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The bi-monocularity of human color sensation and implications for color settings in eye-based devices

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Abstract

It is well established that a small percent of the color deficiency population is monocular (Judd, 1948; Broackes, 2010). On the other hand, it is also well known that under certain conditions, binocular fusion of colors (including brightness) does occur. Considering the two sides together, human color sensation is bi-monocular. Furthermore, relating the La Hire phenomenon about the physiological blind spot to the neuroanatomical finding that the blind spot is represented in V1-L4, we can infer that V1-L4 is the neural substrate for color sensations in the human brain. This neural substrate is bi-monocular in that the excitatory neurons there are monocular in terms of thalamic inputs but the two eyes monocular neurons inhabit there side by side: Together they can represent binocular information. In short, bi-monocularity is a prominent attribute of color vision worthy of further investigation. This quality of color sensation has an obvious and important implication for devices that contain eye-based displays: For example, presently, all the commercially available VR headsets (e.g., Apple s Vision Pro and Meta s Quest products) do not have separate color filter settings for the two eyes of an individual user: This feature is worthy of enhancement for the uniocular color deficient population.

Introduction

As narrated by Mollon (2003, p. 2), Sir Isaac Newton (1642–1727) is one of the pioneers who initiated scientific investigations of colors in the 17th century. Today, Newton’s scientific contributions are mainly perceived as in mathematics, physics, and astronomy; but he had been interested in the human brain—particularly, the visual system—throughout his life, from his college student days to nearly the end of his life when he was still revising his book “Opticks”. Table 1 lists Newton’s writings that touch the subject of human visual perception, together with some related references in his era. In his Trinity notebook, in a section titled “certain philosophical questions”, he wrote down many psychological questions related to vision, audition, olfaction, memory, imagination, and consciousness; concerning vision in particular, he recorded observations on such visual phenomena as afterimage, binocular diplopia, binocular rivalry, and eye movements. Newton picked up the term Sensorium from French philosophers Descartes and Gassendi to denote the place of sensation in the perceiver's brain. Newton (1672) published his theory about light and colors, and this publication is mainly on the physical side. On the human color vision side, an important insight from Newton is that Sensorium is where color fusion (i.e., color compounding) happens. This idea first appeared in Newton (1675), a draft read to the Royal Society to further clarify and expand his theory about light and colors; and it was later more clearly laid out in Newton (1704) where he expanded this idea with the observation of successive color fusion—that is, color fusion must engage some visual short-term memory (vSTM); and this vSTM corresponds to positive afterimage. Today, mapping the monocular and binocular characteristics of color sensations (as discussed by McDougall, 1901) to the neuroanatomical organization of the primate visual system, we can conclude that V1-L4 (Layer 4 in primary visual cortex / cortical area V1) is Newton’s Sensorium for visual sensations. Newton’s Sensorium is essentially the primary part of what has been referred to as the neural correlates of consciousness (NCC) by Crick and Koch (1990) — specifically, the part for color sensations of visual consciousness.

Monocular Color Blindness

A well-established, yet currently under-investigated, aspect of color deficiency is that a small percent of the color deficiency population is uniocular. (Note that the traditional term for this trait is “unilateral”, but this team is ambiguous—as the same team may also be used to refer to the neurological condition where the patient sees only half of their visual field in chromatic colors; here we use the term “uniocular” for the color deficiency exhibited only in an individual's one eye.) Judd (1948) estimated that about 4% of the color deficiency population is uniocular. Since then, there have been a few careful case studies of this peculiar color deficiency (e.g., MacLeod and Lennie, 1976); but as pointed out by Broackes (2010), it still remains largely under-investigated and needs further study. Nevertheless, the very existence of such color deficient individuals attests that human color sensation is monocular. On the other hand, it is also well known that under certain conditions, binocular fusion of colors (including brightness) does occur. Considering the above two sides together, we can refer to human color sensation as bi-monocular.

Table 1. Newton's writings concerning visual neuroscience and some related references before and after Newton.

Author (Year)	Reference and mentioned views / results
Charleton, W. (1654)	*Physiologia Epicuro-Gassendo-Charltoniana.* ● Colors are sensations created in the *Principal Sensory* of the perceiver's brain (p. 190). ● As per Descartes, Common Sensorium is for Perception; and External Sensorium is for Visible Image (p. 151).
Boyle, R. (1664)	*Experiments and Considerations Touching Colours.* ● Colors are generated in the *Sensory* [=Charleton's Principal Sensory] (e.g., pp. 11, 21).
Newton, I. (1664)	Trinity College Notebook (Newton MS Add. 3996) – printed in McGuire, J. E., and Tamny, M. (1983). *Certain philosophical questions: Newton's Trinity notebook*. ● Newton listed many questions and observations related to color vision, binocular vision, afterimage, and space constancy (p. 387). ● The *Common Sensorium* is for the soul (p. 383), and the *Sensorium* [=Charleton's Principal Sensory] is for visual sensations (p. 473). Note: The page numbers are in McGuire and Tamny (1983).
Newton, I. (1666)	Laboratory Notebook (Newton MS Add. 3975) – also printed in McGuire and Tamny (1983). ● Newton drew a diagram of the early stages of the human visual system (p. 484). Note: The page number is in McGuire and Tamny (1983).
Newton, I. (1672)	New theory about light and colours. *Philosophical Transactions of the Royal Society, 6*, 3075–3087. ● There are two sorts of colors: primary and compounded (p. 3082). ● The most surprising and wonderful composition is that of Whiteness (p. 3083).
Newton, I. (1675)	Communication to the Royal Society on December 16, 1675. ● Color compounding and color sensations occur in the Sensorium.
Newton, I. (1682)	Letter to William Briggs dated September 12, 1682. ● Newton wrote a lengthy discussion about binocular vision in humans and some other animals.
Newton, I. (1691)	Letter to John Locke dated June 30, 1691. ● "It [i.e., afterimage] seems rather to consist in a disposition of the Sensorium".
Newton, I. (1704)	*Opticks* (1st ed.) ● Positive afterimage is a form of visual short-term memory (vSTM), and the Sensorium is where this vSTM & color compounding occur (p. 104).
Young, T. (1802)	On the theory of light and colours. *Philosophical Transactions of the Royal Society, 92,* 12–48. ● Young presented a "computational complexity" rationale for the limited number of primary colors and suggested three primary colors: red, yellow, and blue (p. 20).
McDougall, W. (1901)	Some new observations in support of Thomas Young's theory of light- and colour-vision (II). *Mind, 10*, 210–245. ● Visual sensation is produced at a neural stage where both color fusion (i.e., color compounding) and binocular fusion occur (p. 218, Fig. 15).
Hubel, D., and Wiesel, T. (1977)	Functional architecture of macaque monkey visual cortex. *Proceedings of the Royal Society B, 198,* 1–59. ● V1-L4 neurons are monocular per retinal input, comprising ocular dominance columns throughout the cortical sheet of this layer (p. 18, Fig. 11).
Crick, F., and Koch, C. (1990)	Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences, 2,* 263–275. ● Crick and Koch started to use the term *neural correlates of consciousness* (p. 265).
Wu, C. (2025)	Some further developments on a neurobiologically-based model for color sensations in humans. *Human Vision and Electronic Imaging, 37*, 207-1–207-9. ● V1-L4 is the neural substrate for color sensations (i.e., the Sensorium for vision), corresponding to the "visual sensation" stage conceived by McDougall (1901). ● V1-L4 consists of three sub-layers for the 3 primary colors: blue, red, and green.

Blindspot and Bi-monocularity

Another perspective to understand the bi-monocularity of human color sensation is pertinent to the physiological blind spot and its neural representation. In each of our eyes there is a physiological blind spot: Normally we do not see our own blind spots; but under special conditions it is indeed possible for a viewer to see one or both of their eyes' blind spots. A blind spot may manifest itself as a darker spot on a lighter background, a lighter spot on a darker background, or a colored spot on a complementary background. Also, a blind spot may exhibit itself alone or together with its Purkinje Tree (that is, the image of the retinal blood vessels converging on the blind spot). This phenomenon was first reported by the French scholar La Hire in 1694, subsequently rediscovered by several others, and had been actively investigated before World War II; but unfortunately, it has essentially been forgotten after the war. This phenomenon, however, is very prominent as we can relate it to the neuroanatomical finding, first reported by LeVay et al. (1985) in the macaque monkey's brain and then by Adams et al. (2007) in the human brain, that the blind spot is represented in V1-L4 (i.e., the thalamic recipient layer within the primary visual cortex, as illustrated in the figure below); from this relation, we can infer that V1-L4 is the neural substrate for color sensation in the human brain. This neural substrate is bi-monocular in that the principal excitatory neurons there are monocular in terms of their thalamic inputs but such monocular neurons from the two eyes inhabit this neural substrate side by side: Together they can represent binocular information. For this reason, V1-L4 should be referred to as bi-monocular (a concept introduced in Wu, 2021): Throughout the whole human brain only this neural locus possesses this characteristic, and it is prominent as it corresponds to the afore-mentioned bi-monocular quality of human color sensation.

Color Sensation is Monocular

Now we come to an important characteristic of color sensation—that is, its monocularity; in other words, color sensation must occur at a monocular stage within our visual system. This notion is not new: Many researchers have advocated it. Helmholtz (1867/1925) characterizes this notion as follows: "… the content of each separate field [from one eye] comes to consciousness without being fused with that of the other field by organic mechanisms; and that, therefore, the fusion of the two fields in one common image, when it does occur, is a psychic act" (p. 499). Sherrington (1904) and McDougall (1911) later picked up this notion and further developed it.

Here I will use one fascinating visual phenomenon to demonstrate the monocular characteristic of visual sensation. As we know, there is a blind spot (BS) in each of our eyes. The BS was discovered by Edme Mariotte around 1668; Mariotte's method of demonstrating the BS, however, is about how to map it within one's visual field, not about how to (consciously) see it. Presently, any textbook in psychology, neuroscience, and ophthalmology, when teaching about the BS, teaches this method only (e.g., Wolfe et al., 2021, p. 40).

Under special conditions, it is actually possible to see one's own BS in each eye, literally seeing the BS as a black hole on a lighter background or a white hole on a darker background—more generally, a colored spot on a background of the spot's complementary color; the BS may, or may not, be accompanied by the Purkinje Tree (PT) which denotes the image of retinal blood vessels. As far as I have been able to trace back, this phenomenon was first reported by the French scholar Philippe de La Hire (1640-1718) in La Hire (1694). Figure 2 is La Hire's drawing of his entoptic vision when he saw the BS, the PT, and the central blue scotoma (caused by the absence of blue cones in the foveal region of the retina; under special viewing conditions, this region may show up in one's visual field–-see, Magnussen et al., 2004). I have previously suggested that this phenomenon be named the La Hire phenomenon (Wu, 2021b). Over history, the La Hire phenomenon has been re-discovered again and again—see Helson (1929, pp. 352–353), Brøns (1939, Chapter IV), and Wu (2021b) for descriptions of such re-discoveries. In 2012, I serendipitously re-discovered it too and subsequently presented it at that year's annual meeting of the Society for Neuroscience (Wu, 2012b). Strangely, this phenomenon has never entered textbooks and mainstream knowledge—The only textbook that I have found to contain a description of this phenomenon is Titchener (1911), as he relates: "It has recently been asserted that if one looks suddenly, with a single eye, at some uniform and brightly illuminated surface, one sees the projection of the blind spot as a faint grey patch" (p. 328). In recent years, I have been attempting to popularize this wonderful visual phenomenon (Wu, 2021b, 2024).

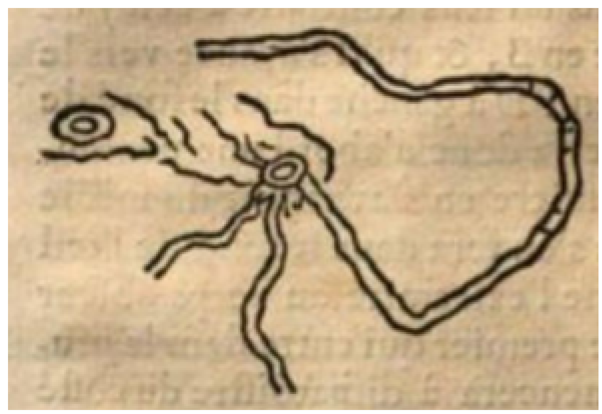

Figure 2. *La Hire's drawing of his entoptic vision: Seeing the BS (the spot at the center) of his left eye, PT (Purkinje Tree; the image of retinal blood vessels, depicted as branches coming out from the BS), and the Central Blue Scotoma (the spot on the left).*

Since the BS in each eye is specific to that eye, the La Hire phenomenon clearly indicates that visual sensation (i.e., color sensation) is monocular.

Mapping the Blind Spot in the Brain

The early stages of the human (or more broadly, the primate) visual system consists of the retina, the lateral geniculate nucleus (LGN) of the thalamus, and the primary visual cortex (i.e., V1). The cortical sheet comprises six layers, with Layer 4 receiving thalamic inputs (i.e., optic radiations in the case of V1). Hereafter, we will denote this layer as V1-L4. Please note that "Layer 4" in V1 has been incorrectly labeled as "Layer 4C" in many textbooks (e.g., Wolfe et al., 2021, p. 71); see Boyd et al. (2000) and Balaram et al. (2014) for the relevant neuroanatomical evidence as to why it should be labeled as "Layer 4" instead of "Layer 4C".

The La Hire phenomenon is a wonderful psycho-anatomical means: As a matter of fact, several neuroanatomical studies have precisely localized a representation of the BS in V1-L4: Figure 3 shows two such studies (LeVay et al., 1985; Adams et al., 2007), with the first one on the monkey brain and the second on a human brain. Though in two species and using different chemical staining methods, both studies clearly indicate that there is a representation of the BS in V1-L4. Please note that V1-L4 is a "bi-monocular" structure in the sense that for each and every tiny patch of the viewer's binocular visual field, the monocular image (i.e., ocular dominance column or ODC) from one eye resides with that for the other eye side by side. For the upper slide in Figure 3, white stripes and areas depict neural tissue regions in V1-L4 predominantly connected with the eye containing the BS, whereas the black stripes and areas depict that connected with the other; for the lower slide in Figure 3, the labeling of the white and the black stripes / areas is just the opposite. From these slides, we should understand that the representation of the BS in V1-L4 does not create any physical "hole" in this neural tissue—instead, the area is invaded and occupied by the input from the other eye.

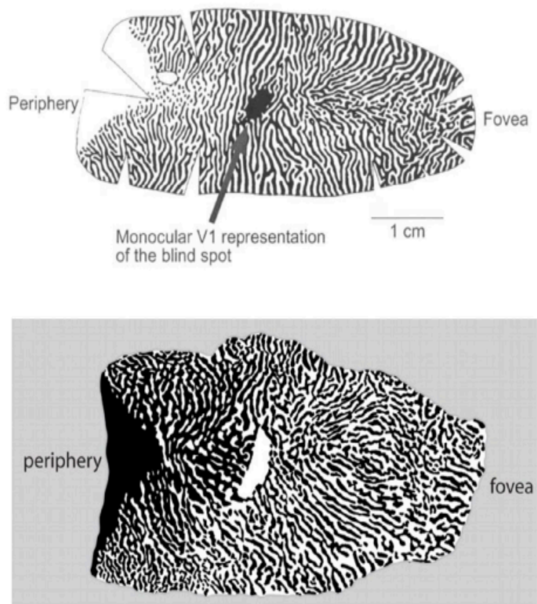

Figure 3. *Two neuroanatomical studies show representations of blind spots in V1-L4 (i.e., the thalamic recipient layer in the primary visual cortex).*

Beyond V1-L4, is there any other neural structure(s) in the primate visual system that may contain representations of the BS? David Hubel and Torsten Wiesel's pioneering exploration of the feline and the primate visual brains had long established that neurons in V1-L4 are primarily monocular whereas that beyond V1-L4 are mainly binocular (e.g., Hubel & Wiesel, 1968). As we already stated, each eye's BS is specific to that eye (i.e., monocular); therefore, the answer to this question is negative.

Correlating the La Hire phenomenon with such neuroanatomical studies, we can conclude that visual sensation is represented in V1-L4. Please note that without knowing the La Hire phenomenon, we cannot argue that the BS representations seen in V1-L4, and this layer in general, are directly correlated with visual sensations—in other words, one may argue that such representations are just for sub-consciousness neural activation; then, with the knowledge of the La Hire phenomenon, we can indeed pinpoint the neural substrate for visual sensations to V1-L4. (The authors of the relevant neuroanatomical studies did not link their results to any visual phenomenon. Therefore, my contribution here is conceptual in linking neuroanatomical studies, on the one hand, with the La Hire phenomenon on the other.)

Implications

Once we understand that human color sensation is bi-monocular, we can explore this notion's implications in display technologies—particulary, in VR (virtual reality) devices with eye-based displays. An obvious and important implication for such devices is that each eye's display should have its own color filter settings. Presently, all the commercially available VR headsets (e.g., Apple's Vision Pro and Meta's Quest products) do not have separate color filter settings for the two eyes of an individual user: This feature is worthy of enhancement and can easily be implemented to better accommodate the population with uniocular color deficiency.

Conclusions

(1) Human color sensation is bi-monocular (i.e., both monocular and binocular); (2) In the human brain, V1-L4 is the neural substrate where color sensation is generated; (3) This very substrate is also the side for both positive & negative afterimages—more generally, for visual sensory memory; (4) Applying the notion of bi-monocularity of human color sensation, it is worthy to have eye-based color settings in display devices where each eye's image is displayed separately.

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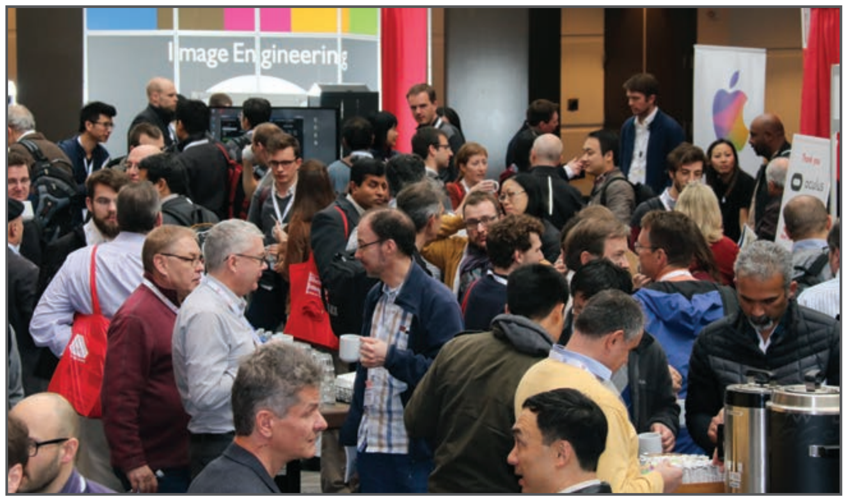

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