Visual purple (*Sehpurpur*)
Franz Boll (1849 – 1879) described the colour of rods dissected from dark adapted frog retinas as *Sehrot* or visual red (Wade 2008). He conducted detailed experiments demonstrating that visual red was bleached by incident light and regenerated in darkness. After initially referring to the colour as reddish-purple he later explicitly stated that the rods were red and not purple. Why is it now referred to as visual purple?

With what Boll saw as unseemly haste, Wilhelm Kühne (figure 1), or Willy as he preferred to be called, not only appreciated the significance of Boll’s research but also reported extensions of it within weeks of its first publication in 1876 (Kühne, 1877a). Because Kühne’s first presentation appeared before Boll’s second (both in January 1877),
he used Boll's initial description of the rods being ‘intense purple-red' and Kühne called it *Sehpurpur*. With little delay, summaries of Boll's and Kühne's reports were translated into English by Arthur Gamgee (Boll 1877a, 1877b; Kühne 1877b). Gamgee wrote: “Kühne's observations were made on the retinae of frogs and rabbits. In the first place, implicitly relying upon the statements of Boll, he examined, as soon as possible after death, the retinae of animals which had been kept for some time in darkness. He soon found that the beautiful purple colour persists after death if the retina be not exposed to light; that the bleaching takes place so slowly in gaslight, that by its aid the retina can be prepared and the changes in its tint deliberately watched; that when illuminated with monochromatic sodium light the purple colour does not disappear in from twenty-four to twenty-eight hours, even though decomposition have set in” (Kühne 1877b, page 156). Boll's *Sehrot* was translated as vision red and Kühne's *Sehpurpur* as vision purple, but Foster (1878, who only published a translation of Kühne's article) referred to the latter as visual purple. Thus, Kühne introduced the term *Sehpurpur* (visual purple) for the colour of the photosensitive pigment in rods and called the chemical responsible for it rhodopsin (see Kühne 1879/1977); these are the terms that are still in use.

Kühne's influence has been far greater than Boll's, perhaps because of Foster's selective translation. Indeed, when Kühne's long review of chemical processes in the retina (from 1879) was translated by Hubbard, to celebrate the centenary of the discovery of rhodopsin, she initially overlooked Boll's earlier research: “A few years ago I read Boll's original note on rhodopsin, published in 1876 and his full length paper of 1877 and realized for the first time how much of what I had come to associate with Kühne's name, Boll also had done” (Hubbard 1977, page 1247).

Kühne came relatively late to the study of the retina. He received a thorough grounding in physiology, chemistry and optics before working (like Boll) for a short time in the laboratory of du Bois-Reymond in Berlin. Kühne's early work was on muscle physiology and digestion and he coined widely used terms in each of these areas: muscle spindles and enzymes. He published an important monograph on the action of nerves on muscles, suggesting that muscle contraction followed the invasion of action currents from the nerves (Kühne 1862). In 1871 he succeeded Helmholtz as professor of physiology at Heidelberg and it was there that he started his investigations of retinal photochemistry (see Crescitelli 1977). Kühne was able to extract rhodopsin from the rods of frogs and rabbits, and his elegant experiments provided the foundations upon which subsequent studies were built. He showed that the rate of bleaching was dependent not only on the intensity of light but also on its wavelength. The visual purple was confined to rods and was not seen in the foveas of humans. Most significantly, Kühne established the ‘visual cycle': visual purple in the rods is bleached by light to form visual yellow which in turn is transformed to visual white. He wrote: “Though the knowledge gained to date about visual purple has left the question whether it has some excitatory, objectively demonstrable effects on the retina completely undecided, the phototropic reaction of the pigment epithelium offers an unambiguous answer, since it shows that light clearly has a stimulating effect on the epithelial protoplasm” (Kühne 1879/1977, page 1314, original italics).

Over half a century later, George Wald (figure 2) fashioned some chemical flesh on Kühne's cyclic skeleton: “It was largely on the basis of Kühne's observations that I could conclude that rhodopsin is a protein” (Wald 1972, page 293). The clue lay in the link between vitamin A and vision: “Animals deprived of vitamin A become night blind: after exposure to bright light, they fail to see at intensities which still readily stimulate the normal eye” (Wald 1935, page 905). Initially working with frog retinas, Wald examined the chemical reactions when it was in the purple, yellow, and white stages.
He established that light converts rhodopsin to retinal and opsin through a series of intermediate reactions involving metarhodopsins; one of the intermediates results in excitation of the photoreceptor cell whereas another releases opsin. Retinal is reduced to vitamin A and regenerates rhodopsin, as does opsin. The diagrammatic representation of these processes can be dimly discerned in figure 2. Wald, who was awarded the Nobel prize for Physiology or Medicine in 1967, started his research in Germany in the 1930s and on his return to the USA continued to elaborate the details of the cycle and to explore the photopigments and processes involved in retinal cones.

Both Kühne and Wald were fascinated by the similarities between the chemical processes in photographic films and in retinas. Kühne described the relationship thus: “Bound together with the pigment epithelium, the retina behaves not merely like a photographic plate, but like an entire photographic workshop, in which the workman continually renews the plate by laying on new light-sensitive material, while simultaneously erasing the old image” (translated in Wald 1950, page 98). In order to display this workshop in action Kühne exposed dark-adapted, living eyes (usually of rabbits) to light and developed the retinas yielding what he called optograms—the final long-lasting stimulus (like a window) on which the eyes were fixed could be captured on the processed retina. He is said to have tried to form an optogram of Helmholtz on a
rabbit’s retina, but only the white collar was rendered visible (Rothschuh 1973)! Of all the scientific work he performed, the optograms had the greatest popular appeal, and they were applied in science fiction in a manner distinctly disapproved of by Kühne. His experiments were reported in newspapers: the notion that the retinal record at the moment of death would be retained captured the imagination of novelists and crime writers. From Jules Verne onwards the possibility that the image of the murderer was retained in their victims' retinas was entertained (see Evans 1993). Wald took the experimental process further but was sanguine about its prospects: “Photography with rhodopsin is only in its first crude stages, perhaps at the level that photography with silver bromide reached almost a century ago. I doubt that it has a future as a practical process. For us its primary interest is to pose certain problems in visual chemistry in a provocative form. It does, however, also add another chapter to the mingled histories of eye and camera” (Wald 1950, page 103).

Boll's Sehrot became Kühne's Sehpurpur. Did the transformation reflect a real difference in the perception of the retinal pigment or was it a consequence of Kühne's reliance on Boll's initial description? On reflection, the name given to the pigment in rods pales into insignificance in comparison to the light cast on the chemistry of the initial stages of vision by the experiments of both Boll and Kühne.

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References
Boll F, 1876 “Zur Anatomie und Physiologie der Retina” Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 783 – 787
Boll F, 1877a “A contribution to the anatomy and physiology of the retina” Quarterly Journal of Microscopical Science 17 152 – 155
Boll F, 1877b “Contributions to the physiology of vision and of the sensation of colour” Quarterly Journal of Microscopical Science 17 226 – 232
Crescitelli F, 1977 “Friedrich Wilhelm Kühne” Vision Research 17 1317 – 1323
Evans A B, 1993 “Optograms and fiction: photo in a dead man's eye” Science-Fiction Studies 20 341 – 361
Foster M, 1878 The Photochemistry of the Retina and On Visual Purple (London: Macmillan)
Hubbard R, 1977 “Preface to the English translation of Boll’s On the anatomy and physiology of the retina and of Kühne’s Chemical processes in the retina” Vision Research 17 1247 – 1248
Kühne W, 1862 Über die peripherischen Endorgane der motorischen Nerven (Leipzig: Engelmann)
Kühne W, 1877a “Zur Photochemie der Netzhaut” Untersuchungen aus dem Physiologischen Institut der Universität Heidelberg 1 1 – 138
Kühne W, 1877b “Kühne's researches on photo-chemical processes in the retina” Quarterly Journal of Microscopical Science 17 155 – 159
Kühne W, 1879/1977 “Chemische Vorgänge in der Netzhaut”, in Handbuch der Physiologie Ed. L Hermann, volume 3 part 1 (Leipzig: Vogel) (translated by R Hubbard in Vision Research 1977 17 1269 – 1316)
Rothschuh K E, 1973 History of Physiology translated by G B Risse (Huntington, NY: Krieger)
Wade N J, 2008 “Visual red (Sehrot)” Perception 37 1467 – 1470
Wald G, 1935 “Vitamin A in eye tissues” Journal of General Physiology 18 905 – 915
Wald G, 1950 “Eye and camera” Scientific American 183 (August) 32 – 41
Wald G, 1972 “The molecular basis of visual excitation” Nobel Lectures. Physiology or Medicine, 1963 – 1970 (Amsterdam: Elsevier) pp 292 – 315