

REVIEW ARTICLE

SUBLIMINAL AFTERIMAGES VIA OCULAR DELAYED LUMINESCENCE: TRANSACCADIC STABILITY OF THE VISUAL PERCEPTION AND COLOR ILLUSION

István Bókkon^{1,2*} & Ram L.P. Vimal²

¹Doctoral School of Pharmaceutical and Pharmacological Sciences, Semmelweis University, Budapest, Hungary

²Vision Research Institute, Lowell, MA, USA

Abstract

Here, we suggest the existence and possible roles of evanescent nonconscious afterimages in visual saccades and color illusions during normal vision. These suggested functions of subliminal afterimages are based on our previous papers (i) (Bókkon, Vimal et al. 2011, J. Photochem. Photobiol. B) related to visible light induced ocular delayed bioluminescence as a possible origin of negative afterimage and (ii) Wang, Bókkon et al. (Brain Res. 2011)'s experiments that proved the existence of spontaneous and visible light induced delayed ultraweak photon emission from *in vitro* freshly isolated rat's whole eye, lens, vitreous humor and retina. We also argue about the existence of rich detailed, subliminal visual short-term memory across saccades in early retinotopic areas. We conclude that if we want to understand the complex visual processes, mere electrical processes are hardly enough for explanations; for that we have to consider the natural photobiophysical processes as elaborated in this article.

Key words: *Saccades; Nonconscious afterimages; Ocular delayed bioluminescence; Color illusion*

1. INTRODUCTION

Previously, we presented a common photobiophysical basis for various visual related phenomena such as discrete retinal noise, retinal phosphenes, as well as negative afterimages. These new concepts have been supported by experiments (Wang, Bókkon et al., 2011). They performed the first experimental proof of spontaneous ultraweak biophoton emission and visible light induced delayed ultraweak photon emission from *in vitro* freshly isolated rat's whole eye, lens, vitreous humor, and retina.

According to our novel photobiophysical interpretation of negative afterimage formation (Bókkon, Vimal et al. 2011), when we gaze at a colored (or white) image for some seconds, external photons can stimulate excited electronic states within different parts of the eye that is followed by a delayed reemission of transiently absorbed photons for several seconds. These reemitted photons can be absorbed by non-bleached photoreceptors, which produce a negative afterimage. We have also emphasized that although photobiophysical source of negative afterimages can be related to the delayed reemission of absorbed photons and the

*Correspondence to: IB: bokkoni@yahoo.com; url: <http://bokkon-brain-imagery.5mp.eu>; RV rlpvimal@gmail.com; url: <http://sites.google.com/site/rlpvimal/Home/>.

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retinal mechanisms, cortical neurons have essential contribution in the modulation and interpretation of negative afterimages.

In this article, we argue about the existence of rich detailed, subliminal visual short-term memory (or transsaccadic visual buffer) across saccades in early retinotopic areas (Bókkon & Vimal, 2010; Melcher, 2005). In addition, some possible roles of subliminal afterimages via ocular delayed luminescence (Wang, Bókkon et al., 2011) in visual saccades and color illusions, during normal vision, are also discussed.

2. DELAYED LUMINESCENCE

Delayed luminescence (DL, also termed as light-induced ultraweak photon emission or delayed biophoton emission) is the long-term ultraweak reemission of optical photons from living cells and various materials when they were exposed to a white or monochromatic light (Ho et al., 2002; Popp & Yan, 2009; Kim et al., 2005). The DL intensity is considerably lower than the known fluorescence or phosphorescence. Although externally measured intensity of spontaneous biophoton emission from mammalian is extremely low intensity (from a few to up to some hundred photons/(cm² x s), it can be increased via external illumination (Kim et al., 2005; Niggli et al., 2005). The decay time of delayed luminescence is dependent on the physiological conditions of the samples and kinds of the tissues as well as intensity, duration, and spectral distribution of illumination (Niggli et al., 2005).

Various experiments demonstrated that the DL is a sensitive indicator of the physiological state of cells that is closely connected to the differentiation stage of the biological system (Kim et al., 2005; Lanzanò et al. 2007; Brizhik et al., 1993; Van Wijk et al., 1993; Musumeci et al., 1997). The DL characteristics largely depended upon structural organization (Ho et al., 2002). According to Ho et al. (2002), DL comes from the excitation and subsequent decay of collective electronic states whose properties depend on the organized structure of the system. Namely, extremely long decay times of DL are due to the interrelated molecular levels that are connected to an ordered spatial structure.

3. AFTERIMAGES BY OCULAR DELAYED PHOTONS

When we gaze at a colored (or white) image for some seconds and then look at a blank screen, we can see a complementary negative afterimage. This negative afterimage is the same shape as the original image but different colors. A generally accepted concept of negative afterimages is based on the photopigment-bleaching hypothesis (Brindley, 1962; Rushton & Henry, 1968). Namely, bleached photoreceptors are significantly less (or not) responsive to relevant visible photon stimuli compared to those photoreceptors that are not affected.

However, there are several contradictions about photopigment bleaching hypothesis (Craik, 1940; Loomis, 1972; Wilson, 1997; Tsuchiya & Koch 2005; Hofstoetter et al., 2004). For example, Craik (1940) reported that positive and negative afterimages could be observed following adaptation to a 60 W illumination, although the eye was pressure-blinded during the 2 min adaptation. Craik concluded that this was proof of a photochemical basis of negative afterimages. Loomis demonstrated (1972) that after long duration illumination, afterimages were correlated with visual appearance, and were quite independent of bleaching. In Lack' experiments (1974), binocular rivalry did not reduce afterimage formation. The motion-induced blindness can occur if a salient static target spontaneously fluctuates in and out of our visual awareness while surrounded by a random moving visual pattern. In 2004, Hofstoetter et al. revealed that motion-induced blindness does not significantly reduce the duration or the strength of negative afterimages. In addition, the negative afterimage does not transfer between eyes (Lack, 1974). Tsuchiya and Koch's (2005)

continuous flash suppression experiments also hint that afterimages are retinal phenomena. According to Tsuchiya and Koch's (2005), "Our results imply that formation of afterimages involves neuronal structures that access input from both eyes but that do not correspond directly to the neuronal correlates of perceptual awareness." From a molecular point of view, recently, Khadjevand et al. (2010) observed reduction of afterimage duration in patients with Parkinson's disease and suggested that this reduction is due to the retinal dopaminergic system deficiency.

The above-mentioned findings all suggest that the source of negative afterimages can be linked to retinal mechanisms in addition to cortical neurons that participate in the modulation of negative afterimages.

We should also mention that phosphene lights can be induced in blind people, for example, in the V1 cortex, by electric or magnetic stimulations (Gothe et al., 2002). However, complementary negative afterimage illusion cannot be elicited in the V1 cortex of blind people via electric or magnetic stimulations. This may also support the notion that the source of negative afterimages are placed somewhere within the eyes.

In addition, since we can see negative afterimages not only through open eyes but also closed eyes without any ambient photons in a dark room, the photopigment bleaching proposal cannot elucidate that where the source is of negative afterimages with closed eyes without any external photon stimulation (Bókkon, Vimal et al. 2011). In other words, what generates this long-lasting signal that produce static pictures inside our eyes, which is interpreted by higher neural processes in the brain?

However, recently, we (Wang, Bókkon et al., 2011) demonstrated the existence of visible light induced delayed ultraweak photon emission from *in vitro* freshly isolated rat's whole eye, lens, vitreous humor, and retina. Based on our experiments, we have suggested a novel photobiophysical interpretation of negative afterimage formation (Bókkon et al., 2011). According to our photobiophysical conception, when we gaze at a colored (or white) image for some seconds external photons can be absorbed and induce excited electronic states within the eyes. Next, there can be a long-term delayed reemission of absorbed photons. Finally, reemitted photons can be absorbed by non-bleached cones (or/and rods) that can produce a negative afterimage. According our estimation (Bókkon et al., 2011), at least in principle, we can calculate with 10^4 photons/sec in the retinal system during DL phenomenon, which could be sufficient to produce an afterimage via retinal MWS and LWS cone photoreceptors.

We must consider that under natural circumstances, ambient photons (for example, under photopic conditions, there is $\approx 10^{11}$ - 10^{14} photons/ (cm² x s) (Augustin, 2008) can induce much stronger delayed photon re-emission within the eyes than in our isolated and dark-adapted experiments (Wang, Bókkon et al., 2011). This also means that a brief light flash can also produce nonconscious (subliminal) afterimages via delayed photon re-emission within the eyes.

To sum up, negative afterimages most likely have a photophysical (photochemical) source that is related to retinal processes in addition to cortical networks that take part in the modulation and interpretation of negative afterimages.

4. RETAINED SUBLIMINAL VISUAL REPRESENTATION IN EARLY VISUAL AREAS AFTER VISUAL PERCEPTION

According to Silvanto et al. (2007) experiments, after 30 sec visual adaptation to a homogeneous color, transcranial magnetic stimulation (TMS) can produce phosphenes that take on the color qualities of the adapting color. For example, when subjects are adapted to a green color, they perceive a red negative afterimage into which the application of TMS induces green phosphenes. The negative afterimages persisted about 69sec after 30 sec visual adaptation and the induced phosphenes persisted for about 91 sec, meaning that the

information of perceived visual color (after 30 sec visual adaptation to a color) was not consciously represented for 91sec in early visual areas. This subliminal short-term representation of a color became conscious information, for a moment, by TMS stimulation.

In Halelamien et al.'s experiments (2007), after the coil position optimization over the occipital cortex to induce intense phosphenes, researchers presented pictures of natural scenes for 100 msec, followed by TMS stimulation. TMS induction shortly after an image presentation caused the re-perception of clearly defined forms that varied according to the content of the flashed image. In the most remarkable cases, volunteers perceived photographic-like re-perception in portions of the display. Halelamien et al. (2007) concluded that after visual perception has finished detailed visual information remained encoded in occipital cortex and that TMS induction could make a conscious access to these subliminal representations. Halelamien et al.'s experiments were also validated by Wu et al. (2007).

According to Harrison and Tong (2009) fMRI experiments, early visual areas can retain specific information about visual features held in working memory for several seconds when no visual stimulus is present.

These mentioned results support the notion that early retinotopic areas able to sustain rich detailed, subliminal visual information for several seconds after visual perception and that subliminal residual states are not being reflected in passive neural recording techniques, but require active stimulation to be revealed as we pointed out it previously (Bókkon and Vimal, 2009, 2010). It is remarkable that only 100 ms duration of a presented image produced subliminal and rich detailed representations in visual cortex (Halelamien et al. 2007). However, humans can process and recognize complex images and objects especially rapidly (Kirchner & Thorpe, 2006; Thorpe et al., 1996), so that 50-80 ms of cortical processing time are enough.

5. EYE MOVEMENTS

While our eyes scan the visual world, the eyes make fast ballistic movements, called saccades. Common types of eye movements (at a macro-level) that can be described during static scene perception are saccades and fixation. Saccades are followed by fixations when the eyes are relative stable (Tatler & Wade, 2003). An average voluntary fixation is approximately 250-300 msec in duration (Irwin & Brockmole, 2000). Saccade duration depends on saccade distance and its duration increases as saccade distance increases. The average saccade duration during picture viewing or reading is around 30-50 msec (Rayner, 1978, 1998). Since a typical observer makes 2-5 eye movements (saccades) per second, a visual scene is processed via discrete snapshots during eye fixations (Henderson & Hollingworth, 1998). Saccades and microsaccades are generally binocular and conjugate (Yarbus, 1967). Although during vision, involuntary micro saccades (usually occur in 30-50 milliseconds) and voluntary macro saccades (usually occur in 150 or more milliseconds) continuously alternate each other (Bahill et al., 1975), it seems that saccades and microsaccades share a common oculomotor basis and there is a microsaccade-saccade continuum (Bahill et. al., 1975; Otero-Millan et al., 2008).

Fixational eye movements include three major types of motion of eyes such as tremor, drift and microsaccades (Martinez-Conde et al., 2004). Tremor is the smallest (amplitudes are about the diameter of a cone i.e., approximately two micrometers (1/500 mm) aperiodic motion of the eyes (Yarbus, 1967; Carpenter, 1988). Drifts take place between microsaccades and are slow motions of the eye that occur simultaneously with tremor (Martinez-Conde et al., 2004). Involuntary microsaccades occur 2-3 times in every second and are the largest and fastest of the three fixational eye movements. Microsaccades are produced involuntarily while the subject is attempting to fixate (Martinez-Conde, 2006).

Saccade depends on eye position (McIlwain, 1986), which is related to activities in superior colliculus (Hartline, Vimal, King, Kurylo, & Northmore, 1995; Kurylo, Vimal & Hartline, 1992).ⁱ Rolfs et al. (2008) suggested that microsaccades could be generated in a motor map, which is commonly used as a coding for microsaccades and saccades in the superior colliculus.

The image of the world moves constantly on our retina because of our eye and head frequent movements. For example, while our eyes scan the visual world, despite the constantly changing retinal images, our perception of the visual world is stable. Thus, one of the essential questions of vision research is how we can keep track of the location of objects across saccades (Melcher & Colby, 2008; Wurtz, 2008).

6. SUBLIMINAL TRANSSACCADIC BUFFER IN EARLY RETINOTOPIC AREAS

As was mentioned, one of the fundamental questions of vision research is how we can keep track of the location of objects across saccades (Melcher & Colby, 2008; Wurtz, 2008). There are three major explanations in literature about the persistence of visual representations across eye movements (Melcher & Colby, 2008):

(I) The first idea is akin to superimposing two patterns from the separate fixations, but it seems that patterns are not fused across saccades.

(II) The second idea proposes that tiny or no visual information is maintained across saccades.

(III) The third conception focus on the visual short-term memory.

However, there is an increasing evidence of the existence of visual short-term memory across eye movements. According to Prime et al (2011)...“transsaccadic memory has a similar capacity for storing simple visual features as basic visual memory, but this capacity is dependent both on the metrics of the saccade and allocation of attention”. There can be a direct relationship between attention, short-term memory, and transsaccadic memory (Khayat et al., 2004). Hollingworth et al. (2008) proposed that visual short-term memory could be utilized to remember the features of the current saccade target so that it can be quickly reacquired after a rambling saccade.

In the previous section we could see that rich detailed, subliminal visual information can be maintained for several seconds after visual perception in early retinotopic areas. In addition, in Halelamien et al.'s experiments when researchers presented pictures for 100 msec, followed by TMS stimulation, TMS caused the re-perception of clearly defined forms. If we calculate with an average eye fixation time, i.e. with about 200-300 ms between saccades

ⁱ As per (McIlwain, 1986), “Stimulation in the anterior two-thirds of the colliculus with long-duration pulse trains produced multiple saccades ... but their directions and amplitudes were influenced significantly by the initial position of the eye. [...] Saccades evoked during bilateral simultaneous stimulation of the superior colliculi were also dependent on the initial position of the eye. [...] These findings indicate that saccadic commands resulting from focal collicular stimulation in the cat can be modified by information about current eye position.” As per (Hartline, Vimal, King, Kurylo, and Northmore, 1995), “The maps of visual and auditory space within the superior colliculus are in approximate register both with each other and with the underlying motor maps associated with orienting responses. The fact that eyes and ears can move independently poses a problem for the sensorimotor organization of these two modalities. By monitoring eye and pinna positions in alert, head-fixed cats, we showed that the accuracy of saccadic eye movements to auditory targets was little affected by eye eccentricity (range +/- 15 deg) at the onset of the sound. A possible neural basis for this behavioral compensation was suggested by recordings from superior colliculus neurons. The preferred sound directions of some neurons in the deep layers of this midbrain nucleus exhibited a shift with the direction of gaze, while in others the response throughout the auditory receptive field was either increased or decreased, suggesting that changes in eye position alter the gain of the auditory response.” As per (Kurylo, Vimal, & Hartline, 1992), “We investigated the characteristics of saccades made by cats in response to single and double stimuli. [...] Cats made saccadic eye movements to positions that ranged between the location of the two targets. If the eye position at the start of a saccade was near the mid point of the targets, cats were less likely to initiate a saccade, and saccadic latencies were longer, compared to when starting eye position was at a distance from this location. These behavioral results are consistent with the hypothesis that the neural representations of briefly presented targets are combined and treated as a unitary, low resolution stimulus from which an orienting motor program is derived. The similarity of responses to double visual, double auditory and bimodal stimuli suggests that a common sensorimotor mechanism applies within and between these sensory modalities.”

(Henderson and Hollingworth, 1998), it means that fixation (and saccade) times are plenty sufficient for the creation and the maintenance of rich detailed, subliminal visual information in early retinotopic areas.

In brief, the above mentioned experimental results and our argumentation can strongly support the conception about the existence of rich detailed, subliminal visual short-term memory (or transsaccadic visual buffer) across saccades in early (V1, V2) retinotopic areas.

7. SACCADES, NONCONSCIOUS AFTERIMAGES, AND THE OCULAR DELAYED PHOTON REEMISSION

If we stare at a colored image for some moment and then look at a blank screen, we can see a negative afterimage. A negative afterimage is the same shape as the original image but different colors. Based on Wang et al. (2011) researches, we proposed a photobiophysical explanation of negative afterimage formation (Bókkon et al., 2011). Namely, if we stare at a colored (or white) image for several seconds outside photons can be absorbed and induce excited electronic states within the eyes. Then, there can be a long-term delayed reemission of absorbed photons. Finally, reemitted photons can be absorbed by non-bleached cones (or/and rods) that can generate a negative afterimage.

However, normally, no afterimages appear during visual perception, because a typical observer makes 2-5 eye movements in every second (saccades) (Yarbus, 1967). This means that a visual scene is processed via discrete snapshots during eye fixations, which is about 300 ms between saccades (Henderson and Hollingworth, 1998).

Under photopic circumstances, the intensity of external photons is about 10^{14} photons/($\text{cm}^2 \times \text{s}$). Although, we cannot perceive consciously afterimages during normal visual perception, nonconscious (subliminal) afterimages could also emerge during 100-300 milliseconds that are due to the external induced (for example, under photopic conditions, there is $\approx 10^{11}$ - 10^{14} photons/ ($\text{cm}^2 \times \text{s}$) (Augustin, 2008)) delayed photon reemission within the eyes (Wang et al., 2011). Thus, saccades not only can prevent the bleaching of photoreceptors but also can inhibit the emergence of conscious afterimages that could perturb our normal visual perception.

Under photopic circumstances, we can easily experience this evanescent afterimage if we look out our window for 2-3 seconds then gaze at our darker wall inside our room. In this case, we can usually see a complement, darker silhouette negative afterimage of window for some seconds.

However, evanescent nonconscious (subliminal) afterimages may also have essential functions in our normal vision. The next possible function of subliminal afterimage (produced via external induced delayed photons) is that this may guarantee extended intrinsic nonconscious retinal visual information between saccades. We could see above in Silvanto et al. (2007) experiments that after 30 sec visual adaptation to a homogeneous color, TMS could induce phosphenes within afterimage took on the color qualities of the adapting color. Namely, when subjects are adapted to a green color, they perceived a red negative afterimage into which TMS induced green phosphenes. It means that information about perceived colors was transmitted to the visual cortex and is not the colors of afterimages. Thus, temporary nonconscious afterimages (produced via external induced delayed photons) can promote (with the original colors and forms) an extended subliminal visual representation across saccades at retinal level.

It may also be possible that extended subliminal visual representation [subliminal afterimages] i.e., visual photonic signals that are produced via external induced delayed photons (Wang et al., 2011)] across saccades at retinal level can serve as photobiophysical sources of subliminal visual short-term memory (or transsaccadic visual buffer) across saccades in early retinotopic areas (Prime et al., 2011).

Under scotopic circumstances, evanescent nonconscious afterimages (produced via external induced delayed photons (Wang et al., 2011)) may also facilitate our scotopic vision. At scotopic luminance level, both contrast sensitivity and acuity are greatly reduced relative to photopic level; there are two spatial frequency tuned mechanism at scotopic vision; the scotopic (rod) visual system appears capable of processing spatial (hyperacuity) information over its restricted dynamic range with at least as much accuracy as the photopic (cone) system (Vimal & Wilson, 1986, 1987). Under scotopic conditions, when we can see our external world in grey colors and there are not strong contrasts, the extended evanescent subliminal afterimages may facilitate our normal vision.

8. PERCEIVE COLOR WHERE THERE IS ONLY BLACK AND WHITE

Attributes of light, such as wavelength and intensity, are physics. For most researchers the attributes of color, such as hue, saturation, and brightness (Vimal et al., 1987), are subjective experiences, which are the mental aspect of color related neural-network (NN)-state; the physical aspect of this NN-state is the color related V4/V8/VO-NN and its activities (Vimal, 2009) in the dual-aspect monism framework (Vimal, 2008, 2010). Electromagnetic light waves (photons) visible to the human eye range from about 400 to 700 nm. A hue is a pure color, i.e. one with no black or white in it.

In our previous paper (Bókkon et al., 2011), we elaborated that the white light (visible electromagnetic photons) is a mixture of all colors. White objects are white because the most of the light that falls on them is reflected by the material. Black objects absorb light of all frequencies but a little light (electromagnetic photons) is reflected from them. Thus, black is also a mixture of all colors! White and black have the same hue and saturation, and the lightness is all that is different (Fig.1).

In 1938, Fechner described that color perception can be induced by rotating a black and white disk at a certain velocity. Benham (1985) constructed a more complex disk (Fig.2) that also induced colors when it was rotated. However, how we can perceive colors where there is only black and white for example, during Fechner's color illusion. Because both the black and the white are composed a mixture of all colors, while we are looking at certain rapidly changing or moving black-and-white patterns, it can be probable that we can see some flashing color components of evanescent subliminal white-and-black afterimages (produced via external induced delayed photons (Wang et al., 2011)). Namely, the pattern induced flicker colors can be due to the flashing color components of perturbed evanescent subliminal white-and-black afterimages.

It is very likely that several further illusions can be explained by the help of the proven external induced ocular delayed photons and/or the subliminal visual short-term memory across saccades in early retinotopic areas.



Figure 1. The complementary afterimages of upper circles can be seen in the lower circles (and vice versa). White and black are a mixture of all colors and they have the same hue and saturation, but the brightness/lightness (a color's lightness also corresponds to its amplitude) varies.



Figure 2. Benham's disk can induce subjective color experience when rotated.

9. DISCUSSION AND SUMMARY

It should be emphasized again that if we want to understand the complex visual processes, electrical processes is scarcely enough for explanations, as indicated in this article. Since all living cells perform delayed luminescence (light-induced ultraweak and long-term ultraweak reemission of optical photons from living cells) phenomenon, it was not surprising for us (i.e. Wang, Bókkon, Dai & Antal, 2011) that spontaneous and visible light induced delayed ultraweak photon emission exists from *in vitro* freshly isolated rat's whole eye, lens, vitreous humor and retina. However, our first experimental results (Wang, Bókkon et al., 2011) made it possible that we support and present common photobiophysical basis for various visual related phenomena such as discrete retinal noise, retinal phosphenes as well as negative afterimages (Bókkon, 2008; Bókkon & Vimal, 2009; Bókkon et al., 2011).

This paper is the next outcome of our common ocular photobiophysical explanations. The evanescent subliminal afterimage (produced via external induced delayed photons during vision) is not a speculation, mainly, if we consider that under natural circumstances, ambient photons can induce much stronger delayed photon emission within the eyes than in our isolated and dark-adapted experiments (Wang & Bókkon et al., 2011).

The extended visual representation via subliminal afterimages during normal vision, could give us several explanations about visual perception related processes such as:

(i). Why we can perceive colors where there is only black and white for example, during Fechner's color illusion. The black and the white are created via mixture of all colors. When we are looking at certain quickly changing or moving black-and-white patterns, we might be experiencing some flashing color elements of nonconscious white-and-black afterimages (produced via external induced delayed photons (Wang et al., 2011)).

(ii). Subliminal afterimages can guarantee extended intrinsic nonconscious retinal visual information between saccades that could facilitate our photopic vision.

(iii). Subliminal afterimages could also assist our scotopic vision. Under scotopic vision, we can see our external world in grey-like colors and there are not strong contrasts. Thus, the extended evanescent subliminal afterimages may facilitate our scotopic vision.

(iv). We can explain why we need saccades. For example, saccades not only can prevent the photoreceptor bleaching but also can inhibit the appearance of conscious afterimages that could perturb our waking state visual perception.

(v). It is also possible that extended subliminal visual representation (i.e. afterimages produced via external induced delayed photons) across saccades at retinal level can be a photobiophysical source (or supporting) of the rich detailed, subliminal visual short-term memory (or transsaccadic visual buffer) across saccades in early retinotopic areas.

(vi). It is very likely that several further illusions can be elucidated in future with the help of the proven external induced ocular delayed photons and/or the subliminal visual short-term memory across saccades in early retinotopic areas.

We termed our new photobiophysical concepts as a natural photobiophysical area, because its ultraweak photon sources are originated within visual systems during natural vision. We hope that this new natural photobiophysical area of visual researches can get more interest in the future.

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DECLARATION OF INTEREST

The authors declare that they have no competing financial interests. The authors alone are responsible for the content.

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