



## Review article

## Bongard and Smirnov on the tetrachromacy of extra-foveal vision

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## ABSTRACT

In Moscow in the 1950's, the physicist M. M. Bongard developed the use of silent substitution to establish the number of dimensions of human or animal colour vision and to derive colour-matching functions either for whole organisms or for individual neuronal channels. In 1956, he and his colleague M. S. Smirnov reported that extra-foveal human vision was tetrachromatic when tested by the silent-substitution method that they called 'replacement colorimetry'. In the steady state, trichromatic matches were possible in extra-foveal regions, but transients were visible when one such match was replaced by another. If, however, a match was made with four primaries, then a silent substitution was possible; and such matches – unlike trichromatic ones – were stable with light level and with changes in the state of chromatic adaptation. Bongard and Smirnov believed that the fourth receptor had the spectral sensitivity of the rods, but of course they were working long before the discovery of intrinsically photosensitive retinal ganglion cells. On the fiftieth anniversary of Bongard's grievous death, we provide a translation of Bongard and Smirnov's paper on the tetrachromacy of extra-foveal vision. In a commentary, we give the background to their work and provide further details of their apparatus and procedure. We briefly discuss related research and the reception in the West of Bongard and Smirnov's claims. We suggest that an analogy can be made between the tetrachromacy of the parafovea and the 'weak tetrachromacy' of heterozygotes for anomalous colour vision, whose trichromatic matches are not stable with chromatic adaptation.

## 1. Introduction

In 1956, M. M. Bongard and M. S. Smirnov, from the Institute of Biophysics in Moscow, reported that extra-foveal vision is four-dimensional (Bongard & Smirnov, 1956). Their paper is of renewed interest today, owing to the possibility that melanopsin-containing ganglion cells contribute to the appearance of peripheral stimuli. On the 50th anniversary of Bongard's unhappy and untimely death, we give a translation of the 1956 paper. We also offer some background to the work and its novel experimental method; and we comment briefly on subsequent developments in the field. The core paper on tetrachromacy contains only limited details of apparatus and procedure, and so our commentary draws together information that is distributed among several papers in *Doklady Akademii Nauk SSSR* and *Biofizika*, including those by Liselotte Fridrikh (Friedrich) – a PhD student from the Deutsche Demokratische Republik who had previously worked on colour metrics at the Agfa Wolfen film company (Friedrich, 1954).

## 2. The authors

As students, Mikhail Moiseevich Bongard and Mikhail Sergeevich Smirnov (See Fig. 1) were near-contemporaries in the Physics Faculty of Moscow University. They remained good friends, and they were still sharing an office in the year of Bongard's death. A recent memoir of Smirnov, marking the 100th anniversary of his birth (Anon., 2021), recounts how the two colleagues were known in the lab as 'dva Mishki': this affectionate Russian phrase means both 'the two Michaels' and 'the two bears'.

When Nyuberg, at the suggestion of the mathematician Kolmogorov, transferred his Biophysics of Vision Laboratory to the Institute for Problems of Information Transmission, Bongard and Smirnov were part of the move. Their colleagues in this distinguished lab during the 1960's included A. L. Yarbus (celebrated for his work on eye movements), A. L. Byzov, V. V. Maximov and O. Y. Orlov (Rozhkova & Sobolevski, 2015).

Smirnov is now best remembered as a pioneer in the measurement of ocular aberrations (Howland, 2000): he used a subjective vernier task to measure the retinal misalignment of rays entering through different

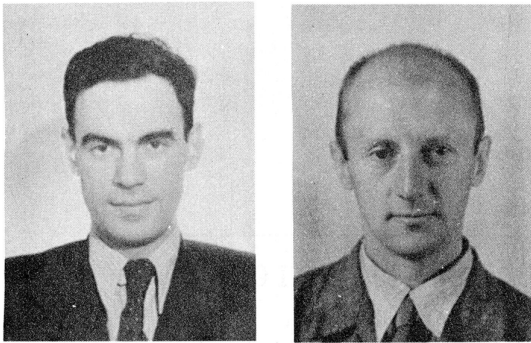
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**Fig. 1.** M. M. Bongard, 1924–1971 (left) and M. S. Smirnov, 1921–2008. (Photographs from the Proceedings of the 1957 NPL Symposium on Colour Vision).

parts of the pupil, allowing third- and fourth-order aberrations to be estimated; and he concluded that it would be in principle possible to construct a contact lens that compensated for the aberrations (Smirnov, 1961). Bongard became particularly well known in computer science for ‘Bongard Problems’, which were introduced as a challenge for AI programs; and his book *Pattern Recognition* was translated into English (Bongard, 1970). Yet he continued to take an interest in colour vision and in the year of his death he was an author of two papers on colour constancy. In 1967, members of the laboratory voted for Bongard (rather than Byzov) to succeed Nyuberg as head of the laboratory. He proved an inspiring and popular leader.

Bongard was a keen alpinist and annually enjoyed a mountaineering holiday in the summer. In 1971, however, he expressed to Smirnov a strange reluctance to go on holiday (Vishnevets, 2005). He spoke of withdrawing his application for holiday leave from the Institute. But nevertheless, he went. On August 5th, he and a companion were roped together in the Pamir mountains when they slipped while descending an icy and rocky slope. They then fell 800 m vertically into a gorge. Their bodies remain buried close by (Tamm, 2001).

### 3. The tetrachromacy of the peripheral retina

To understand Bongard and Smirnov’s claim that four variables are needed for a peripheral match it is necessary to consider the severe criterion they set for a satisfactory match: When one field is replaced by the second, the transition should be undetectable. They call their method ‘replacement colorimetry’. In the second edition of his textbook *Physiology of the Retina and Visual Pathway* (1970), Giles Brindley describes how Bongard demonstrated the phenomenon to him in Moscow: “At 160 cd m<sup>-2</sup> on a 1.5° field placed 5° from the fixation point, the mismatch takes the form that on changing either from red + blue-green to yellow + violet or the reverse, there is a momentary apparent brightening. The steady appearances of the two fields do not, for me, differ.” (Brindley, 1970 pp. 204–205).

Bongard and Smirnov found that the transient could be eliminated if a fourth variable was included in the match. Such a tetrachromatic match was stable as light level or chromatic adaptation were varied, whereas peripheral trichromatic matches are unstable when conditions are changed. These observations were later confirmed by Clarke and Trezona (1976) using more conventional, side-by-side, matching.

The instability of trichromatic peripheral matches with variation in chromatic adaptation is reminiscent of the instability of foveal matches found in some carriers of anomalous trichromacy when the wavelength of a background field was changed (Nagy, Macleod, Heyneman, & Eisner, 1981). In the latter study, all the heterozygotes for anomaly accepted a trichromatic foveal match, even though four of them made non-additive matches, in that the match was different when different background fields were used. Jordan and Mollon (1993) termed this condition ‘weak tetrachromacy’. The usual explanation of weak

tetrachromacy is that four types of receptor are present but there are only the normal number of post-receptor channels, into which the receptors feed. Different adapting fields differentially adapt the four receptors and so the relative contributions of the individual receptors to the post-receptor channels are changed. ‘Strong tetrachromacy’, where the observer cannot make a trichromatic foveal match and has independent access to four cone signals, appears to be a very rare condition – perhaps confined to observers whose anomalous photopigment occupies a spectral position almost midway between the normal long-wave and middle-wave pigments (Jordan & Mollon, in press).

So should we call the tetrachromacy of the periphery ‘weak’ or ‘strong’? Bongard and Smirnov show that the normal observer can consciously detect the transition between the two fields of a trichromatic peripheral match. However, we are inclined to classify this as ‘weak tetrachromacy’. One can assume that the four underlying receptors are differentially adapted by the two fields of the trichromatic match; and that this is how a transient signal arises in post-receptor channels at the moment of replacement. Bongard and Smirnov’s result does not, in itself, require us to conclude that the responses of four receptors are independently available to the cortex. It is possible that replacement colorimetry would offer an efficient way to test for weak tetrachromacy in the foveae of heterozygotes for anomalous trichromacy.

To a modern reader, one of Bongard and Smirnov’s most unexpected claims is that a tetrachromatic match made in the periphery is then accepted by the fovea. If the only difference between the periphery and the fovea were the presence of an additional receptor in the periphery, and if the spectral sensitivity of each receptor were unchanged in different regions, then the result would be expected. Yet we usually assume that the spectral sensitivity of the fovea is altered by the macular pigment – and also by variations in the optical density of central cones (e.g. Pokorny, Smith, & Starr, 1976; Wyszecki & Stiles, 1982). Interestingly, Clarke and Trezona (1976) confirmed Bongard and Smirnov’s result for tetrachromatic matches. They write: “the tetrachromatic match is unaffected by reducing the field size from 10° to 1° 20’ ...”. They also note that Maxwell’s spot, often visible at the centre of a large matching field, is not seen with tetrachromatic matches (see also Trezona, 1973b). However, their claims were not supported by Palmer (1981). And indeed, Liselotte Friedrich, who used Bongard and Smirnov’s colorimeter to make tetrachromatic matches, wrote in her own account: “Strictly speaking, four-colour matches were correct over the whole retina except for the yellow spot. Therefore in the appropriate experiments a 2° sector of the 5° comparison field in the yellow spot region was cut off by a screen.” (Fridrikh, 1957b) See also: Bongard, Smirnov, and Friedrich (1958). An explanation for these discrepancies may lie in individual differences in the optical density of the macular pigment, which are known to be large (Bone & Sparrock, 1971; Hammond, Wooten, & Snodderly, 1997).

Bongard and Smirnov believed that the fourth signal in the periphery came from the rods and that these ‘twilight receivers’ are active at high levels of photopic luminance. However, Bongard and Smirnov worked at a time when there was no suggestion of a fifth class of photoreceptors in the retina – the melanopsin-containing ganglion cells. Today of course there is active interest in the question of whether peripheral colour appearance is modified by melanopsin signals (e.g. Horiguchi, Winawer, Dougherty, & Wandell, 2013; Lucas, Allen, Milosavljevic, Storchi, & Woelders, 2020; Spitschan et al., 2017; Yamakawa, Tsujimura, & Okajima, 2019). The ‘momentary apparent brightening’ that Brindley saw in 1969 does not sound dissimilar from the ‘diffuse, minimal brightening of the visual field’ experienced by Spitschan and colleagues after onset of a stimulus designed to give a pulse in the melanopsin signal.

Bongard and Smirnov themselves were satisfied that the additional signal had approximately the spectral sensitivity of the rods, but, for them, the only other signal needing to be ruled out was that of the short-wave cones. The spectral sensitivity of melanopsin is much closer to that of the rods: the separation is of the order of 20 nm (e.g. Enezi et al., 2011; Gamlin et al., 2007). Nevertheless, Bongard’s ‘replacement

colorimetry' may well have the potential resolution to distinguish whether the fourth signal comes from rods or from melanopsin. For – in use in Moscow in 1956 – replacement colorimetry appeared to have the spectral resolution to detect individual differences in the colour-matching functions of normal human trichromats (Fridrikh, 1957a). It might be thought that replacement colorimetry would be insensitive to changes in a melanopsin signal, since the melanopsin component of the response of intrinsically photosensitive ganglion cells has a famously long time constant (Dacey et al., 2005); but in fact a brief flash does initiate action potentials within a few hundred milliseconds (Do et al., 2009).

If Bongard and Smirnov were correct in identifying the transient as a rod signal, then they may turn out to have been prescient in their claim that rods are functional at high levels. Their claim appeared to contradict the finding of Aguilar and Stiles (1954) that rods saturate at moderate photopic levels. Measuring increment thresholds under conditions of wavelength and pupil entry chosen to isolate the rod response over a large range of intensities, Aguilar and Stiles reported that the Weber fraction increased rapidly at levels equivalent to 120–200  $\text{cd}\cdot\text{m}^{-2}$  – although the intrusion of cone responses meant that the rod response could not be followed to higher light levels. Those results set the predominant view in visual science for many years. However, recent work suggests that mammalian rods escape saturation at high levels (Tikidji-Hamburyan et al., 2017), as result of an adaptive mechanism that moves transducin from the outer segment to the inner segment (Frederiksen et al., 2021).

#### 4. Apparatus and methods

In their 1956 paper Bongard and Smirnov give few details of their apparatus. They refer the reader to an earlier paper on the analysis of colour vision in animals (Bongard, 1955). Fig. 2 shows that apparatus – a prism monochromator with multiple entrance slits, on the principle of the colour-mixing box of Clerk Maxwell (1860) or the anomaloscope of Nagel (1907). The inset shows the arrangement of entrance slits. The upper slits define the fixed primary wavelengths. Only two are shown in use here, but in later versions of the instrument there were more. The lower slit is the comparison wavelength. Opaque occluders allow arbitrary changes to be made in the amount of light passing through each of the slits.

One set of slits are covered with polarising sheet (поляроид, 'polaroid') of one orientation ( $I_3$ ) and the second set with polaroid of orthogonal orientation ( $I_2$ ). A rotatable polaroid common to all beams ( $I_1$ ) allows a transition to be made between one set of slits and the other, replacing one stimulus field by the other. Lens  $L$  forms the image of lens  $O_2$  on the internal surface of an integrating sphere ( $III$ ). When recordings are being made from an animal, the eye is placed at  $\Gamma$ .

It was for analysing the colour vision of animals that Bongard first introduced his method of 'replacement colorimetry'; and it is a powerful one. The experimenter records, say, the electroretinogram and seeks what Rushton would later call a 'silent substitution', a transition between fields that evokes no response (Bongard, 1955; Donner & Rushton, 1959). By this means, and by varying the wavelength passed by the lower slit, the arrangement of Fig. 2 allows colour-matching functions to be established for a dichromatic animal.

Bongard and Smirnov note several advantages of 'replacement colorimetry' (Bongard & Smirnov, 1957b; Smirnov & Bongard, 1956): (i) The method avoids the danger, present when the fields are side by side, that the two retinal areas are exposed to different colours during the approach to a match; (ii) It is ideal for studying peripheral vision, where the line dividing two side-by-side fields would not be clearly resolved; and (iii) The eye is maximally sensitive to departures from the current state of adaptation (Rautian & Solov'eva, 1954), and so the replacement method will allow precise matches to be achieved. Fridrikh (1957b) adds a fourth point: (iv) when a side-by-side comparison is used, the distribution of receptors may be different in the two half-fields,

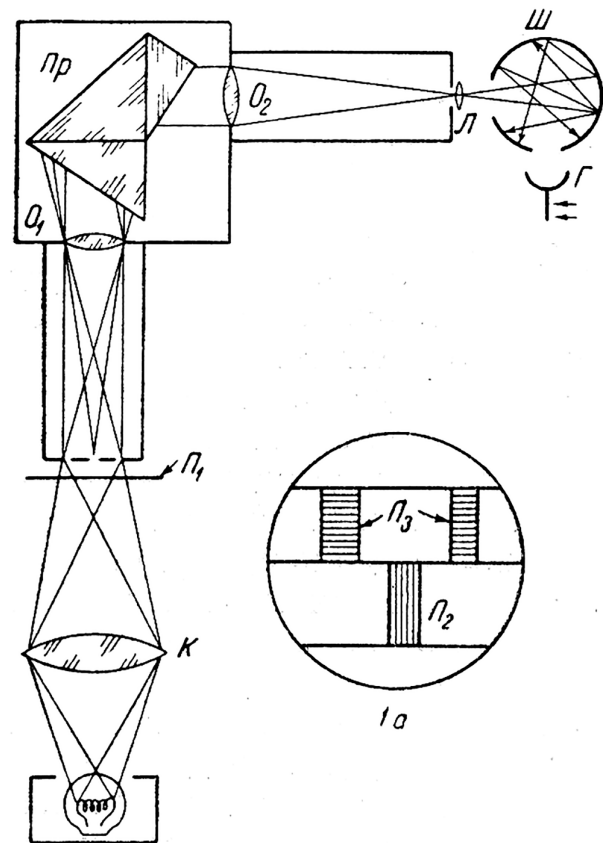


Fig. 2. Bongard's apparatus as illustrated in his 1955 paper on testing colour vision in animals. The inset shows the arrangement of the input slits of the monochromator (see text).

a consideration that is especially relevant in peripheral work.

By adding more slits, Bongard and Smirnov could examine more complicated visual systems. Fig. 3(a), taken from a methodological paper they published in *Biofizika* (Bongard & Smirnov, 1957b), illustrates two possible arrangements of five slits (four primaries and one variable slit). The vertical and horizontal hatching shows how fixed polaroids could be used to combine the primaries and the variable in different combinations. Fig. 3(b) gives further detail of the mechanical features of the slits. Slit  $I$  can be moved horizontally to change the variable wavelength, and its width can be varied with the screw 3. The four fixed primaries correspond to slits  $RGBV$ , and the amount of light passed by each can be adjusted by slides (4), which are controlled by screws (5) linked by flexible cables to four knobs adjacent to the observer's hand.

At moderate light levels, the observer viewed an aperture of the integrating sphere (Fig. 2,  $III$ ), but to obtain very high levels, the output of the monochromator was focussed on a piece of ground glass; and the latter was relayed to the eye in Maxwellian view (Bongard & Smirnov, 1957b).

Bongard and Smirnov give no details of the procedure by which their observers reached the tetrachromatic match. Given four independent adjustments, a naïve observer would readily become confused. Even at the anomaloscope, it is wise to ask the untrained observer to adjust one variable at a time. Pat Trezona (who advocated a systematic iteration to reach a tetrachromatic match, alternating between photopic levels and a strictly scotopic one) referred to Bongard and Smirnov's method as 'trial and error' (Clarke & Trezona, 1976; Trezona, 1973a). In fact, the Moscow method is set out by Fridrikh (1957b) and depended on predicting

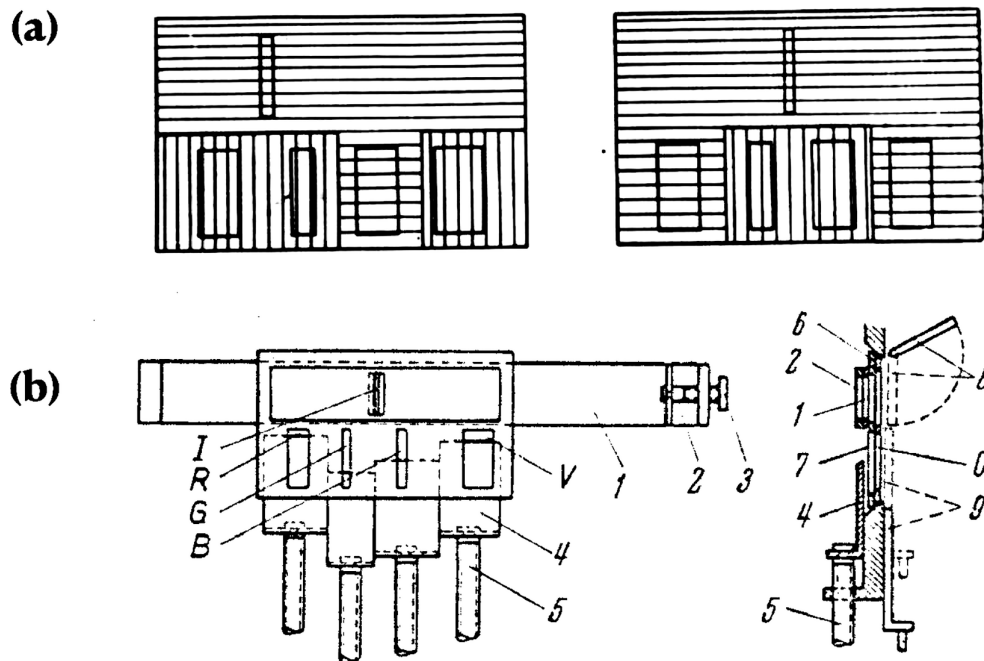


Fig. 3. Arrangements of the colorimeter slits for studying tetrachromacy. See text for details.

the approximate match in advance by calculation. Foveal colour-matching functions were obtained for the same observers and with the same instrument; and estimates of scotopic spectral sensitivity were obtained by extrafoveal matches made at low intensities. From these measurements, four-dimensional matches were set up on the instrument in advance and the subjects then made small adjustments to establish an experimental match.

## 5. Related work

Bongard was a pioneer in the use of ‘silent substitution’, but he was not the very first to use such a method. Estévez and Spekreijse (1982), in a review in honour of William Rushton, identify a use of silent substitution by Makoto Ishihara in 1906; and the method was used explicitly by Forbes, Burleigh, and Neyland (1955) to show, in frog and turtle, that more than one receptor was contributing to the ERG. However, most early experiments using silent substitution were limited to the replacement of one wavelength by a second. The originality of Bongard’s ‘colorimetric’ use of silent substitution lay in its extension to the case where there were two, three or even four primaries. This extension allowed the method to be applied to organisms, or neural channels, that were dichromatic, trichromatic or even tetrachromatic.

Already in 1957, in a paper that has not enjoyed the recognition it deserves, Bongard and Smirnov used a microelectrode to isolate action potentials from single ganglion cells in frog retina. They identified single, chromatically sensitive cells for which no silent substitution could be made between two monochromatic lights, a result implying the cell was connected to more than one type of receptor. However, a silent substitution was possible when two primaries and a variable test light were available; and dichromatic ‘colour-matching functions’ could be measured rather precisely for an individual fibre (Bongard & Smirnov, 1957a). The application of Bongard’s methods to vertebrates and invertebrates was carried forward in Moscow by Orlov, Maximov and Mazokhin-Porshnajkov in the Laboratory for Biophysics of Vision (e.g., Maximov, Orlov, & Reuter, 1985; Orlov, 1961).

Together with Liselotte Fridrikh, Bongard and Smirnov submitted a short account of their work on human tetrachromacy to the 1957

symposium that Stiles organised at the National Physical Laboratory, although they were unable – or, most probably, were not permitted – to attend in person (Bongard *et al.*, 1958). Fridrikh herself used the method of substitution colorimetry to measure colour-matching functions for a 1.5° central field in five normal trichromats (Fridrikh, 1957a; Fridrikh, 1956). She made a point of making direct, absolute, measurements of the radiances of the primaries, for her supervisor was especially critical of Guild and Wright’s failure to adopt this approach (Niuberg, 1956). Submitting her Moscow work as a dissertation, she was awarded a doctorate by the Karl Marx University, Leipzig (Fridrikh, 1957).

It seems likely that Western workers, aware only of the summary given in the proceedings of the NPL symposium, often did not fully grasp Bongard’s method. Thus F. J. J. Clarke (1960) wrote: ‘Bongard *et al.* ... have recently claimed that extra-foveal vision is tetrachromatic, in spite of the (admitted) fact that trichromatic matches are always possible; since four primary matches cannot be unique, it is difficult to see how reproducible data were obtained.’ This passage should be read in conjunction with the comments of Brindley (a Russian speaker): ‘I know of no published report of any attempt, successful or unsuccessful, to confirm [Bongard’s finding]. Dr. F. J. J. Clarke tells me that he knows of three independent unpublished attempts, all unsuccessful. Nevertheless, Dr Bongard has demonstrated the phenomenon to me (in Moscow in 1969), and I believe it to be real.’ (Brindley, 1970, p. 205)

When silent substitution is used today to study a system with  $n$  independent signals, the strategy is usually to equate  $n-1$  signals by calculation and then to examine the effect of modulating the remaining signal. The method depends critically on the accuracy with which the spectral sensitivities of the  $n-1$  signals are known for a given observer. In particular, it assumes that the original colour-matching functions and the scotopic sensitivity – from which the estimates of photoreceptor sensitivities must derive – were themselves wholly (and curiously) uncontaminated by melanopsin signals. Bongard limited himself to establishing full silence empirically and to measuring the colour-matching functions that then maintained the null.



## 6. Translators' notes

Russian famously has two basic colour words for the region of colour space that is designated as 'blue' in English (Martinovic, Paramei, & MacInnes, 2020; Paramei, 2007). Here we translate синий ('sinij') as 'blue' or 'violet-blue' and голубой ('goluboj') as 'cyan' or 'blue-green'. In the subscripts of section 4, we have used 'C' for cyan and 'V' for violet-blue, i.e. 'sinij'. We translate базисные цвета ('basis colours') as 'primaries'.

We translate приемник ('receiver') throughout as 'receptor'. However, the reader should be aware that in this period Bongard and Smirnov, impressed by the similarity of visual acuity in white and in monochromatic light (Smirnov, 1955), explored the possibility that a single cone contains three independent 'receivers' (Smirnov & Bongard, 1959). This does not affect either the arguments or the theory of their 1956 paper on tetrachromacy – and of course we now know of cases of mammalian cones that contain more than one opsin (Applebury et al., 2000).

Where proper names have more than one transliteration from Cyrillic (e.g. Niuberg, Nyuberg; Fridrikh, Friedrich), we give the version that appears on the published paper.

Bongard and Smirnov give luminance in apostilbs. 1 apostilb =  $0.3183 \text{ cd.m}^{-2}$  (Le Grand, 1968, Table 11)

### The four-dimensionality of human colour space

Bongard, M. M. and Smirnov, M. S.

*Doklady Akademii Nauk SSSR*, 1956, vol. 108, No. 3, pp 447–449

1. The twilight receptor in the frog operates not only at threshold levels but also in visual fields of high luminance ( $>100$  apostilbs) (1). Twilight vision in frogs and in man is made possible by the same visual pigment (rhodopsin) and that is why we set out to understand whether the human twilight receptor operates at high light levels. We needed to study the functioning of one (twilight) receptor while the other three (daylight) receptors were operating as well. The only reliable method for such studies is colorimetry. The results of colorimetric experiments in the periphery of the visual field ( $>5$  deg from the centre) have not, so far as we know, been published. We were interested in this area of the retina because it is easier to detect the activity of the twilight receiver where there is a large percentage of rods. Colorimetric studies using standard methods are difficult in the periphery, owing to the low visual acuity. The observer does not see clearly the line that divides the visual fields and cannot judge whether these fields are identical or not. That is why we chose a procedure of separating the fields for comparison not in space but in time. The comparison fields were presented to the observer in succession. The two fields were considered equal in colour when the observer could not detect the moment of substitution of one field for the other. It turns out that the differential sensitivity of the periphery is much better using such a method than it is with normal colorimetry. For these experiments, the same apparatus was used as for studies of colour vision in animals (1).

2. First we checked whether the observer accepted in the periphery matches that he had made in the fovea. The observer adjusted a mixture of red (640 nm) and green (550 nm) to be indistinguishable from monochromatic yellow (590 nm) in the fovea. Then the observer fixated  $10\text{--}20^\circ$  from the field of the colorimeter. The compared fields became strongly unequal. Monochromatic yellow looked dark red, whereas the mixture of red and green looked light green. The luminances of the fields could reach 1000 apostilbs in this experiment.

It is possible to postulate two reasons for the failure of the match:

(a) In the periphery in this spectral region, as in the fovea, there are only two receptors but their spectral sensitivity curves are slightly different from the spectral sensitivity curves for the fovea. The reason for this difference could be, for example, pigmentation of the yellow spot.

(b) In the periphery, in addition to the two receptors that operate in the fovea, some other receptor is active.

If the first hypothesis is correct, then in the periphery matches could be achieved by different mixtures of the same primaries (red and green colours). If another receptor is present in the periphery, then to achieve a colorimetric match one needs to use three and not two primaries.

The experiment showed that it is not possible to achieve a match with any adjustment of the intensities of the red and green lights. However, if a third light was introduced, a good match could be achieved. The central part of the retina fully accepted the matches made for the periphery. This means that a third receptor operates in the periphery. The two receptors that function in the fovea in this part of the spectrum ( $\lambda > 550 \text{ nm}$ ) are not different in their properties from the corresponding receptors in the periphery.

3. The question of the nature of the additional receptor was solved by means of measuring colorimetric summation curves for the periphery. For simplicity, the experiment was conducted only in the spectral range  $> 535 \text{ nm}$ , that is, where the blue receptor in man has such low sensitivity that it can be considered as non-functional. On account of this fact, it was possible to use 3-, and not 4-dimensional, colorimetry.

The primaries were 538, 592 and 640 nm. The resulting summation curves are shown in Fig. 4 (Figure 1 of Bongard and Smirnov's paper), where  $\alpha$  is the curve corresponding to the 538-nm primary,  $\beta$  corresponds to 592 nm and  $\theta$  corresponds to 640 nm. The solid line is the theoretical curve that would correspond to the 538-nm primary if the third receptor is the twilight receptor. The dashed line is the theoretical curve if it were the 'blue' receptor. The comparison of these curves shows that it is the twilight receptor that operates.

The experiments described above prove that the twilight receptor in man does not stop working at high luminances but continues functioning with the daylight receptors.

4. In order to check additionally that the phenomena described above were not caused by the activity of the blue receptor but by a twilight receptor, colorimetric experiments were made in the spectral range where the colour space of the fovea is three-dimensional.

The inner surfaces of an averaging sphere were illuminated by a mixture of red and cyan (goluboj) or a mixture of yellow and violet-blue (sinij) lights. [ $\lambda_R > 630 \text{ nm}$ ,  $\lambda_Y = 592 \pm 2 \text{ nm}$ ,  $\lambda_C = 490 \pm 10 \text{ nm}$  and  $\lambda_V = 435 \pm 15 \text{ nm}$ .] With the visible diameter of the aperture of the sphere at  $0.5\text{--}2^\circ$ , the best match was found for the fovea. Then the fixation point was moved to the side and the match was broken. All the observers estimated the mixture of red and cyan as bright green and the mixture of yellow and blue as rose-purple and seriously darker. A prominent inequality was noticeable as soon as the fixation point was moved from the central field by  $1$  or  $2^\circ$ .

In peripheral vision, it was not possible to achieve even an approximate match by any changes in the proportions of red, yellow, cyan and violet-blue. From this it directly follows that the colour space of the periphery of the retina is more than three-dimensional. Therefore we ran

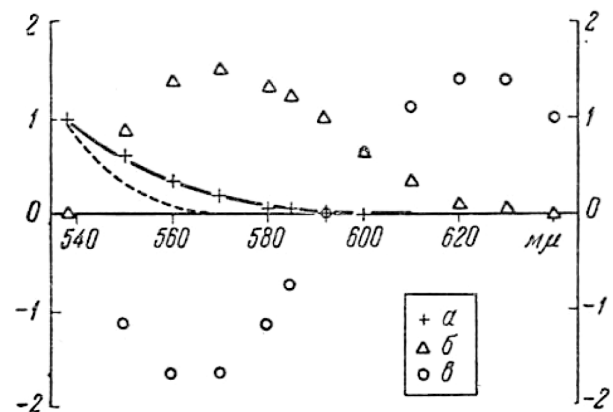


Fig. 4. Fig. 1 of Bongard and Smirnov's paper.

experiments with five radiations. With any choice of wavelengths for these radiations, it is possible to adjust their intensities so that the mixture of two of them is not distinguishable from a mixture of the remaining three. Such four-dimensional matches found for the periphery also satisfy well the central retina. These experiments once again show that in the periphery four receptors are active concurrently.

Four-dimensional matches turned out to be stable with respect to changes in adaptive state. After light-adaptation or long dark-adaptation and after adaptation to bright red, green or blue light, the previously established matches were fully accepted.

5. The existence of a fourth receptor in the periphery, which operates at high intensities \*, explains well many phenomena that were considered unexplainable from the point of view of three-component theory. Such phenomena are, for example: different perimetric borders for a yellow made of a mixture of red and green and for a monochromatic yellow; disruption of the match of a mixture of red and green to yellow with increase in visual angle and with changes in adaptive state etc (2).

6. The twilight receptor, both in man and frog, operates not only under low but also under high luminances. Two fields cannot be matched in colour if the twilight receptor is differentially activated. This means that in both man and frog it plays a role in colour vision. In humans, owing to the presence of several photopic receptors, the role of the twilight receptor is relatively small. This smaller role of the twilight receptor in human colour vision is certainly also due to a sharp decrease in the number of rods in the central retina. However, in high-precision colorimetric experiments in the periphery, and possibly in the fovea, the fourth receptor should be taken into account. In our experiments, it is noted that four-dimensional matches for the fovea are of "higher quality" than are three-dimensional ones (Three-dimensional matches seem less precise). This can be explained by the fact that part of the dispersed light in the eye falls on the periphery but also by the existence of a small number of rods in the fovea. Evidence that there are functional rods in the fovea is given by the work of V. G. Samsonova (3).

\* In the periphery, two-dimensional matches in the range of  $\lambda > 550$  nm were found to be disrupted up to the highest field luminances that were used – 100,000 apostilbs. However, we did not explore in detail whether these disruptions can be explained by only the twilight receptor even under such high luminances.

1. M. M. Bongard, *Doklady Akademii Nauk*, 103, No. 2 (1955).
2. G. Hartridge, *Modern achievements in the Physiology of Vision*, 1952.
3. V. G. Samsonova, *Problemy fiziologicheskoy optiki*, 8, 26 (1953).

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## References

- Aguilar, M., & Stiles, W. S. (1954). Saturation of the rod mechanism of the retina at high levels of stimulation. *Optica Acta*, 1(1), 59–65.
- Anon.. (2021). Mikhail Sergeevich Smirnov (1921–2008 ГГ.). *Sensornye Systemy*, 35(2), 175–176.
- Applebury, M. L., Antoch, M. P., Baxter, L. C., Chun, L. L. Y., Falk, J. D., Farhangfar, F., ... Robbins, J. T. (2000). The murine cone photoreceptor: A single cone type expresses both S and M opsins with retinal spatial patterning. *Neuron*, 27(3), 513–523.
- Bone, R. A., & Sparrock, J. M. B. (1971). Comparison of macular pigment densities in human eyes. *Vision Research*, 11(10), 1057–1064.
- Bongard, M. M. (1955). Kolorimetriya na Zhivotnykh [Colorimetry in animals]. *Doklady Akademii Nauk SSSR*, 103(2), 239–242.
- Bongard, M. M. (1970). *Pattern recognition*. New York: Spartan Books.

- Bongard, M.M., Smirnov, M.S., & Friedrich, L. (1958). The four-dimensional colour space of the extra-foveal retinal area of the human eye. In: *Visual Problems of Colour*, 1. London: Her Majesty's Stationery Office.
- Bongard, M. M., & Smirnov, M. S. (1956). Chetyrekhmernost' tsvetovogo prostranstva cheloveka. [The Four-Dimensionality of Human Colour Space]. *Doklady Akademii Nauk SSSR*, 108(3), 447–449.
- Bongard, M. M., & Smirnov, M. S. (1957a). Spectral sensitivity curves for receptors connected to single optic nerve fibres in the frog. *Biophysics*, 2, 328–333.
- Bongard, M. M., & Smirnov, M. S. (1957b). A substitution method of visual colorimetry (A new system of colorimetry for investigating colour vision in Man). *Biophysics*, 2, 124–128.
- Brindley, G. S. (1970). *Physiology of the retina and visual pathway*. London: Arnold.
- Clarke, F. F. J. (1960). Extra-foveal colour metrics. *Optica Acta*, 7(4), 355–384.
- Clarke, F. F. J., & Trezona, P. W. (1976). *Towards general systems of colorimetry and photometry based on the tetrachromatic colour match*. Paris: Bureau Central de la CIE.
- Dacey, D. M., Liao, H.-W., Peterson, B. B., Robinson, F. R., Smith, V. C., Pokorny, J., ... Gamlin, P. D. (2005). Melanopsin-expressing ganglion cells in primate retina signal colour and irradiance and project to the LGN. *Nature*, 433(7027), 749–754.
- Do, M. T., Kang, S. H., Xue, T., Zhong, H., Liao, H. W., Bergles, D. E., & Yau, K. W. (2009). Photon capture and signalling by melanopsin retinal ganglion cells. *Nature*, 457(7227), 281–287.
- Donner, K. O., & Rushton, W. A. (1959). Retinal stimulation by light substitution. *Journal of Physiology*, 149, 288–302.
- Enezi, J.A., Revell, V., Brown, T., Wynne, J., Schlagen, L., & Lucas, R. (2011). A "melanopic" spectral efficiency function predicts the sensitivity of melanopsin photoreceptors to polychromatic lights. *Journal of Biological Rhythms*, 26(4), 314–323.
- Estévez, O., & Spekreijse, H. (1982). The "silent substitution" method in visual research. *Vision Research*, 22(6), 681–691.
- Forbes, A., Burleigh, S., & Neyland, M. (1955). Electric responses to color shift in frog and turtle retina. *Journal of Neurophysiology*, 18(6), 517–535.
- Frederiksen, R., Morshedian, A., Tripathy, S. A., Xu, T., Travis, G. H., Fain, G. L., & Sampath, A. P. (2021). Rod photoreceptors avoid saturation in bright light by the movement of the G protein transducin. *Journal of Neuroscience*, 41(15), 3320–3330.
- Friedrich, L. (1954). Prüfung der Gültigkeit des Beerschen Gesetzes am Agfacolorfilm. *Zeitschrift für wissenschaftliche Photographie, Photophysik und Photochemie*, 49, 114–118.
- Fridrikh, L. (1957a). Colour-combination curves for normal trichromats determined by direct energy measurements. *Biophysics*, 2(1), 129–132.
- Fridrikh, L. (1957b). The part played by rod vision in the light-adapted human eye. *Biophysics*, 2(3), 334–339.
- Friedrich, L. (1956). Bestimmung der Spektralwertkurven normaler Trichromaten durch direkte Messungen nach einer neuen Methode. *Die Farbe*, 5, 201–209.
- Friedrich, L. (1957). Foveale und extrafoveale Charakteristik der Netzhaut des menschlichen Auges. Mathematisch-Naturwissenschaftlichen Fakultät, Inauguraldissertation. Leipzig: Karl-Marx-Universität.
- Gamlin, P. D. R., McDougal, D. H., Pokorny, J., Smith, V. C., Yau, K.-W., & Dacey, D. M. (2007). Human and macaque pupil responses driven by melanopsin-containing retinal ganglion cells. *Vision Research*, 47(7), 946–954.
- Hammond, B. R., Wooten, B. R., & Snodderly, D. M. (1997). Individual variations in the spatial profile of human macular pigment. *Journal of the Optical Society of America A*, 14(6), 1187–1196.
- Horiguchi, H., Winawer, J., Dougherty, R. F., & Wandell, B. A. (2013). Human trichromacy revisited. *Proceedings of the National Academy of Sciences of the United States of America*, 110(3), E260–E269.
- Howland, H. C. (2000). The history and methods of ophthalmic wavefront sensing. *Journal of Refractive Surgery*, 16(5), S552–553.
- Jordan, G., & Mollon, J.D. (in press). Tetrachromatic Vision. In: R.M. Luo (Ed.) *Encyclopedia of Color Science and Technology*. New York: Springer.
- Jordan, G., & Mollon, J. D. (1993). A study of women heterozygous for colour deficiencies. *Vision Research*, 33(11), 1495–1508.
- Le Grand, Y. (1968). *Light, colour and vision*. London: Chapman & Hall.
- Lucas, R. J., Allen, A. E., Milosavljevic, N., Storchi, R., & Woelders, T. (2020). Can we see with melanopsin? *Annual Review of Vision Science*, 6(1), 453–468.
- Martinovic, J., Paramei, G. V., & MacInnes, W. J. (2020). Russian blues reveal the limits of language influencing colour discrimination. *Cognition*, 201, 104281. <https://doi.org/10.1016/j.cognition.2020.104281>.
- Maximov, V. V., Orlov, O. Y., & Reuter, T. (1985). Chromatic properties of the retinal afferents in the thalamus and the tectum of the frog (*Rana temporaria*). *Vision Research*, 25(8), 1037–1049.
- Maxwell, J. C. (1860). On the theory of the compound colours and the relations of the colours in the spectrum. *Philosophical Transactions of the Royal Society*, 150, 57–84.
- Nagel, W. A. (1907). Zwei Apparate für die Augenärztliche Funktionsprüfung. *Adaptometer und kleines Spektralphotometer (Anomaloskop)*. *Zeitschrift für Augenheilkunde*, 17, 201–222.
- Nagy, A. L., Macleod, D. I. A., Heyneman, N. E., & Eisner, A. (1981). Four Cone Pigments in Women Heterozygous for Color Deficiency. *Journal of the Optical Society of America*, 71(6), 719–722.
- Niuberg, N.D. (1956). Colorimetric experiments as a means of studying colour vision: their basic requirements. *Biophysics*, 2 (2), 157–156.
- Orlov, O. Y. (1961). Receptors of the retina and visual pigments. *Biophysics*, 6(3), 368–377.
- Palmer, D. A. (1981). Nonadditivity in Color Matches with 4 Instrumental Stimuli. *Journal of the Optical Society of America*, 71(8), 966–969.

- Paramei, G.V. (2007). Russian 'blues'. Controversies of basicness. In: R.E. MacLaury, G. V. Paramei, & D. Dedrick (Eds.), *Anthropology of Color*. Amsterdam: John Benjamins Publishing Co.
- Pokorny, J., Smith, V. C., & Starr, S. J. (1976). Variability of color mixture data - II. The effect of viewing field size on the unit coordinates. *Vision Research*, 16(10), 1095–1098.
- Rautian, G. N., & Solov'eva, V. P. (1954). Vlijanie svetlogo okruženija na ostrotu cvetorazloženija. [The effect of a light surround on the acuity of colour discrimination.]. *Doklady Akademii Nauk SSSR*, 95, 513–515.
- Rozhkova, G. I., & Sobolevski, A. N. (2015). Scientific activity of Alfred Yarbus: The stages of research work, senior and younger colleagues, conditions of investigations. *Perception*, 44(8–9), 837–850.
- Smirnov, M. S. (1955). Raspolozhenie tsvetovospriimajuschikh priemnikov v fovea cheloveka. [The arrangement of colour-perceiving receivers in the human fovea.]. *Doklady Akademii Nauk*, 103(3), 427–429.
- Smirnov, M. S. (1961). Measurement of the wave aberration of the human eye. *Biophysics*, 6, 687–703.
- Smirnov, M. S., & Bongard, M. M. (1956). Porogovyj i kolorimetriceskij metody izuchenija tsvetovogo zrenija [Threshold and colorimetric methods of studying colour vision]. *Biofizika*, 1(2), 158–162.
- Smirnov, M. S., & Bongard, M. M. (1959). Hypothesis concerning the mechanism of photoreception in the retina (An analogy between retinal photoreceptors and semiconducting photoelements). *Biophysics*, 4, 57–63.
- Spitschan, M., Bock, A. S., Ryan, J., Frazzetta, G., Brainard, D. H., & Aguirre, G. K. (2017). The human visual cortex response to melanopsin-directed stimulation is accompanied by a distinct perceptual experience. *Proceedings of the National Academy of Sciences of the United States of America*, 114(46), 12291–12296.
- Tamm, E. I. (2001). *Zapiski al'pinista. [Memoirs of an alpinist]*. Moscow: Fizicheskij Institut Akademii Nauk.
- Tikidji-Hamburyan, A., Reinhard, K., Storch, R., Dietter, J., Seitter, H., Davis, K. E., ... Münch, T. A. (2017). Rods progressively escape saturation to drive visual responses in daylight conditions. *Nature Communications*, 8(1). <https://doi.org/10.1038/s41467-017-01816-6>.
- Trezona, P. (1973a). Tetrachromatic colour measurement. Second Congress, Association Internationale de la Couleur: London: Adam Hilger.
- Trezona, P. W. (1973b). The tetrachromatic colour match as a colorimetric technique. *Vision Research*, 13(1), 9–25.
- Vishnevets, Y. (2005). "[Mikhail Sergeevich]." Livejournal <https://kunstkamera.livejournal.com/109610.html> Accessed 21 August 2021.
- Wyszecki, G., & Stiles, W. S. (1982). *Color science*. New York: Wiley.
- Yamakawa, M., Tsujimura, S., & Okajima, K. (2019). A quantitative analysis of the contribution of melanopsin to brightness perception. *Scientific Reports*, 9, ARTN 7568.