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On G. E. Müller's colour sensations

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Resumen

The current paper deals with Müller's contributions to visual perception, which originated from the Heringhian model of chromatic opponence based on the principle that the three primary colours were distributed into three antagonistic pairs of colours (red-green, yellow-blue, black-white), each of them corresponding to a specific retinal channel. The nature of the channel responses was chemical and not physical. Moreover, Hering supposed that, when these couples were in equilibrium, one would see nothing, but actually one sees grey. Müller further developed Hering's theories about the colour grey by adding a cortical grey as the zero-point from which all colour sensations diverged. In other words, there was a «cortical» or «intrinsic/subjective» grey (*Augengrau*), which was used as a device for placing the opponent processes in a single cortical, but not receptor, cell. The present paper focuses in particular on this last attractive theme.

Keywords: Visual perception, colour sensations, cortical grey.

In a letter of April 1928 from Georg Elias Müller to Edwin Boring in answer to a question about his early formative years, the former wrote: «With quick determination I now turn myself energetically toward natural science, and bury myself in Helmholtz's *Physiologische Optik* and the like» (Boring, 1935, p. 345). It was this «burial» that led to his involvement in a third field of interest, the psychology of vision. In fact, best-known for his research on memory, Müller also developed a theory that attempted to go beyond the empirism *versus* nativism debate by improving on Hering's idea of colour vision. In 1896-1897 he published *Zur Psychophysik der Gesichtsempfindungen*, in which he adopted Hering's theory of the three reversible photochemical substances (he held that the processes were chemical rather than metabolic, as Hering had thought) and added his concept of cortical grey as the zero-point from which all colour sensations diverge.

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While Hermann von Helmholtz has probably been given most of the credit for the trichromatic theory of colour vision, he was not the first to postulate such a theory.

The discovery in 1665 by I. Newton that light from the sun could be bent to varying degrees by a prism so as to produce a spectrum of colours ranging from red (least bent rays) to violet (most bent rays) (*degree of refrangibility*) provided the basis for the rejection of Aristotle's view that colours came from objects and led to its being replaced with the view that colour was a property of light. Basing himself on Newton's theory (Newton, 1706), on 12th November 1801 Thomas Young affirmed in *Hypothesis II* of his Bakerian Lecture:

> I use the word «undulation», in preference to «vibration», because «vibration» is generally understood as implying a motion which is continued alternately backwards and forwards, by a combination of the momentum of the body with an accelerating force, and which is naturally more or less permanent; but an «undulation» is supposed to consist of a vibratory motion, transmitted successively through different parts of a medium, without any tendency in each particle to continue its motion (Young, 1802, p. 16).

Young carried out an experiment that allowed light to pass through two pinholes set close together on a screen where he observed that the beams spread out, or diffracted, and overlapped. In areas where the light beams overlapped, bands of brightness alternated with bands of darkness. This phenomenon was called *interference* and Young compared it to waves in water, where the crests meet and combine to make bigger waves and troughs meet and cancel each other out. In 1817, he concluded that they propagate as transverse waves, not longitudinal waves as he originally proposed.

However, the ondulatory theory of light instead of the Newtonian corpuscular opinion was the final point of previous research on the visual system and the starting point of research on chromatic vision. In the same year of the Lecture Young showed that astigmatism was due to irregular curvature of the cornea (Young, 1801) providing its first measurement; this discovery closed the investigations carried out in the 1790s on vision and, more precisely, on the process of focusing of the eye (accommodation), that was achieved by a change of shape in the lens of the eye, the lens being composed of muscle fibres (Young, 1793). Then, in 1800 he talked about a possible analogy between the propagation of the sound waves and of the light ones (Young, 1800). It was in this context that Young reread the Newtonian principle according to which colour sensation depended upon the wavelength of the light entering the eye. For him, «as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance, to the three principal colours, red, yellow, and blue (Young, 1802, p. 21).

Consequently, he proposed a trichromatic theory of colour according to which colours result from the mixture of the three primary colours (red, yellow, and blue). As a result of learning from his friend, William Hyde Wollaston, that red light mixed with green light gave a yellow sensation, Young changed the primary colours to red, green, and violet, following their respective correspondence to a long wavelength (the first), intermediate wavelength (the second), or short wavelength (the third). In Young's opinion, such a trichromatism would not have been determined by light properties, but by physiological peculiarities of the human eye;

more precisely, by the different tension degree of three types of receptors for daytime or photopic vision connected to primary colours. Therefore, any other colour would have resulted from the simultaneous stimulation of the three types of receptors (Young, 1802).

Young's hypothesis, afterwards justified by the discovery of retinal cones, gave rise to many investigations that aimed at quantifying the constituents of colour mixtures.

Young's model was –as Helmholtz suggested– «nothing more than a further extension of Johannes Müller's law of special sensation» (Helmholtz, 1962, p. 134), according to which the quality of an experience was related to some specific quality of the energy in the nerves. In fact, in 1826 Müller stated the principle that the kind of sensation following stimulation of a sensory nerve did not depend on the mode of stimulation but upon the nature of the sense-organ. Thus light, pressure, or mechanical stimulation acting on the retina and optic nerve invariably produced luminous impressions. This he termed the law of *specific nerve energies*, better clarified in his 1833-1840 *Handbuch der Physiologie des Menschen für Vorlesungen*. Therefore, the visual experience from light shining into the eye, or from a poke in the eye, arose from some special quality of the energy carried by optic nerve. «(S)ensation is not the conduction of a quality or state of external bodies to consciousness, but the conduction of a quality or state of our nerves to consciousness, excited by an external cause», wrote Müller in 1833 (Müller, 1833, Bd. I, p. 583). It was not by chance that Helmholtz observed: «the perception of each of the three fundamental colours arises from the excitation only one kind of sensitive fibres, while the two others are at rest, or at any rate are but feebly excited» (Helmholtz, 1862, p. 280).

In line with Young, Helmholtz realized that the correspondence between the various wavelengths of light and colour perception was achieved solely within organism; it was not the rays of light that were coloured and produced that various colour perception. Therefore, he proposed the existence of three types (violet, green, and red) of retinal nerve fibres or receptors. Each fibre class was differentially sensitive to wavelengths of light ranging from approximately 400 nm to 700 nm, with the violet-coding fibre maximally sensitive to the short wavelengths, the green-coding fibres maximally sensitive to the middle wavelengths, and the red-coding fibres maximally sensitive to the long wavelengths. Consequently, three mechanisms were sufficient to account for colour perception.

Within this tri-receptor model, different colour sensations were the outcome of the relative strengths which with these three fibre types were activated by physical light. Since these fibres were assumed to have a direct connection to the brain, stimulation of one or a combination of these fibres generated the various psychological experiences of colour. In particular, equal activation of all three fibre types created the sensation of whiteness (Helmholtz, 1862, p. 369). The blackness sensation occurred when none of the fibres were stimulated by light.

However, Helmholtz went beyond Young's theory in the introduction of three variables to characterise a colour, hue, saturation, and brightness, whereas Young showed that any hue could be produced by mixing no more than two coloured lights: every colour in the spectrum could be replicated by a mixture of just two of the *primaries*, red, green, and blue. In this way, Helmholtz was the first to demonstrate that the colours which Newton had seen in his spectrum were different from colours applied to a white base using pigments. The spectral colours shone more intensely and possessed greater saturation. They were mixed additively, whereas pigments were mixed subtractively. In each case, a different set of rules governed their combination.

While Helmholtz's theory was guided by the physics of light, Ewald Hering's was strongly influenced by the phenomenological experience of colour. Persuaded that uncoloured sensations did not derive from coloured ones, he started from the Helmholtzian trichromatic theory, observing that it could not account for why certain pairs of colours were not perceived together at the same place and at the same time, e.g. reddish greens or yellowish blues (Hering, 1878, pp. 9-23): when the different hues were arranged in a circle there was a great number of dichromatic mixtures, but none of them could be described as yellow-blue or red-green.

Similarly, the theory could not explain the phenomenon of *afterimages*, i.e. negative-coloured images seen after extended viewing of a coloured object (*e.g.* red after green, or yellow after blue).

Arguing (Hering, 1888; 1897) that this mutual exclusivity between yellow-blue and between red-green originated in neurophysiologically based chemical processes of the visual system, Hering interpreted this perceptual constraint as evidence for an antagonistic relation between the chemical processes mediating yellow and blue, and red and green. Consequently, he postulated two chromatic opponent processes (red-green and blue-yellow) (*Gegenfarben*), each of them having an excitatory and inhibitory component, referred as assimilation (anabolism) and dissimilation (catabolism). This required that each opponent process received inputs from more than one class of cone, and that some were excitatory, others inhibitory. The antagonistic processes struggled to maintain a state of equilibrium in the visual system, although under normal viewing conditions there was usually an imbalance. The vast array of chromatic perceptions, therefore, arose from the degree of imbalance within the opponent processes.

In addition, Hering proposed a third, achromatic channel: it was a white-black chemical process and viewed as the oldest of the three systems, partly because it was the most stable. This inference was based on the reciprocal relation observed between black and white under conditions of spatial and temporal contrast, but not on mutual exclusivity, since there was a continuous transition from white to black passing through the various shades of grey. Moreover, against the generally accepted opinion that black was the absence of retinal stimulation, Hering argued that there was a considerable degree of brightness remaining with the total exclusion of light from the eye. He called this «mean grey» or «middle grey». True black, he maintained, occurred only under conditions of simultaneous or successive contrast; black demanded external stimulation, not its absence.

Hence, if the intensity of a white annular light increased around a centre stimulus, dissimilation of the affected areas of the visual field would increase and at the same time this activity would induce assimilation into the surrounding areas of the visual field. If this surround induced more assimilation into the centre such that it cancelled or inhibited the dissimilation already present in that visual area, the centre would appear black. Under conditions of temporal contrast, a white inducing stimulus would generate dissimilation in the visual area excited by it. After termination of the white stimulus, the process of assimilation would dominate over dissimilation in an attempt to restore the system to a state of equilibrium. Before equilibrium would be reached, a black afterimage would be perceived.

Hering's theory of middle grey was improved by Georg Elias Nathanael Müller, who was one of the first to distinguish between retinal and cortical activities in the visual pathway. He suggested (Müller, 1896; 1897) the presence of three reversible or antagonistic chemical reactions in the retina: white-black, red-green, and blue-yellow. If light produced a white reaction in the retina, an opposing reaction neutralized the white reaction and the retina returned to a state of equilibrium. The reverse occurred during a black reaction. Similar reciprocal processes were assumed to exist for the red-green and blue-yellow pairs.

According to Müller, in the cortex existed an endogenous white process and an endogenous black process that were also antagonistic with each other and dominated over the weaker chromatic excitations. The active retinal processes determined which of the cortical processes were in an excited state. If a white reaction dominated the retina, the white-black balance was disturbed, causing the white excitation in the cortex to increase and signal the perception of whiteness. Similarly, if a black reaction prevailed in the retina, it increased the black excitation in the cortex to signal the sensation of blackness. Lastly, if the black and white reactions in the retina were in equilibrium, *Augengrau* was perceived.

Ten years after his retirement, namely in 1930, Müller published a 648-page book: *Ueber die Farbenempfindungen: psychophysische Untersuchungen*, reviewing and evaluating much of the literature that had been accumulating in this very active field. Unfortunately, this work is still almost unknown by the scientific community.

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