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Sensitivity of Rods and Cones in the Parafovea

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Commentary by Oscar Estévez-Uscanga

By his own account, Stiles¹ produced 93 publications as listed in the bibliography included at the end of his book, Mechanisms of Colour Vision, Selected Papers of W. S. Stiles F.R.S. with a new introductory essay. This makes then a total of 94 publications, if we include the introductory essay to the reprinted collection of papers that form the bulk of the book. While I haven’t read or consulted all of Stiles’ papers, most of those I did read have, in one way or another, been influential in the course of my own scientific development.

In the Preface to Stiles’ book, W. A. H. Rushton writes: ‘‘It has now become accepted that Stiles’ conclusions are authoritative and deep and most of those working in this field wish to consult them.’’ This is as true now as it was when Rushton wrote the Preface in 1977, twenty years ago. ‘‘Unfortunately . . . ’’, Rushton continues, ‘‘. . . Stiles has not published his important series of papers in sequence in one journal but seems to have given his latest paper to whatever conference asked him for it when it was ready, and then he felt it redundant to say the same again in a more accessible publication.’’ Not only were his papers often published in little known journals or difficult to find places such as conference or symposia proceedings, but two of his papers are not even in English: one is in German (Stiles²) and another in Spanish. This last was the result of a collaboration with Cabello, who visited the National Physical Laboratory at the end of the 1940s and who was probably responsible for writing the paper for the Spanish journal, ‘‘Anales de Física y Química.’’ It is fortunate that Geller and Herrero de Tejada have undertaken the chore to translate—and to some extent correct some mistakes in the original—the
last mentioned paper to English as it is now published here.

The significance of Stiles’ work can hardly be overemphasized. His contributions to Visual Science are many and varied. In the first place, he made accurate measurements of many of the basic characteristics of the human visual apparatus, from the passive optics of the eye and pigments absorbing light in the path to the retina, up to important optical properties of the receptors themselves. In the second place, he developed several theoretical frameworks that have proven to be of fundamental importance to understand, among others, brightness and colour vision as well as the ways that different receptor types interact with light and with each other to yield the visual impression. Finally, all throughout his work, he developed and applied several original methodologies that have, by themselves, proven to be of great value in the study of human vision. Not only have these “Stiles’ methodologies withstood the test of time and continue to be used, but they have also been further developed and perfected leading, in some cases, to even newer methodologies of great value in vision research.

Besides the above mentioned merits of Stiles’ work, his papers are also significant in yet another and different way: they often contain remarks, observations or even unanswered questions that provide us with a rich source of research ideas still deserving to be further investigated. The article with Cabello published here is a case in point: in this article, two of the methodologies developed by him—selective chromatic adaptation and directional receptor sensitivity—were ingenuously combined to study an important question, namely that of the receptors’ sensitivity at the near-fovea where the transition from rod to cone vision takes place. While the Cabello and Stiles article purports to study and clarify the change in threshold sensitivity of rods as one approaches the central fovea from the near periphery, it also reports in its conclusions an interesting finding bearing on the possible mechanism of the rod–cone interactions.

In my opinion, the way or ways in which rods and cones interact and contribute to vision is not yet fully understood. A prevalent view is that at photopic levels rods do not contribute to vision—coloured or not—because they become “saturated” and at lower scotopic levels cones’ signals cannot pass a threshold; this view is too simplistic. We know, of course, that both types of receptors must share the available and scarce neural channels, i.e., that they must use the same ganglion cells to send their signals to the brain. It should be obvious that a mechanism is called for that ought to take care of locally regulating the momentary rod–cone participation for any given visual stimulus, at any given part of the retina, and for any given light level. A simple, global mechanism working all over the retina switching “systems” fully, as it were, simply will not do. The structure and composition of the retina vary much according to the part of the visual field being examined, and the visual stimulus itself is not projected on the retina in a uniform way: several optical effects combine to affect the image quality depending on eccentricity. Even if an even and uniform stimulus is presented, the retinal intensity distribution of its projection becomes highly nonuniform in the periphery and is certain to be affected as well near the fovea and perifovea due to the nonuniform localization of screening pigments, the rapidly changing structure of the receptor mosaic, and the numerosity and specific mixture of rod and cone photoreceptors.

The Cabello and Stiles study reports on an investigation of that part of the retina where the rod–cone transitions are certain to occur due to the characteristics of the retinal topology and receptor distributions. By studying this part of the retina, one might be able to throw some light on the ways those receptors interact. Indeed, Cabello and Stiles’ most significant conclusion is that a change in rod sensitivity takes place that cannot be accounted for in terms of biochemical processes nor in terms of receptor numerosities only. Rather, they conclude, “changes in the characteristics of the rods themselves or in the nervous conductors which carry the signal to the brain” must take place (my italics). I believe this last explanation—with some qualifications—to be most likely the correct one.

In the first place, it is important to realize that, contrary to widespread belief, rods can contribute to both peripheral colour vision and central colour matches, and can do this even at low or near photopic levels. Perhaps one of the most convincing results showing rod participation in colour vision in central fields and at low photopic levels is that of Smith and Pokorny. They studied the colour vision of dichromats—protanopes and deuteranopes—with an 8º centrally fixated field. Their study was motivated by the finding that dichromats could continue to make dichromatic matches at the red end of the spectrum, where otherwise they would be expected to make monochromatic matches due to the fact that only one type of cone is available to them in this region. Similarly, it is well known that subjects with normal colour vision actually make trichromatic matches past about 600 nm up to the extreme reds. In both cases, normals and dichromats, a second (in dichromats) or third (in normals) receptor must be participating in the colour match. Smith and Pokorny showed, by analyzing anomaloscope matches of these observers, that their extra color receptors must be rods.

In a reanalysis of the Smith and Pokorny results, motivated by colorimetric arguments, I also could show (Estévez), and convinced myself, that indeed, the small but quite apparent curvature in the spectrum locus past 600 nm up to 700 nm or further, which is obtained for both large field (10º) and small field (2º) normal colour matches, must be attributed to rod participation in the colour match. This appears to be the case even at low but nevertheless photopic levels and for near foveal small fields (2º) when one analyzes not the Standard Colorimet-
stronger if their signals are to reach the corresponding existence of these two arms does not agree with what cones are hindering the rod receptor signals at the given vs. intensity curves of cone vision showed two arms that sensitivity loss found by Cabello and Stiles can readily resulting in an increased perceptual threshold. The great constant measured with a constantly present red (630 nm) adapt-

A model yielded spectral loci that agree qualitatively well with those observed. My own unpublished calculations and analysis of those data with such a model yielded spectral loci that agree qualitatively well with those observed. With this in mind, we can return to the Cabello and Stiles finding that neither the amount of sensitivity changes of rods, nor the shape of t.v.i. rod curves obtained in the near fovea agree with a uniform behavior of rods between the periphery and the central region. After introducing all possible relevant corrections, their computations allow them to account for only part of the total rod loss of sensitivity, leaving some 0.7 log units unexplained.

However, if we recall that these rod sensitivities were measured with a constantly present red (630 nm) adapting field, and realize that the local rod signals must make up their way past ganglion cells that are also receiving a strong and constant signal from red cones, the extra sensitivity loss found by Cabello and Stiles can readily be explained: the near-periphery relatively numerous red cones are hindering the rod receptor signals at the given region so that these must be stimulated about 5 times stronger if their signals are to reach the corresponding ganglion cells and produce a sensory response.

Is my explanation right? Perhaps yes, probably no, but it is a plausible one. I would be happy and satisfied, if some younger vision scientist, after reading these speculations of mine and the accompanying translation of the original Cabello and Stiles article published here, would be stimulated as well to go ahead and study the matter further. Many questions concerning rod—cone interactions are still waiting to be investigated and the near-peripheral retina seems an ideal object for further research.

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Abstract: The transition from cone to rod vision was studied by measuring the variation in absolute threshold across the retina with a small monochromatic test stimulus (λ = 490 nm). The shift from one mechanism to the other was determined by means of directional sensitivity. In the retinal region corresponding to rod vision, the test sensitivity (reciprocal threshold) decreased closer to the fovea. This variation may be attributed to three causes: a) the reduction in the number of rods; b) the increase in absorption of the yellow macular pigment; c) changes in the characteristics of the rods themselves or in the nervous conductors, which carry the signal to the brain, resulting in an increased perceptual threshold. The great importance of the latter cause is discussed. The threshold vs. intensity curves of cone vision showed two arms that may be attributed to the action of cone mechanisms. The existence of these two arms does not agree with what is expected from the simple trichromatic analysis of the