resistance of 40-80 MOm. Microelectrodes were inserted into tissue in steps of 1 - 3 microns using a computerized microelectrode driving system MS-314 (WPI, Sarasota, USA).

### *Data Collection and Statistical Analysis*

Statistical analyses were performed using 'CONAN' (Kulaichev, 2002) and 'STATISTICA-5.0' software. The non-parametric rank Wilcoxon T-test was used to evaluate the reliability of differences between averaged quantities of experimental data.

## Results

In 68 experiments on 75 animals intracellular (and in some cases extracellular) recordings from 94 cells were successfully collected and analyzed. Based upon the sign of the light response (sustained depolarization or sustained hyperpolarization) most of the cells were divided into two main groups. In the first group white light or monochromatic colored light of any wavelength depolarized the cells (designated as B-type cells). Cells in the second group responded to light of any wavelength or to white light with hyperpolarization (designated as D-type cells). Below we summarize the characteristics of B- and D-cells and of other photosensitive elements discovered in the snail's retina.

### *B-cells*

The resting membrane potential of 35 B-cells varied within the interval 40-70 mV. A typical response of a B-cell to light is shown in Figure 4 A.

Some B-cells exhibited dark background spike activity interrupted by light-sensitive depolarization (Figure 4 B). The range of maximal amplitudes of light responses was 4 - 20 mV. The value of maximal amplitude of a light response increased monotonically with the logarithm of light intensity (Figure 4 C). Response latency decreased with increasing stimulus intensity and varied between 200 ms and 400 ms. Response duration was 3 - 4 seconds. The spectral response characteristic, which was successfully calculated for four B-cells corresponded closely to that of rhodopsin (Figure 4 D).

### *D-cells*

The resting membrane potential of 41 D-cells varied between -5 and -35 mV and differed significantly from that of the B-cells (T-test: $p < .05$). A typical response of a D-cell to light is presented in Figure 5 A.

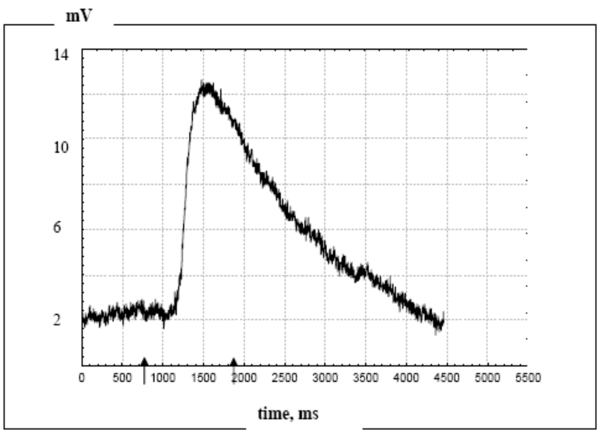


**Figure 4 A**

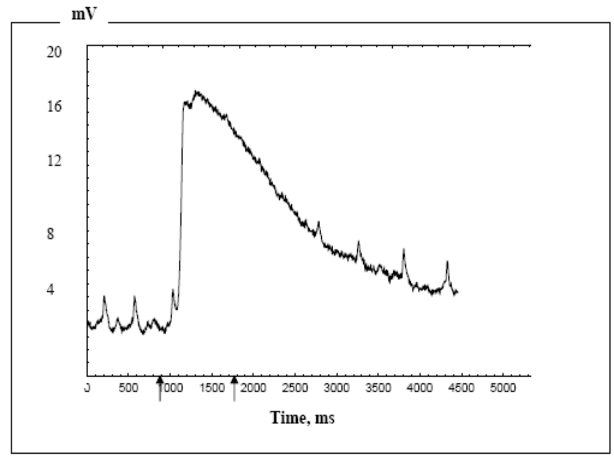


**Figure 4 B**

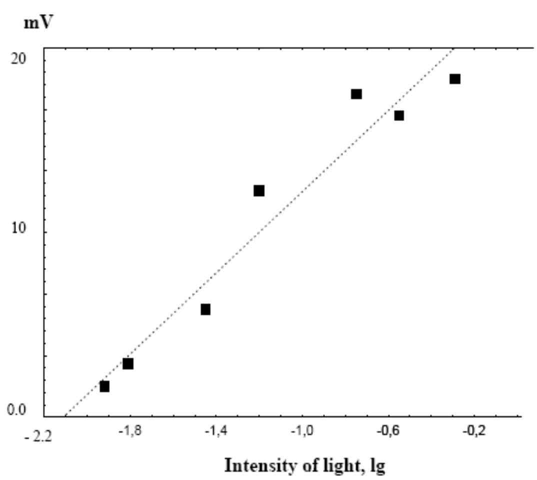


**Figure 4 C**

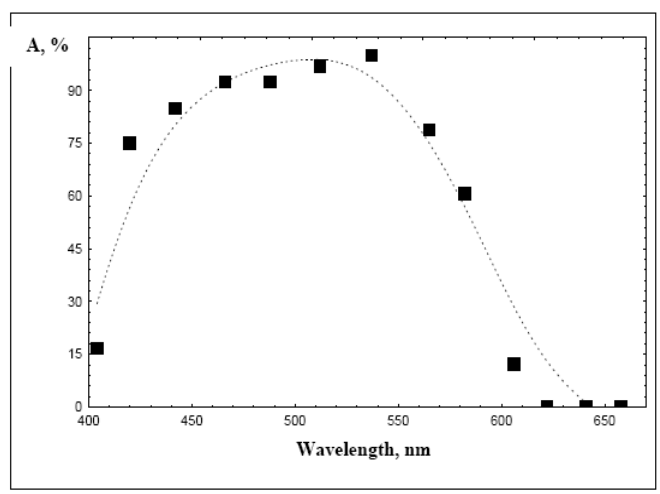


**Figure 4 D**

*Figure 4*. B-cell response to light.

A: Typical response of B-cell to flash of diffuse white light. Axis X: duration of light stimulation (ms); axis Y: amplitude of response (mV). Flash duration: 1000 ms; intensity: .0 log units. Arrows correspond to onset and offset of light stimulus.

B: Tonic response of B-cell accompanied by spike-like activity. Parameters as in panel A.

C: Amplitude of B-cell responses as a function of light intensity. Stimuli are diffuse 1000 ms flashes of white light. Axis X: log magnitude of light intensity (common logarithm units); Axis Y: amplitude of peak depolarization response (mV). Dark level of B-cell membrane potential before light stimulation = –18 mV. Dotted line: linear regression of response magnitude on stimulus intensity.

D: Response amplitude of a B-cell as a function of wavelength. Stimuli: diffuse light flashes (1000 ms and .0 log units) of equiquantum monochromatic radiation of different wavelengths. Axis X: wavelength, nm; Axis Y: amplitude of peak spectral response normalized to maximal response (A, %). Dark level of B-cell membrane potential before light stimulation = – 18 mV. Dotted line: best fit approximation by least squares method.

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Amplitude versus light intensity functions for D-cells (Figure 5 B) looked similar to those for the B-cells (compare Figure 5 B and Figure 5 C). However, the spectral response characteristic, obtained adequately for only one D-cell (Figure 5 C), differed from that obtained for B-cells (compare with Figure 4 D) in that it was shifted along the wavelength axis towards shorter wavelengths peaking around 450 nm.

### *ON-, OFF- and ON-OFF-photosensitive elements*

In addition to B- and D-cells we also recorded from 18 cells that responded to diffuse light flashes not with graded polarization responses, but instead with spike discharges. Among them were cells with:

1. equally strong phasic responses to the onset and offset of a diffuse light flash (*ON/OFF-elements* (Hartline, 1940)) (Figure 6);
2. weak responses to light onset but with powerful discharges to light offset (*OFF-elements* (Hartline, 1940));
3. weak responses to light offset but with powerful discharge to light onset (*ON-elements* (Hartline, 1940)).

## Discussion

### *Photosensitive cells of snail's eye in situ and in isole*

The B- and D-type cells described in this study correspond with two analogous types of photosensitive cells extracted from the dark-adapted snail retina using tripsin (Shekhter & Grechenko, 2009). Similar to our B-cells, the first type of cells described by Shekhter & Grechenko (2009) *in isole* responded to white light stimulation with long-lasting (1.2 - 2.5 s) depolarization.

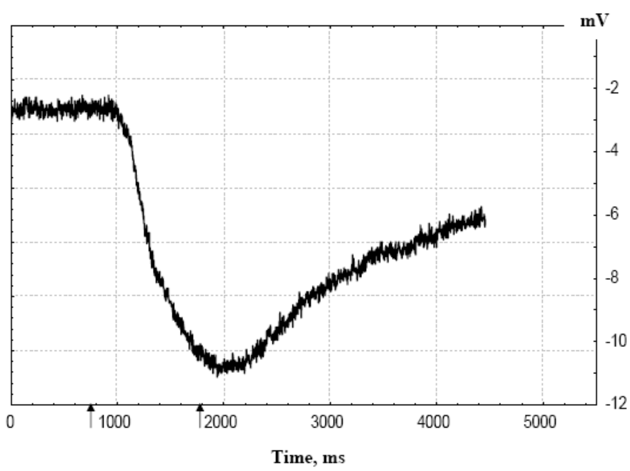


Figure 5 A

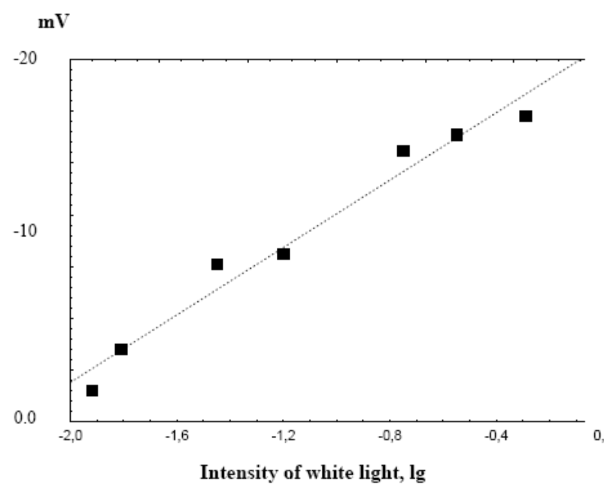


Figure 5 B

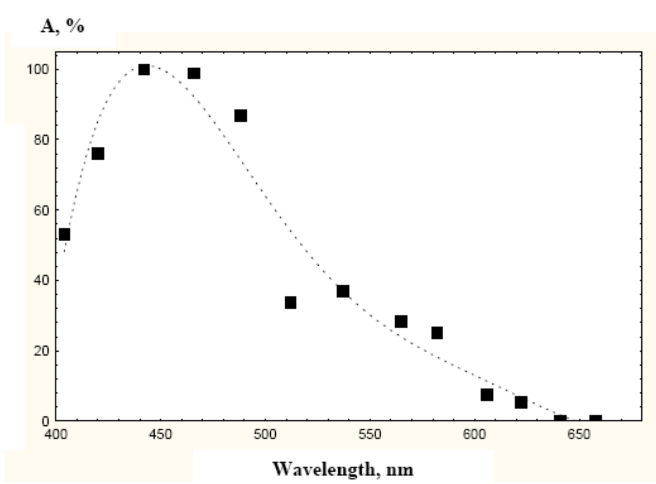


Figure 5 C

*Figure 5*. D-cell response to light stimuli.
A: Typical response of D-cell to flash of diffuse white light. Axis X: duration of light stimulation (ms); axis Y: amplitude of response (mV). Flash duration: 1000 ms; intensity: .0 log units. Arrows correspond to onset and offset of light stimulus.
B: Amplitude of D-cell responses as a function of light intensity. Stimuli are diffuse 1000 ms flashes of white light. Axis X: log magnitude of light intensity (common logarithm units); Axis Y: amplitude of peak hyperpolarization response (mV). Dark level of D-cell membrane potential before light stimulation = – 5 mV. Dotted line: linear regression of response magnitude on stimulus intensity.
C: Amplitude of D-cell as function of light wavelength. Specification of stimuli and designations see Figure 4 D. The dark level of D-cell membrane potential equaled - 5 mV.

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Cells from their second group were hyperpolarized by white lights and were similar to our D-cells. Thus data from *in situ* and *in isole* experiments are consistent in their demonstration of two types of photosensitive elements in the snail eye that have responses of opposite polarity to light stimuli.

### *Morphological types of retinal cells generating B- and D-responses: hypothesis as to two types of photoreceptors in snail retina*

One question arises regarding the anatomy of brightness cells in snail retina, namely, what are the morphological types of retinal cells that generate the B- and D-responses? Are they photoreceptors, interneurons, pigment cells or glial cells? Considering currently available data (for review see: Musio, 2001), we propose that there are two morphological types of photoreceptors in the snail retina. The first is a rhabdomeric type (Eakin & Brandenburger, 1967) which generates light induced depolarization. The second is a ciliar type (Musio, 2001) which responds to light by hyperpolarization. Such a combination has only been observed in the retina of two other mollusks, – *Lima scarba* and *Pecten irradians* (Gomez & Nasi, 1998, 2000; McReynolds & Gorman, 1970; Musio, 2001; Nasi, 1991a, b, c).

### *B- and D-type cells in the mollusk retina as analogues of Br- and Da-type neurons in the vertebrate visual system*

Our research shows that D-type cells are hyperpolarized by light and depolarized in darkness, whereas B-type cells respond in the opposite fashion. The functional characteristics of D- and B-cells in the mollusk retina closely resemble those of spike-generating Da- and Br-cells in higher vertebrates (Figure 1) and ON- and OFF-bipolar cells in lower vertebrates (Chernorizov, 1999; Chernorizov & Sokolov, 2001; R. DeValois & K. DeValois, 1975; Jung, 1973; Kolb et al., 2008). We suggest that the D- and B-type cells are analogues to darkness (Da-type) and brightness (Br-type) neurons in the visual system of vertebrates (Jung, 1973). Such an analogy suggests that there is a common mechanism of light encoding in the visual systems of vertebrate and invertebrate animals. This commonality is based on opponent cell mechanisms for encoding brightness - B- and D-cells in mollusks and Br- and Da-neurons in vertebrates. Like Br- and Da-cells in the vertebrate eye, opponent B- and D-cells in mollusks (*Lima scarba, Pecten irradians, Helix pomatia L.)* generate a 2-dimensional vector of excitation already at the level of the retina.

### *Geometric model of achromatic vision in the snail based on responses of B- and D-cells*

Figure 7 A shows a two-dimensional achromatic space for snail responses reconstructed using normalized peak amplitudes of one D-cell as coordinates along axis X1 and normalized peak amplitudes of one B-cell - as coordinates along axis X2 (Chernorizov & Sokolov, 2001).

This achromatic space can be approximated by 2-dimensional plane where different intensities of light are represented by points distributed along the circumference of a quadrant of the circle. Note that the points are at the ends of corresponding 2-dimensional vectors of approximately constant length (coefficient of variability = 5.2 %) whose components in Euclidean coordinates are the values of the responses of D- and B-cells to light. The direction of the vector, defined by the relationship between the B- and D-cell responses varies with the value of brightness while the length of vector is constant.

The achromatic 2 – dimensional space obtained in intracellular experiments is approximately isomorphic to the two-dimensional achromatic space constructed by multidimensional scaling of ERG responses recorded from the intact eye of the snail (Figure 7 B) (Chernorizov, 1999; Izmailov et al., 1998; Shekhter, Zimachev, & Arakelov, 1992). Comparison of the independently constructed models of achromatic vision based on psychophysical data from the human (Figure 2 B), behavioral and neurophysiological studies in lower vertebrates and mammals (Evtikhin et al., 2008; Izmailov et al., 2006; Polianskii et al., 2008; Sokolov, 2003), these intracellular data (Figure 7A) and ERG responses (Figure 7 B) in the

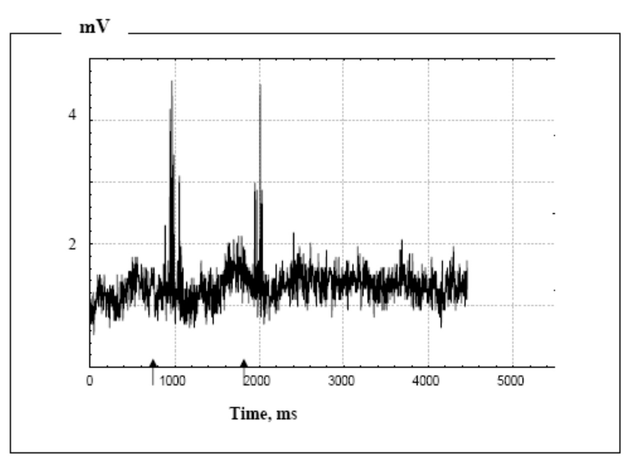


**Figure 6**

*Figure 6.* Response of ON/OFF-element in snail retina.
Axis X: duration of light stimulation (ms); axis Y: response amplitude (mV). Flash duration: 1000 ms; intensity: .0 log units. Arrows correspond to onset and offset of light stimulus.

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mollusk, confirms our hypothesis that, in the invertebrate visual system, as in the visual system of vertebrates, ‑ the encoding of brightness can be represented by the direction of a 2-dimensional vector composed of the opponent responses of B- and D-cells. This conclusion is consistent with psychophysical studies of achromatic vision in the human, which demonstrate the existence of two independent processes in the visual system, which mediate separately the perception of "whiteness" and "blackness" (Heggelund, 1992; Magnussen, Bjorklund, & Kruger, 2008; Vladusich, Lucassen, & Cornelissen, 2007).

The principle of vector encoding widely verified in vision can be applied to other sensory systems and executive mechanisms where it may be considered an appropriate methodological basis for the integration of traditionally opposing "detector" and "ensemble" theories (Sokolov, 2003; Vaitkevichius, Shatinskas, Stanikunas, Shvegzhda, & Sokolov, in press).

## Conclusions

1. Intracellular recording experiments in the retina of the snail reveal two types of cell with opponent responses to flashes of diffuse light. Under light stimulation by white or monochromatic stimuli

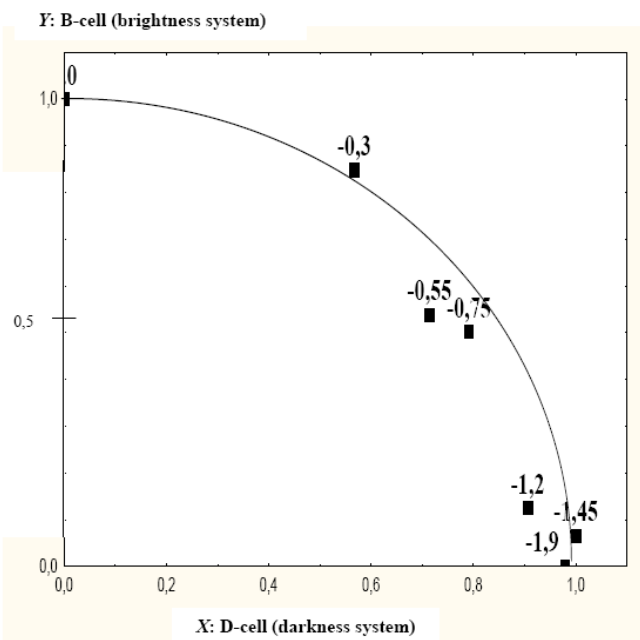


**Figure 7A**

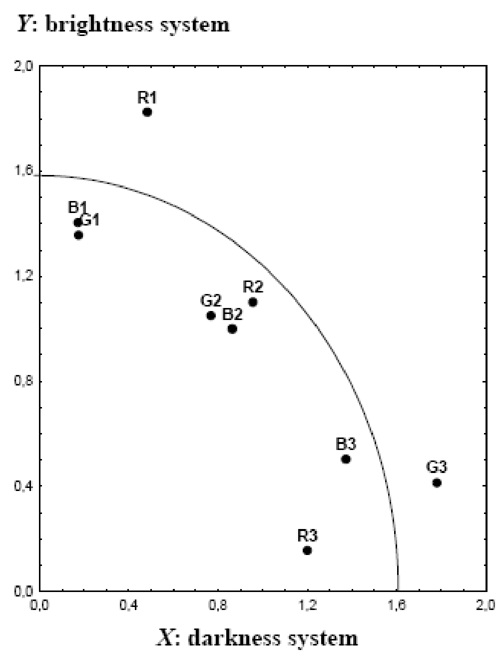


**Figure 7 B**

*Figure 7.* Two-dimensional model of achromatic vision in the snail.
A: Two-dimensional spherical model of achromatic vision based on intracellular recordings from light-sensitive retinal cells. Model constructed by plotting normalized peak amplitude of a D-cell on axis X and normalized peak amplitude of a B-cell on axis Y. Intensities of white light are specified in log units by the numbers near rectangles representing white light stimuli. The values of X and Y coordinates of light stimuli in framework of the model are interpreted as representing the responses of darkness (D-cells) and brightness (B-cells) neuronal systems in the snail retina.
B: Two-dimensional model of achromatic vision based on extracellular recordings from intact eye-ball of snail. Model constructed by multidimensional scaling of electroretinogram (ERG) registered to abrupt substitution of one light stimulus for another of different color and intensity (Chernorizov, 1999).
Designations. The diffuse blue (B), green (G) and red (R) color stimuli were generated on a computer monitor. The intensities of the colors, indicated by numbers 1, 2 and 3 near the color designations, varied within the range 20-30 Nit for R1, G1, B1 (high level of brightness); 12-17 Nit – for R2, G2, B2 (medium level of brightness), and 3-10 Nit – for R3, G3, B3 (low level of brightness). The Euclidean coordinates X and Y obtained by multidimensional scaling of the ERG confusion matrix are represented in reference units (Chernorizov, 1999).
The figure shows that the stimuli are located on the circumference of a circle where they are ordered in a systematic way according to their intensity, not by color, from the darkest stimuli (R3, G3, B3) and medium bright stimuli (R2, G2, B2) to the brightest (R1, G1, B1).

B-cells demonstrate sustained depolarization, sometimes accompanied by spikes, and D-cells, which respond with sustained hyperpolarization.

2. Preliminary data suggest that the peak of spectral sensitivity for both B- and D-cells falls in the range of 450-500 nm, which coincides with maximal sensitivity range for the rhodopsin family of photopigments.
3. Intracellular data from the snail taken together with data from vertebrate animals support the hypothesis that a 2- dimensional model of brightness and darkness encoding utilizes a universal mechanism of ‘vector encoding’ of light intensity in neuronal vision networks.

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