

Explanations step by step about Bókkon's biophysical picture representation model (also called intrinsic biophysical virtual visual reality) during visual perception and imagery

2014 by Bókkon

In 2013, I have managed to take several emails with Prof Kosslyn and explained him my biophotonic molecular picture model. Prof Kosslyn wrote me: "I think I understand this much better now, and it strikes me as a very interesting hypothesis. It's well worth testing -- especially if the tests can pit the electrical view against your view."

*My idea of biophysical visual virtual reality in retinotopic areas can be the first possible biophysical basis of Kosslyn's **reality simulation principle** in the case of visual imagery. Retinal visual information can be re-represented (re-experience) through regulated biophotons in retinotopically organized, mitochondrial cytochrome oxidase-rich V1 visual areas during visual imagery,*

PHOSPHENES

- Press gently and continuously your closed eye for some seconds by your finger and you will see lights.
- Phosphenes represent the perceived sensation of flashes of light **in the absence of external photon visual stimulation**.
- The perceived **phosphene** lies within the visual hemifield contra-lateral to the stimulated cortical hemisphere, at a location **reflecting the retinotopic organization of the visual cortex**.
- Phosphenes can be produced by various stimuli (mechanical, electrical, magnetic, etc.) of cells in the visual pathway as well as random firing of cells in the visual system.

BIOPHOTONS

- Many experiments proved that all living cells and neurons emit ultraweak biophotons that are originated from free radical (oxidative) reactions. Mitochondrial oxidative processes, lipid peroxidation are the main sources of biophotons.

*Isojima, Y., Isoshima, T., Nagai, K., Kikuchi, K., and Nakagawa, H. (1995). Ultraweak biochemiluminescence detected from rat hippocampal slices. *NeuroReport* 6, 658–660.*

*Jansen, K. (1989). Near death experience and the NMDA receptor. *Br. Med. J.* 298, 1708.*

*Kataoka, Y., Cui, Y., Yamagata, A., Niigaki, M., Hirohata, T., Oishi, N., Watanabe, Y., (2001). Activity-Dependent Neural Tissue Oxidation Emits Intrinsic Ultraweak Photons. *Biochem. Biophys. Res. Commun.* 285, 1007–1011.*

*Kobayashi, M., Takeda, M., Ito, K., Kato, H., and Inaba, H., (1999a). Two-dimensional photon counting imaging and spatiotemporal characterization of ultraweak photon emission from a rat's brain in vivo. *J. Neurosci. Methods.* 93, 163–168.*

*Kobayashi, M., Takeda, M., Sato, T., Yamazaki, Y., Kaneko, K., Ito, K., et al. (1999b). In vivo imaging of spontaneous ultraweak photon emission from a rat's brain correlated with cerebral energy metabolism and oxidative stress. *Neurosci. Res.* 34, 103–113.*

- The phrase “ultraweak biophoton emission” a bit confusing, since biophoton intensity can be considerably higher inside cells and neurons than that expected from biophoton measurements, which are performed at a distance of several centimeters away from the cells. What we can measure in biophoton experiments are biophotons principally produced from natural oxidation processes **on the surfaces of cellular membranes** as was demonstrated by Blake et al. (2011).

Blake, T., Dotta, B. T., Buckner, C. A., Cameron, D., Lafrenie, R. M., and Persinger, M. A. (2011). Biophoton emissions from cell cultures: biochemical evidence for the plasma membrane as the primary source. *Gen. Physiol. Biophys.* 30, 301–309.

NOW SEE THE CONNECTION BETWEEN RETINAL PHOSPHENES AND BIOPHOTONS

• Several factors – *as electrical or magnetic stimulation of the visual system, mechanical effects on the visual system, various drugs, stress, high-energy ionizing radiation optic nerve diseases, etc.* – can induce phosphenes. **However, these factors have a common feature, i.e., all of them can cause overproduction of free radicals and excited biomolecules, as I pointed out it.**

Bókkon I. (2008) Phosphene phenomenon: a new concept. *BioSystems* 92, 168-174.

My prediction about one kind of retinal phosphenes (i.e. phosphene perception during space travel (Bókkon, 2008)) was experimentally supported by Narici et al. According to his work, ionizing radiation induced free radicals produce ultraweak photons through processes including by lipid peroxidation. These photons are then absorbed by the photoreceptors and initiate a photo-transduction cascade, which results in the perception of phosphenes. Namely, Narici et al. (2013) revealed that the lipid peroxidation of the photoreceptors can produce ultra-weak biophotons that generate anomalous visual effects, such as those associated with retinal phosphenes.

Narici L, Paci M, Brunetti V, Rinaldi A, Sannita WG, Carozzo S, Demartino A. Bovine rod rhodopsin: 2. Bleaching in vitro upon 12C ions irradiation as source of effects as light flash for patients and for humans in space. *Int J Radiat Biol.* 2013 Oct;89(10):765-769.

In addition, recently, we, Wang, **Bókkon et al.** (2011) presented first experimental demonstration of spontaneous and visible light-induced photon emission from freshly isolated whole eye, lens, vitreous humor and retina samples from rats. Our results also suggest that the source of retinal phosphenes, can originate from natural biophotons within the eyes.

Wang C, **Bókkon I**, Dai J, Antal I. (2011) presented first experimental demonstration of spontaneous and visible light-induced photon emission from rat eyes. *Brain Res.* 1369. 1-9.

Although intensity of biophoton emissions is weak, biophotons can have direct effect in the retinal layers of photoreceptors, thus it can create relatively strong light sensation. During natural sight, the external photon intensity is strong, but most photons are absorbed before they reach the retinal photoreceptors.

When you press your eyes or perform electric stimulation in retina etc., you induce an excess biophoton production, and if it goes above a distinct threshold, it can emerge as phosphene light in our mind since the brain interprets these absorbed retinal biophotons as if they originate from the external world. Now you may understand that several evidence support that retinal phosphenes really can be originated from intrinsic biophotons of retinal oxidation/free radical reactions and our brain interprets these absorbed retinal biophotons as if they were originated from the external world.

INDUCED PHOSPHENES IN V1

- **Phosphenes lights can also be easily induced in V1 without any retinal input** (without photo-transduction cascade). You know that during visual perception, we can see by V1 (V2) visual areas (not directly by our eyes) that **have "perfect" retinotopic maps**. Furthermore, phosphenes are only perceived by blind subjects who have prior visual experience, suggesting that early visual exposure is essential to maintain any level of residual visual function.

- Several experiments proved that **all living cells and neurons produce biophotons, but what the specific is regarding to V1 (and V2)?** The specificity is the **structure**, namely **good retinotopic structure of V1 and V2**, they areas preserve the local spatial geometry of the retina, so patterns of activation in them depict shape. Motor or auditory cortex cannot perform biophysical picture representation via biophotons because there is the lack of structural retinotopic representation.

- I have proposed a molecular hypothesis about the natural biophysical substrate of visual perception and imagery (Bókkon, 2009. *BioSystems*; Bókkon and D'Angiulli, 2009. *Bioscience Hypotheses*). Namely, **the retina absorbs external photons during vision, and then transforms photon signals into electrical signals that are carried to the V1. Then, V1 retinotopic electrical signals (*spike-related electrical signals along classical axonal-dendritic pathways*) can be converted into regulated biophotons within retinotopic neurons that make it possible to create internal biophysical pictures (intrinsic re-representation of perceived external objects) during visual perception and imagery**. Therefore, information in the brain appears not only as electrical (chemical) signal but also as a controlled biophoton signal of synchronized V1 neurons.

Bókkon I. (2009) Visual perception and imagery: a new hypothesis. BioSystems 96, 178-184.

Bókkon I, D'Angiulli A. (2009) Emergence and transmission of visual awareness through optical coding in the brain: A redox molecular hypothesis on visual mental imagery. Bioscience Hypotheses 2, 226-232.

- Recent experiments by Sun et al. (2010) revealed that biophotons can conduct along the neural fibers that can support the relevance of our biophysical picture hypothesis. It seems that biophoton and neuroelectronic activities are not independent biological events in the nervous system, and their synergistic action may play an important role in neural signal processes.

Sun, Y., Wang, Ch., and Dai, J. (2010). Biophotons as neural communication signals demonstrated by in situ biophoton autography. Photochem. Photobiol. Sci. 9, 315–322.

- Newly, Dotta, Saroka and Persinger (2012 *Neurosci. Lett.*) performed some novel experiments. Specifically, volunteers who imagined a white light in a dark room were compared to those who engaged in simple casual thinking. The authors found significant increases in biophoton emissions (300%) from the right hemisphere but not from the left in the former participant group. Namely, there was a cognitive coupling with biophoton emission in the brain during subjective visual imagery. They emphasized that the emissions of biophotons are strongly correlated with the action potentials of axons. These results support our biophysical picture hypothesis that subjective visual imagery is strongly correlated with the release of biophotons and may be the actual experience of organized matrices of biophotons.

Dotta, B.T. Saroka, K.S. Persinger, M.A. (2012). Increased photon emission from the head while imagining light in the dark is correlated with changes in electroencephalographic power: Support for Bókkon's Biophoton Hypothesis. Neuroscience Letters, doi:10.1016/j.neulet.2012.02.021

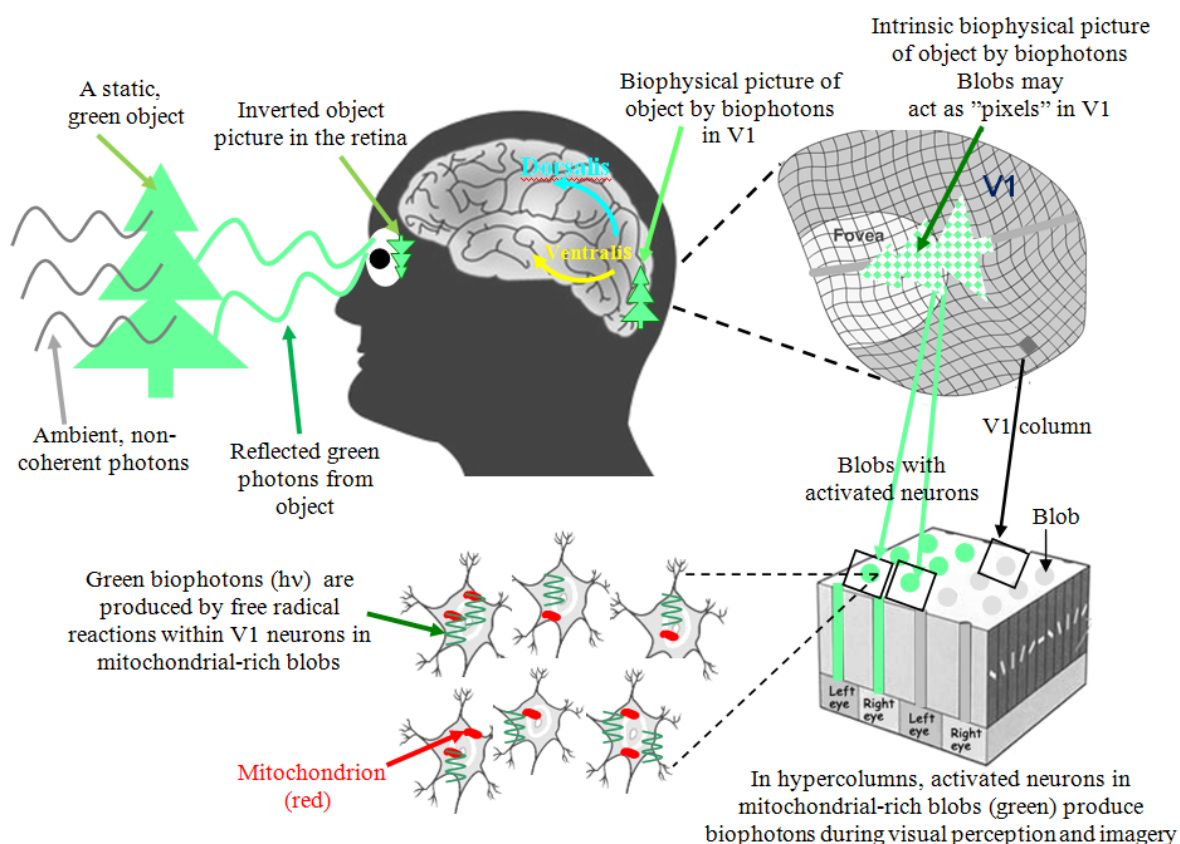


Figure. A simple illustration of the biophysical picture representation idea (also called intrinsic biophysical virtual visual reality) during visual perception and imagery (Bókkon, 2009; Bókkon and D'Angiulli, 2009). External photon signals reflected from an object are converted into retinotopic electrical signals inside the retina. Next, retinotopic electrical signals are conveyed to the V1 and transformed into controlled biophotons by mitochondrial redox processes within the V1 neurons. Specifically, spike-related, retinotopic electrical signals create synchronized biophotons along classical axonal-dendritic pathways through a redox reaction within retinotopic V1 neurons. Small groups of visual neurons can function as “visual pixels” that are appropriate to the topological distribution of the retina’s photonic signals. Thus, we can get an intrinsic computational biophysical picture of the object created by biophotons in the retinotopic V1. The long-term visual information is not stored as pictures but as epigenetic codes. We are able to identify objects since the same epigenetic processes are activated every time we see an object. Therefore, the representation stored in long-term visual memory will match the representation that is created while the object is seen again. Top-down mechanisms control the epigenetically encoded, long-term visual information during visual processing. Then, according to this retrieved epigenetic information, synchronized retinotopic neurons generate dynamic patterns of biophotons through redox reactions. Finally, biophotons within the millions of synchronized neurons (Bókkon et al., 2011a; 2011b) can create biophysical pictures in the early retinotopic visual area. During visual perception and imagery, visual information is linked and combined with different sensory modalities and *higher-order associational areas* during multisensory interactions. It should be emphasized that neural electrical signals are transmitted between neurons, but biophotons are generated within retinotopic visual neurons. In addition, intrinsic biophysical pictures (images) are not like rigid objects but we can alter images *ad-lib*, which make it possible that the visual system can also produce *irrationally* assembled pictures and scenes during REM dreams and visual hallucinations. **Figure source is: Bókkon I, Mallick BN and Tuszyński JA (2013). Near death experiences: A multidisciplinary hypothesis. *Front. Hum. Neurosci.* 7:533.**

- The long-term visual biophysical pictures are not stored as pictures but as epigenetic codes. We are able to identify objects since the same epigenetic processes are activated every time we see an object. Therefore, the representation stored in long-term visual memory will match the representation that is created while the object is seen again. During visual perception and imagery, visual information is linked and combined with different sensory modalities and *higher-order associational areas* during multisensory interactions. **It should be emphasized that neural electrical signals are transmitted between neurons, but biophotons are generated within retinotopic visual neurons.** In addition, intrinsic biophysical pictures (images) are not like rigid objects but we can alter images *ad-lib*, which make it possible that the visual system can also produce *irrationally* assembled pictures and scenes during REM dreams and visual hallucinations.

Rudenko, A., and Tsai, L. H. (2013). *Epigenetic regulation in memory and cognitive disorders. Neuroscience pii: S0306-4522(12)01222-5*

- What can be happened with produced biophotons within neurons? Photosensitive biomolecules of neurons can absorb produced biophotons and transfer the absorbed biophotons energy to nearby biomolecules, which can induce conformation changes and trigger complex signal processes.

- **Since retinal and cortical induced phosphenes may have a similar molecular biophysical basis, if it can be demonstrated that perception of V1 cortical induced phosphenes is due to biophotons, intrinsic regulated biophotons in early retinotopic visual system can be seen to serve as a natural biophysical substrate of visual perception and imagery.**

- If biophotons would play a significant role in visual imagery within the brain, then we would expect that simply shining a bright visible or infrared light into the (during open brain surgery) skull would swamp normal visual imagery. NO NO. The energy of external visible or infrared photons are too weak to perturb visual perception and imagery or produce phosphenes (i.e. inducing strong, excess biophoton emission), so we cannot experience phosphenes upon open brain operations.

HOMUNCULUS

We presented an iterative model of the *homunculus*. Namely, we suggest that during visual imagery, iterative feed forward and feedback processes can be interpreted in terms of a *homunculus* ("little man") looking at the biophysical picture-representation by biophotons. There is a real possibility that biophysical pictures are part of the re-entrant feed forward and feedback processes, and they are not separate from each other because of the re-entry. **Thus, a separate *homunculus* looking at biophotonic representations can be a misleading concept, because it is a iterative matching process.** The matching element is both in physical and mental aspects of feed forward and feedback signals. However, we can render the visual *homunculus* and its mind's eye by showing that it may be reduced to a set of nonlinear biophysical iterative processes.

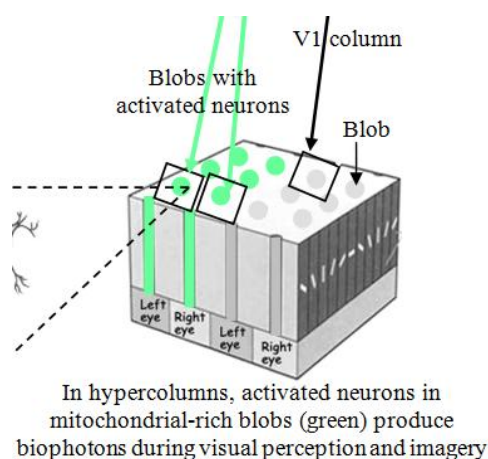
Bókkon I, Salari V, Tuszyński J. (2011) Emergence of intrinsic representations of images by feedforward and feedback processes and bioluminescent photons in early retinotopic areas (Toward biophysical homunculus by an iterative model). *J Integr Neurosci.* 10, 47-64.

The visual content of biophysical representations generated from regulated biophotons is progressively degraded during the transmission along pathways from V1, V2 (extrastriate visual cortical area), and additional visual areas to higher-level associative regions. Furthermore, higher-level cognitive processes might become progressively more abstract or

schematic. The biophysical representation hypothesis suggests that binding between analogic-perceptual and propositional-abstract formats might appear as a natural consequence of the dynamic “crosstalk” between the visual system and the rest of the brain. Thus, retinal visual information can be re-represented through regulated biophotons in retinotopically organized, mitochondrial cytochrome oxidase-rich visual areas during visual imagery, visual perception as well as during REMS associated dreams or visual hallucination.

Cytochrome c- oxidase is a mitochondrial enzyme and is an **endogenous metabolic marker** for **neuronal activity**. **Most neuroscientists do not know that the highest density of neurons in neocortex devoted to representing the visual field is found in V1**, but it has central importance. This means that the highest mitochondrial (and biophoton) activity can be achieved in the color representation cytochrome oxidase-rich blobs. (as mentioned, one of the major source of biophotons are mitochondria, and **cytochrome c-oxidase** is the terminal enzyme of the **mitochondrial** respiratory chain).

So, **cytochrome c-oxidase blobs can work as pixels by their regulated biophotons** during synchronized **spike-related processes in V1 neurons**, and produce internal pictures, internal virtual reality, i.e., produce internal **reality simulation**. The biophysical picture representation may be typically different from other representation forms (i.e., propositional descriptions) up to a point (at least at the level of V1 and V2 areas) in the stream of information processing.



We proposed that detailed and realistic visual representation in early V1 and V2 areas cannot be guaranteed by mere electrical representations. However, the biophysical picture concept may guarantee the detailed and realistic visual representation of objects in retinotopic V1 and V2 areas by congruent patterns of regulated biophotons. In addition, visual cortex not only processes visual signals but also is involved in the processing of mathematical thinking and auditory signals among them. We argued about the essential (and more ancient) role of picture representation over linguistic representation.

Previously, we suggested that dynamic series of picture-representations can carry unambiguous meaning of words. The human memory can operate through inherent dynamic picture representations and we link these biophysical pictures to each other during language learning processes. It means that our brain can use both picture-like and language-like representation processes. The language-like processes can become the basis of abstract thinking, interpersonal communication, etc., while the picture-like biophysical representation processes can guarantee computational geometric imaginary events.

I. Biophysical picture during visual perception

Retinal system is a photon detector and converter. External photons reflected from an object are absorbed by retinal system that begin to process and convert absorbed external photon signals into electrical signals. Next, these object related retinal electric signals are conveyed to the retinotopic V1. The conveyed retinal electric signal stimulate visual V1 cortex and generates synchronized neural spikes/discharges along classical axonal-dendritic pathways. **Simultaneously with synchronized neural spikes, excess biophotons are also produced within discharged retinotopic V1 neurons** (see related experiments and text below). These biophotons that are produced within discharged retinotopic V1 can produce the biophysical picture, i.e. these biophotons **can re-represent of** object (reality simulation). Small neural groups (blobs) work as “pixels” by their biophotons **in retinotopic V1**.

Experiments proved that there is a direct relationship between the intensity of biophotons and neural activity in rat hippocampal slices. In *in vivo* experiments, the biophoton emission from a rat's brain is associated with cerebral energy metabolism, EEG activity, and oxidative processes. Thus, we can conclude that neuronal biophoton emission is in direct relationship with neural activity and neurobiochemical processes. Moreover, it was *demonstrated* that biophotons can conduct along the neural fibers. Latest experiments provided evidence that the glutamate-induced biophotonic activities reflect biophotonic transmission along the axons and in neural circuits, which may be a new mechanism for the processing of neural information. Since regulated electrical signals of neurons can be converted into regulated biophoton signals, external photonic representation can emerge not only as electrical signals but also as regulated biophoton signals in the brain.

Tang R, Dai J. Spatiotemporal imaging of glutamate-induced biophotonic activities and transmission in neural circuits. PLoS One. 2014 Jan 15;9(1):e85643.

Kobayashi K, Okabe H, Kawano S, Hidaka Y, Hara K. Biophoton emission induced by heat shock. PLoS One. 2014 Aug 25;9(8):e105700.

Tang R, Dai J. Biophoton signal transmission and processing in the brain. J Photochem Photobiol B. 2013 Dec 25. pii: S1011-1344(13)00288-1.

Y. Sun, Ch. Wang, J Dai. (2010) Biophotons a neural communication signals demonstrated by in situ biophoton autography. Photochem Photobiol Sci 9:315–322.

Y. Isojima, T. Isoshima, K. Nagai, K. Kikuchi, H. Nakagawa, Ultraweak biochemiluminescence detected from rat hippocampal slices, NeuroReport 6 (1995) 658-660.

M, Kobayashi, M, Takeda, K, Ito, H, Kato, H, Inaba, Two-dimensional photon counting imaging and spatiotemporal characterization of ultraweak photon emission from a rat's brain in vivo, J. Neurosci. Methods 93 (1999) 163-168.

Y. Kataoka, Y. Cui, A. Yamagata, M. Niigaki, T. Hirohata, N. Oishi, Y. Watanabe, Activity-Dependent Neural Tissue Oxidation Emits Intrinsic Ultraweak Photons, Biochem. Biophys. Res. Commun. 285 (2001) 1007-1011.

M. Kobayashi, M. Takeda, T. Sato, Y. Yamazaki, K. Kaneko, K. Ito, H. Kato, H. Inaba, In vivo imaging of spontaneous ultraweak photon emission from a rat's brain correlated with cerebral energy metabolism and oxidative stress, Neurosci. Res. 34 (1999) 103-113.

II. Biophysical picture during visual perception

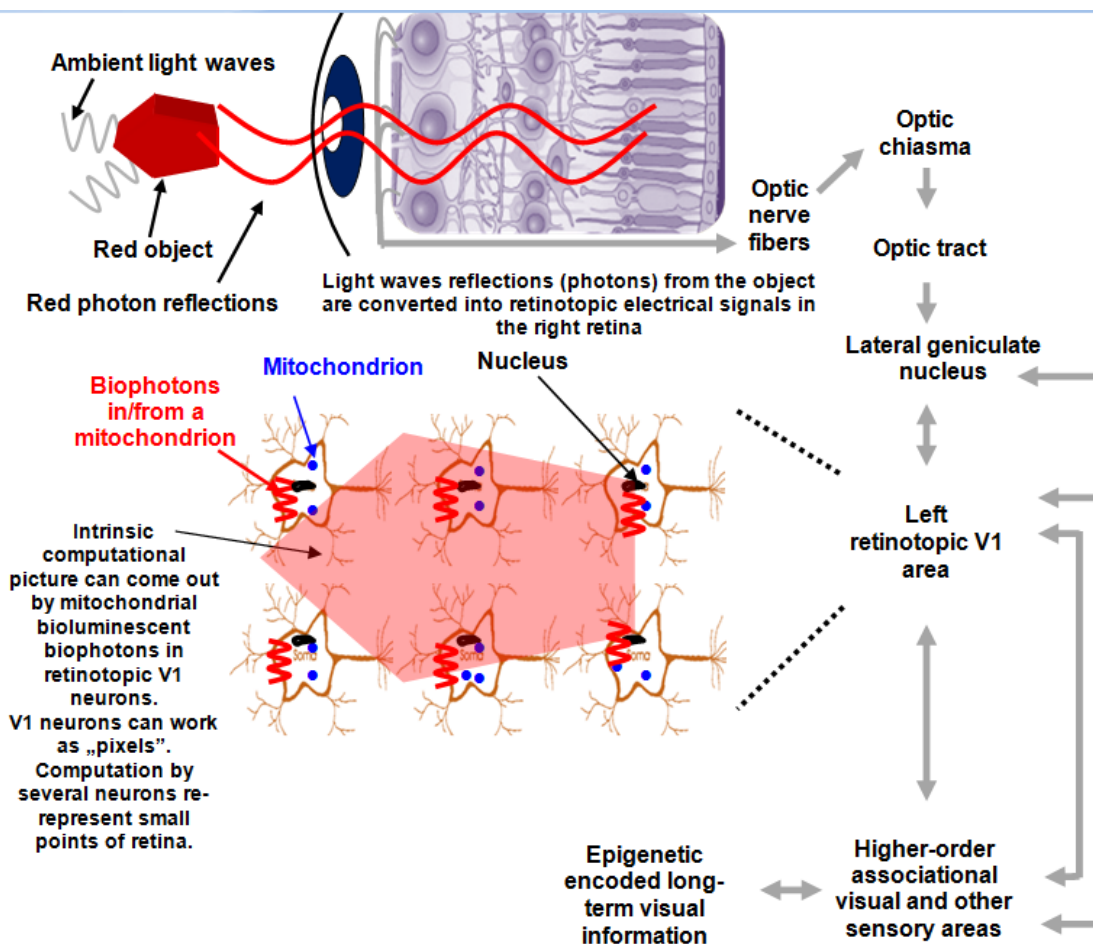


Figure 1. During visual perception, the retinotopic V1 neurons (and extrastriate cortex) are activated by conveyed retinotopic electric signals.

*The conveyed retinal electric signal stimulate V1 cortex and generates synchronized neural discharges along classical axonal-dendritic pathways. **Simultaneously with synchronized neural spikes, excess biophotons are also produced within discharged retinotopic V1 neurons.** These biophotons that are produced within discharged retinotopic V1 can produce the biophysical picture, i.e. these biophotons **can re-represent of object** (reality simulation). Of course, produced biophysical picture interpretation performed by **the long-term memory and higher association areas.***

III. Biophysical picture during visual imagery

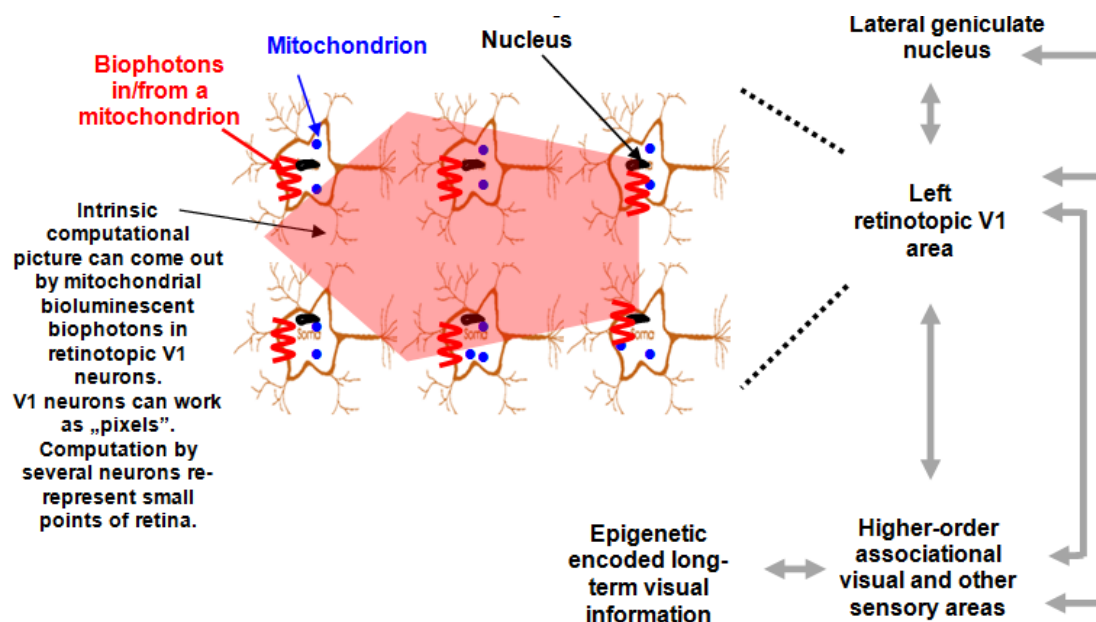


Figure 2. During visual imagery, the retinotopic V1 neurons (and extrastriate cortex) are activated by long-term memory and higher association areas.

Now, close your eyes or go into a dark room and imagine something. There is not any external photon absorbed by retina, but there are discharged retinotopic neurons of V1 related to your actual visual imagery. In this case, retinotopic V1 neurons and extrastriate cortex are activated by your long-term memory and higher association areas. While you imagine something it also produce synchronized neural spikes, and simultaneously with synchronized neural spikes, biophotons are also produced within discharged retinotopic V1 neurons, which produce the internal biophysical picture based on your long-term memory.

Of course, imagery, *per se*, does not produce strong internal biophysical pictures compared to normal visual perception.

Note: But your eye moving reflects your imagery, the retinal system has not too much role in it. A blind person (for example with removed eyes), can also imagine something via activated long-term memory, but without eye moving.

I wrote that every cell, so the retina also, can produce spontaneous biophotons. However, retinal biophoton intensity is much weaker than photons what come from the outside in visual perception, so retinal biophotons are negligible during visual imagery and perception. But when we excite the retina, for example by electric stimulation, the intensity of biophoton emission increases and the brain interprets these retinal excess biophotons similarly to external photons in visual perception.

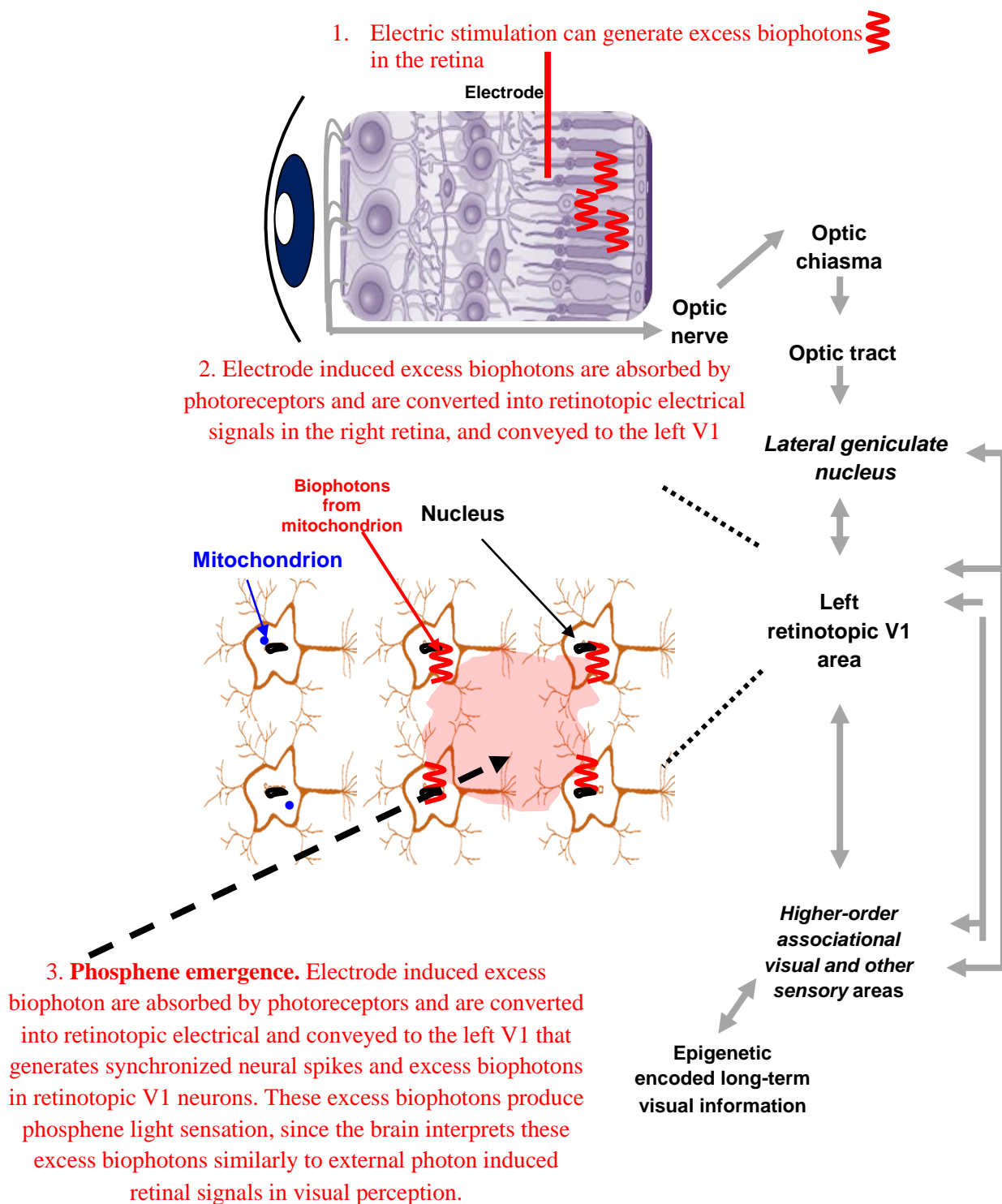
First biophoton experiments may support the biophysical pictures representation. Namely, Dotta et al. (2012) observed cognitive coupling with biophoton emission in the brain during subjective visual imagery. In addition, the biophoton emissions were strongly correlated with EEG activity and the emergence of action potentials in axons.

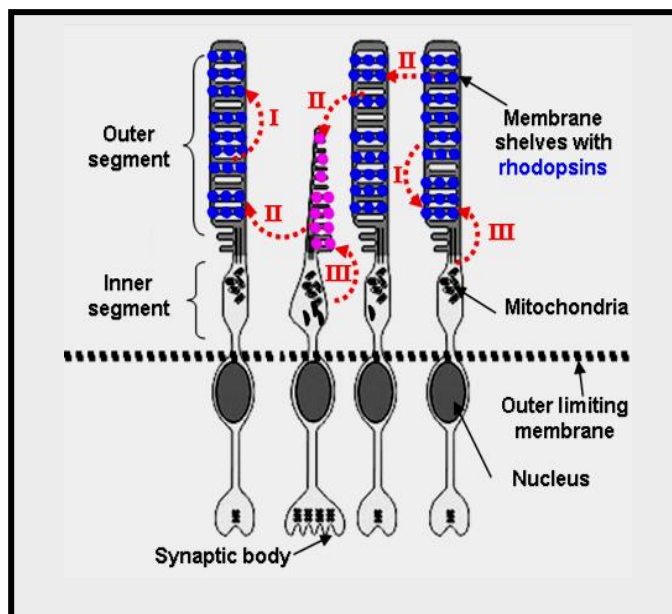
Dotta, B. T., Saroka, K. S., and Persinger, M. A. (2012). Increased photon emission from the head while imagining light in the dark is correlated with changes in electroencephalographic power: Support for Bókkon's Biophoton Hypothesis. Neurosci. Lett. 513, 151–154

IV. Retinal phosphene induction

(for example, with closed eyes or in the blind)

Figure 3.





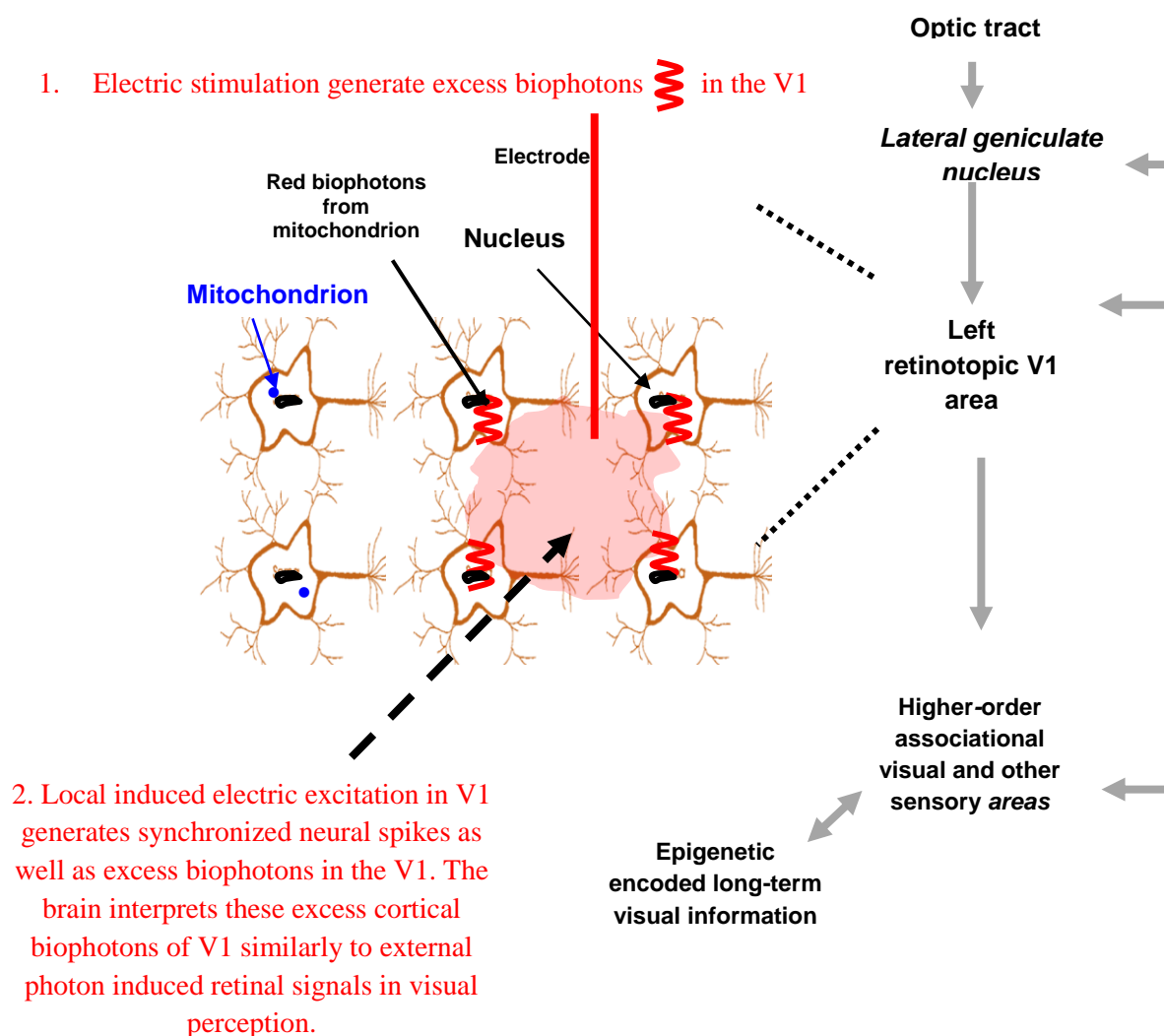
This figure is copyrighted!!

This figure (Wang C, Bókkon I, Dai J, Antal I. (2011) *Brain Res*) may help understand that how biophotons produced and absorbed within photoreceptor layer. **I.** It is possible that a given rod or cone emits a bioluminescent photon that changes its direction, and a subsequently can absorb its own bioluminescent photon. **II.** A rod or cone can absorb bioluminescent photons from the lipid peroxidation of PUFA of adjacent rods or cones. **III.** Bioluminescent photons, emitted from the mitochondrial oxidative metabolism in the inner segment, can also be absorbed by opsins.

This figure also helps understand why weak biophotons can produce strong retinal phosphene perception. In natural vision, external photon intensity is much more stringer compared to biophotons. But, while external photons go across several parts of the eye and several retinal layers, the intensity of external photons are greatly reduced. But retinal biophotons are absorbed where they produced, retinal (namely, biophotons from photoreceptors) biophotons do not need to go across several parts of the eye. Thus, this weak biophotons can produce strong retinal phosphene perception in many cases.

V. Seeing of cortical induced phosphene does not need retina (for example, in the blind)

Figure 4.



Artem'ey, V.V., Goldobin, A.S., Gus'kov, L.N., 1967. Recording the Optical Emission of a Nerve. Biophysics 12, 1278-1280.

Unfortunately, to date, only one experiment proved that a nerve of frog emitted visible biophotons when the nerve was excited by 10-15 V. It was long time ago with more outdated device, but it produced biophotons only via single neuron excitation!!!

6.State-dependent phosphenes

Phosphenes can originate at different levels in the visual system. Several studies demonstrated that patients could perceive phosphenes only in the presence of an intact V1 visual area (Cowey and Walsh, 2000). Recently, Silvanto et al. (2007) carried out a number of transcranial magnetic stimulation (TMS) researches. After 30 sec visual adaptation to a homogeneous color, TMS stimulation was applied on the occipital cortex. This TMS induction could elicit phosphenes that took on the color qualities of the adapting color. For instance, if voluntaries were adapted to a green color, they perceived a red negative afterimage into which the application of TMS induced green phosphenes (Fig.). The negative afterimages lasted about 69 sec. In these experiments, state-dependent 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 91 sec in early visual areas. This subliminal temporary representation of a color became explicit/conscious information, for a moment, by TMS stimulation.

These experiments may support the idea that V1 able to sustain transient subliminal visual information for several seconds. This sustained, transient subliminal visual information is also necessary for iterative/recursive feedforward and feedback neurocomputation between higher and lower areas.

Silvanto, J., Muggleton, N.G., Cowey, A., Walsh, V., 2007. Neural adaptation reveals state-dependent effects of transcranial magnetic stimulation. Eur. J. Neurosci. 25, 1874–1681.

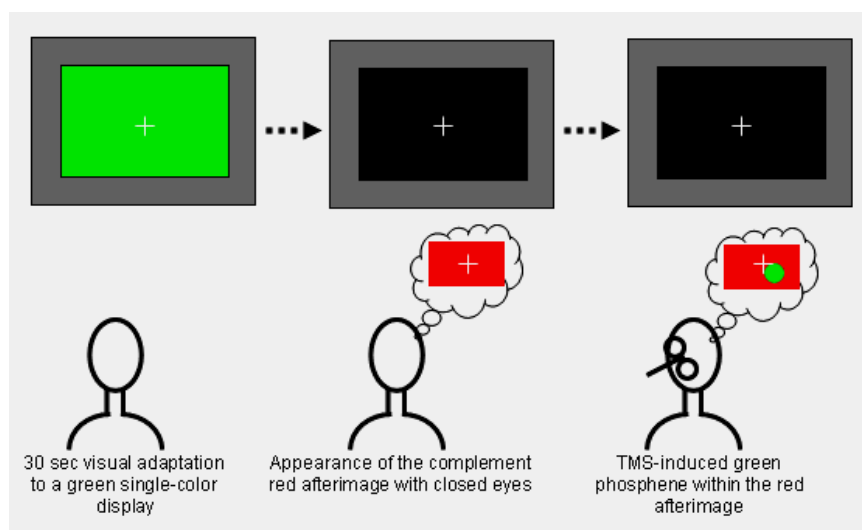


Fig. A schematic drawing of TMS-induced phosphene within the afterimage. Figure source: Bókkon I, Vimal RLP. (2010). Implications on visual apperception: energy, duration, structure and synchronization. *BioSystems* 101, 1-9.

Early visual areas can preserve specific information about visual features for many seconds

According to Harrison and Tong (2009), early visual areas can maintain specific information about visual features held in working memory for many seconds when no physical stimulus is present. Harrison and Tong found that early visual areas are not only important for processing information about the immediate sensory environment, but can also maintain information in the absence of direct input to support higher-order cognitive functions. During their orientation-selective tasks, fMRI was used to determine whether activity in early visual areas could reflect the contents of working memory. Although decoding of low amplitude signals led to reliable prediction of the orientation held in memory, Harrison and Tong found that the overall activity in the visual cortex fell to near-baseline levels after prolonged delays.

Harrison, S.A., Tong, F., 2009. Decoding reveals the contents of visual working memory in early visual areas. Nature 458, 632–635.

Long-lasting subliminal visual representation in early visual areas after visual perception

The experiments by Harrison and Tong (2009) and Silvanto et al. (2007) suggest that residual brain states are not fully reflected in active neural patterns after visual perception. Namely, subliminal residual states are not being reflected in passive neural recording techniques, but require active stimulation to be revealed. This required active stimulation can be realized by artificial (*external*) stimulations, like TMS, or by natural (*internal*) stimulations, like active visualization processes. However, it should be considered at the perceptual experiments to be made in the future that in many cases this retained, subliminal visual representation processes cannot be seen inevitably by the most modern neural recording procedures, but require active stimulation to be emerged.

TMS induces detail-rich “instant replays” of natural images

Wu performed several experiments on the interaction of phosphenes and visual stimuli. He found that the TMS effect is dependent on ongoing neural activity. When a flashed visual disk was timed with TMS so that the phosphene and disk were perceived at the same time, the area of overlap between the disk and phosphene was seen as a more intense color disk version of the disk's color. When TMS was timed so that the subject would see the colored disk and phosphene separately, one after the other, the percept induced by TMS was not an average phosphene. Instead, in the area where the phosphene and disk would have overlapped, the subject saw a repetition of that portion of the colored disk. **Under optimal conditions, the instant replay had a certain photographic-like quality.** When stimulation intensity was lowered, or the delay between the disk and TMS was lengthened, the replay effect became weaker.

Recently, Halelamien et al. and Wu et al. confirmed the neurobiological state-dependency of transcranial magnetic stimulation during visual perception. In Halelamien et al.'s experiments, the coil position was optimized over the occipital cortex to elicit vivid phosphenes in a darkened room and subjects were screened to find those that perceived large, bright phosphenes near fixation. Then, researchers presented pictures of natural scenes and animals for 100 msec, followed by TMS. **They found that TMS delivered shortly after image presentation led to the re-perception of clearly**

defined forms that varied according to the content of the flashed image. In the most notable cases, subjects perceived nearly photographic repetitions in portions of the display. In other cases, subjects perceived uniformly-filled, phosphene-like figures whose outlines matched, in detail, contours drawn from the preceding image. Halelamien et al. concluded that rich, detailed visual information remains encoded well after visual perception has ended and that TMS can allow conscious access to these nascent low-level representations.

In 2013 Liao et al. validated that TMS reactivates visual experience (i.e. induces instant replays).

Neil, H., Wu, D. A. & Shimojo, S. TMS induces detail-rich “instant replays” of natural images. *J. Vis.* 7(9), 276 (2007).

Wu, D. A., Neil, H., Hoeft, F. & Shimojo, S. TMS “instant replay” validated using novel double-blind stimulation technique. *J. Vis.* 7(9), 275 (2007).

Wu, D. A., Neil, H., Hoeft, F. & Shimojo, S. TMS “instant replay” validated using novel double-blind stimulation technique. *J. Vis.* 7(9), 275 (2007).

Jolij, J. & Lamme, V. A. F. Transcranial magnetic stimulation-induced ‘visual echoes’ are generated in early visual cortex. *Neurosci. Lett.* 484, 178–181 (2010).

Hsin-I Liao, Daw-An Wu, Neil Halelamien, Shinsuke Shimojo. Cortical stimulation consolidates and reactivates visual experience: neural plasticity from magnetic entrainment of visual activity. *Sci Rep.* 2013; 3: 2228.

TMS cortical stimulation consolidates and reactivates visual experience

Liao HI, Wu DA, Halelamien N, Shimojo S. Cortical stimulation consolidates and reactivates visual experience: neural plasticity from magnetic entrainment of visual activity. *Sci Rep.* 2013 18;3:2228.

Experiments support the hypothesis that replayed and entrained visual percepts are processed by mechanisms similar to those of regular visual processing (Liao, Wu et al. 2013).

A previous study (Jolij and Lamme, 2010) of the perceptual replay or ‘visual echo’ examined the effect of the visual surround on replayed images, measuring the amount of tilt repulsion between the two. Results showed that the replayed image interacted with the visual surround presented at the time of replay, not at the time of the original visual stimulus presentation.

This suggests that the replay effect involved a recapitulation of normal low-level visual processing (Liao, Wu et al. 2013).

Jolij J, Lamme VA. Transcranial magnetic stimulation-induced ‘visual echoes’ are generated in early visual cortex. *Neurosci Lett.* 2010 Nov 5;484(3):178-81.

Abstract

Transcranial magnetic stimulation (TMS) of the early visual areas can trigger perception of a flash of light, a so-called phosphene. Here we show that a very brief presentation of a stimulus can modulate features of a subsequent TMS-induced phosphene, to a level that participants mistake phosphenes for real stimuli, inducing ‘visual echoes’ of a previously seen stimulus. These ‘echoes’ are modulated by visual context at the moment of magnetic stimulation, showing that they are generated in early visual areas, and that the brain processes these ‘echoes’ as if they are factually presented stimuli. This shows that TMS can re-activate weak visual representations in early visual areas. Based on the pattern of contextual modulation of visual echoes, we theorize that perception of these echoes is not a passive reactivation of residual activity in early visual cortex, but an active interpretation of the combined activity of TMS-induced neural noise and cortical state.

Our results from the TMS-replay learning trials provide further support for this hypothesis, as masking interactions are also mediated in early visual cortex. Further, the results from the TMS-test trials extend the same implications to the entrained percepts (Liao, Wu et al. 2013).

One may alternatively consider the entrained percepts as visual imagery extracted by TMS (Kosslyn, S.M. et al 1999; Silvanto, & Cattaneo, 2010); however, the temporal and spatial specificity found in our results suggest a representation more closely locked to the original 'real' retinally-driven percept (Liao, Wu et al. 2013). Our data, particularly the spatial selectivity, should be interpreted in the context of the continuum from percept to iconic storage to visual memory (Liao, Wu et al. 2013)..

Kosslyn, S.M. et al. The Role of Area 17 in Visual Imagery: Convergent Evidence from PET and rTMS. Science 284, 167–170 (1999).

Silvanto, J. & Cattaneo, Z. Transcranial magnetic stimulation reveals the content of visual short-term memory in the visual cortex. Neurolmage 50, 1683–1689 (2010).

We know that phosphenes can be easiest induced by TMS in the V1.

In all above experiments, subjects were selected if researches could easily induce phosphenes in subjects. We should see, that the same process, i.e. TMS, that produced phosphenes, also could produce TMS induced re-perception of clearly defined forms that varied according to the content of the flashed image and in the most notable cases, subjects perceived nearly photographic repetitions in portions of the display!!!!

Thus, when TMS is applied in right time after visual perception it does not produce phosphenes but produces re-representation that is closely locked to the original 'real' retinally-driven percept. It also evident that conscious re-representation was essentially performed by V1 in these experiments. However, if V1 induced TMS phosphenes can be bioluminescent photons, TMS induced nearly photographic re-representation may also due to the bioluminescent photons. We should think about it!!!!

7.The phosphene is phosphene

As was mentioned, the hypothesis that retinal phosphene lights are due to biophotons is supported by several sets of experiments.

Catalá (2006) has shown that radicals from lipid peroxidation of the photoreceptors can create (bio)chemiluminescent photons (bioluminescence is a type of chemiluminescence, which naturally occurs in living organisms) in the visual spectrum. (there are different name of ultra weak biophotons, such as ultra weak chemiluminescence, eutoluminsecence, ultra weak bioluminescence, etc.)

Catalá A. An overview of lipid peroxidation with emphasis in outer segments of photoreceptors and the chemiluminescence assay. Int J Biochem Cell Biol. 2006;38(9):1482-95

My prediction regarding one specific kind of phosphenes (i.e. retinal phosphenes during space travel) was essential supported by two papers of Narici et al. (2012, 2013). According to this work, ionizing radiation induced free radicals which produce bio/chemiluminescent photons through processes including by lipid peroxidation. Chemiluminescent photons are then absorbed by the photoreceptors and initiate a photo-transduction cascade, which results in the perception of phosphenes. Narici et al. (2013) also revealed that the lipid peroxidation of the photoreceptors can produce (bio)chemiluminescent photons that generate anomalous visual effects, such as those associated with retinal phosphenes. Narici cited my several papers in his 2013 paper.

Narici L, Paci M, Brunetti V, Rinaldi A, Sannita WG, Carozzo S, Demartino A. Bovine rod rhodopsin: 2. Bleaching in vitro upon (12)C ions irradiation as source of effects as light flash for patients and for humans in space. Int J Radiat Biol. 2013 Oct;89(10):765-9

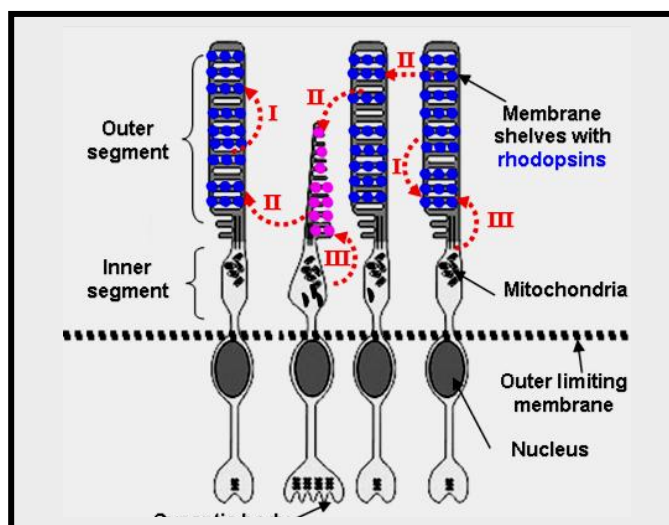
Narici L, Paci M, Brunetti V, Rinaldi A, Sannita WG, De Martino A. Bovine rod rhodopsin. 1. Bleaching by luminescence in vitro by recombination of radicals from polyunsaturated fatty acids. Free Radic Biol Med. 2012 Aug 1;53(3):482-7.

Bókkon I, Vimal RLP. (2009) Retinal phosphenes and discrete dark noises in rods: a new biophysical framework. J. Photochem. Photobiol. B Biology. 96, 255-259.

In addition, recently, we presented the first experimental *in vitro* evidence (Wang, Bókkon et al., 2011) for the existence of spontaneous and visible light induced biophoton emission from freshly isolated whole eye, lens, vitreous humor and retina samples from rats. It also supports the hypothesis that retinal phosphene lights are produced by biophotons.

Wang C, Bókkon I, Dai J, Antal I. (2011) First experimental demonstration of spontaneous and visible light-induced photon emission from rat eyes. Brain Res. 1369. 1-9.

As we can see, there is strong experimental evidence that retinal phosphene lights are due to biophotons.



This figure is copyrighted!!

This figure (Wang C, Bókkon I, Dai J, Antal I. (2011) *Brain Res*) may help understand that how biophotons produced and absorbed within photoreceptor layer. I. It is possible that a given rod or cone emits a bioluminescent photon that changes its direction, and a subsequently can absorb its own bioluminescent photon. II. A rod or cone can absorb bioluminescent photons from the lipid peroxidation of PUFA of adjacent rods or cones. III. Bioluminescent photons, emitted from the mitochondrial oxidative metabolism in the inner segment, can also be absorbed by opsins.

This figure also helps understand why weak biophotons can produce strong retinal phosphene perception. In natural vision, external photon intensity is much more stronger compared to biophotons. But, while external photons go across several parts of the eye and several retinal layers, the intensity of external photons are greatly reduced. But retinal biophotons are absorbed where they produced, retinal (namely, biophotons from photoreceptors) biophotons do not need to go across several parts of the eye. Thus, this weak biophotons can produce strong retinal phosphene perception in many cases.

Now, you may agree with me that **The phosphene is phosphene**, namely, spontaneous retinal phosphenes of Leber Congenital Amaurosis patients (Ashtari et al 2013) (*spontaneous retinal phosphenes activated occipital lobes covering all retinotopic visual centers, and you could see that free radicals takes part in LCA*) are phosphenes like ionizing radiation induced phosphenes Narici et al. (2012, 2013), which due to the free radicals and ultra weak biophotons.

Manzar Ashtari, Laura Cyckowski, Alborz Yazdi, Kathleen Marshal, Amanda Viands, **István Bókkon**, Albert Maguire and Jean Bennett. (2013). *fMRI of Retinal Originated Phosphenes Experienced by Patients with Leber Congenital Amaurosis*. *PLoS One*. Under review.

But it has not proved yet that cortical phosphene lights are due to biophotons, however, the next logical step can be: that retinal and visual cortical phosphenes are generated by similar mechanisms, and both may be due to the transiently and locally increased ultraweak biophotons.

However, cortical phosphenes can be produced by direct electric stimulation of the visual cortex without retinal photo-transduction cascade. **If we can prove that cortical V1 phosphenes can be biophotons, it essentially supports biophysical picture hypothesis.**

However, as mentioned, unfortunately, to date, only one experiment proved that a nerve of frog emitted visible biophotons when the nerve was excited by 10-15 V. It was long time ago with more outdated device, but it produced biophotons only via single neuron excitation!!! Artem'ey, V.V.,

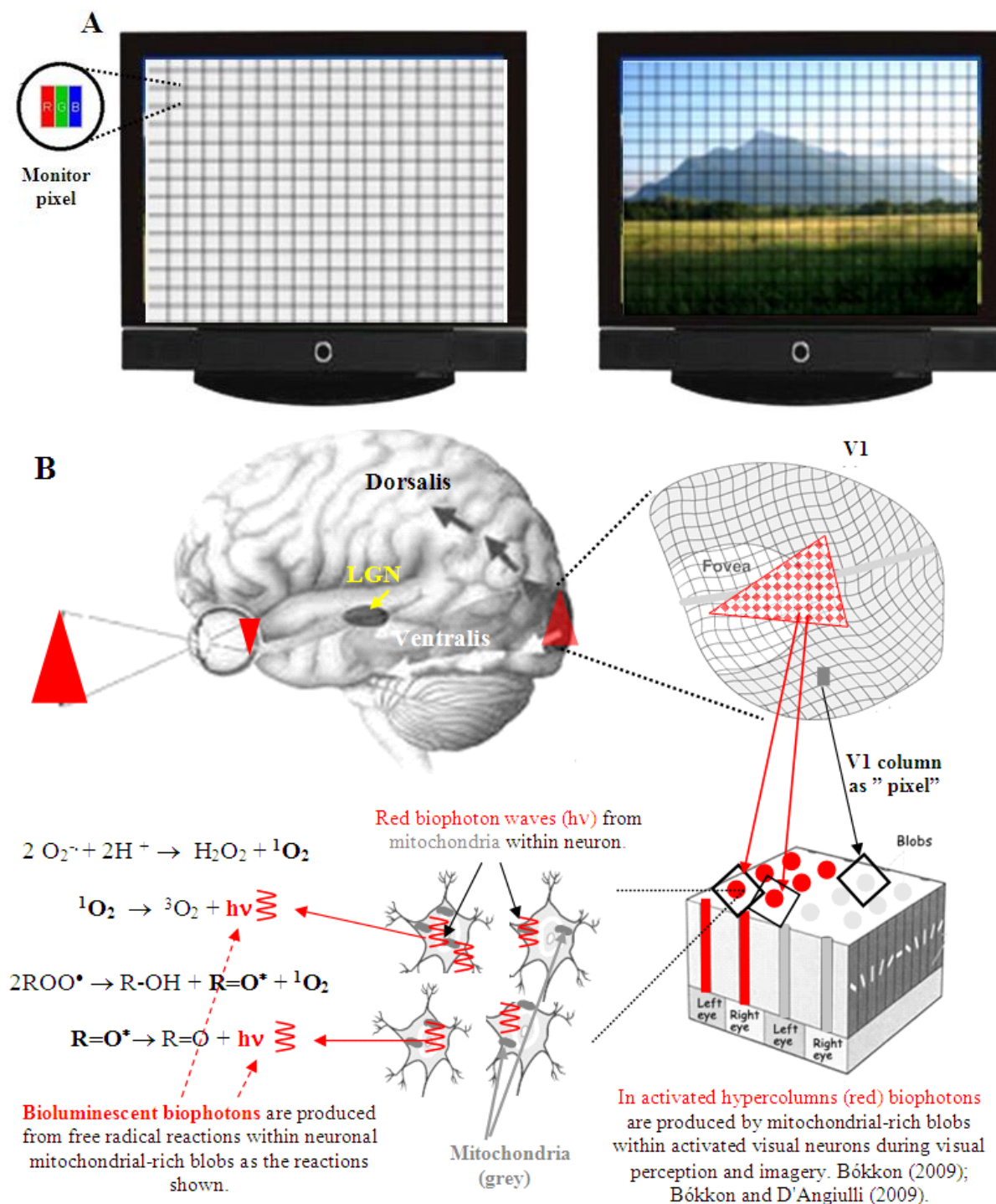


Figure. Biophysical picture representation. (A) Kosslyn's original but simple Cathode Ray Tube metaphor concept about V1 retinotopic structure related to computer monitor. (B) Biophysical picture model by Bókkon (2009), and Bókkon and D'Angiulli (2009). The B is based on the Hubel and Wiesel ice-cube model to describe the biophysical picture idea. In reality (C), V1 structure has not strict geometric like an ice-cube or a monitor pixel. In V1 cytochrome oxidase patches (mitochondrial-rich blobs as local neuron clusters) may constitute the basic modules of striate cortex and may act as "pixels". Since living cells and system use non linear processes, it is not a matter to utilize quasi-irregular geometric organization for visual representation in retinotopic areas.

The human memory (unconscious) can operate through intrinsic dynamic pictures and we link these picture-representations to each other during language learning processes.

Recently, Bókkon and Malick 2012, we have suggested that characteristics of homeothermic state make the development of explicit memory possible in evolution. Our idea may be related to Hobson's protoconscious notion, i.e. protoconscious state may be emerged form implicit memory in homeotherms during evolution of REMS. We also suggested that REM protoconscious state may be essentially visual-based process.

István Bókkon & Birendra Nath Mallick. ACTIVATION OF RETINOTOPIC VISUAL AREAS IS CENTRAL TO REM SLEEP ASSOCIATED DREAMS: VISUAL DREAMS AND VISUAL IMAGERY POSSIBLY CO-EMERGED IN EVOLUTION *Activitas Nervosa Superior* 2012, 54, No. 1-2

Recently, we have proposed a theoretical model involving a biophysical picture-representation without *homunculus* during visual imagery (BÓKKON, SALARI, TUSZYNSKI.2011). We have shown that the somewhat mysterious *homunculus* phenomenon may be elucidated with the help of retinotopic representation, rapid feedforward and feedback connections (*between V1 and V2*), and non-linear iterative processes during visual imagery. We also proposed that emergence of an iterative biophysical picture-representation in retinotopic V1/V2 and the semantic interpretation of an emerged biophysical picture are two different things, although they may be tightly connected. The first is a biophysical picture-representation generating process (*picture-like*) while the second is a language-like semantic interpretation process. However, they can induce each other's representations.

The human memory can operate through intrinsic dynamic pictures and we link these picture-representations to each other during language learning processes. During language learning processes, development of picture-like and language-like systems becomes a quasi-independent neural process. An important implication of this hypothesis is that long-term information storage of the language-like and picture-like representations can be encoded by non-linear epigenetic redox processes. The evolutionary advantage of the biophysical picture representation is that it makes possible, for example, for us to imagine events, compose and design objects, etc.

However, if it can be proved that perception of cortical induced phosphene lights is due to biophotons; intrinsic regulated biophotons in the brain may serve as a natural biophysical (redox molecular) substrate of visual perception and imagery. In other words, intrinsic biophysical visual virtual reality may emerge from feedback and feedforward iterative operation processes and biophotons in early retinotopic V1 and V2 areas. Kosslyn's reality simulation principle [40] states that mental imagery mimics the corresponding events in the world. However, our concept of intrinsic biophysical visual virtual reality (*by iterative processes*) in retinotopic areas may be nothing else than a possible biophysical basis of the reality simulation principle in the case of visual imagery.

BÓKKON, SALARI, TUSZYNSKI. EMERGENCE OF INTRINSIC REPRESENTATIONS OF IMAGES BY FEEDFORWARD AND FEEDBACK PROCESSES AND BIOLUMINESCENT PHOTONS IN EARLY RETINOTOPIC AREAS *Journal of Integrative Neuroscience*, Vol. 10, No. 1 (2011) 47–64

BELOW SEVERAL LATEST PAPERS' ABSTRACTS RELATED TO V1 AND PHOSPHENES

Feedback to Early Visual Cortex Contributes to Perceptual Completion

1. Martijn E. Wokke^{1,2},
2. Annelinde R. E. Vandenbroucke¹,
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4. Victor A. F. Lamme^{1,2}

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1. Martijn E. Wokke, University of Amsterdam, Department of Psychology, Weesperplein 4, 1018 XA, Amsterdam, The Netherlands E-mail: martijnwokke@gmail.com

Abstract

A striking example of the constructive nature of visual perception is how the human visual system completes contours of occluded objects. To date, it is unclear whether perceptual completion emerges during early stages of visual processing or whether higher-level mechanisms are necessary. To answer this question, we used transcranial magnetic stimulation to disrupt signaling in V1/V2 and in the lateral occipital (LO) area at different moments in time while participants performed a discrimination task involving a Kanizsa-type illusory figure. Results show that both V1/V2 and higher-level visual area LO are critically involved in perceptual completion. However, these areas seem to be involved in an inverse hierarchical fashion, in which the critical time window for V1/V2 follows that for LO. These results are in line with the growing evidence that feedback to V1/V2 contributes to perceptual completion.

Neuropsychologia. 2013 Feb;51(3):482-7. doi: 10.1016/j.neuropsychologia.2012.11.020. Epub 2012 Nov 21.

Conscious processing during retrieval can occur in early and late visual regions.

Thakral PP, Slotnick SD, Schacter DL.

Source

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Abstract

Previous evidence has suggested a functional-anatomic dissociation between conscious and nonconscious processing during retrieval where early visual regions BA17/18 are associated with nonconscious processing and late visual regions BA19/37 are associated with conscious processing. However, evidence for this dissociation has only been observed using a limited number of experimental paradigms. In the present functional magnetic resonance imaging (fMRI) study, we

tested the hypothesis that conscious processing during retrieval can occur in BA17/18 using memorial paradigms that recruited processing in these early visual regions. During the encoding phase of Experiment 1, abstract shapes with colored and oriented internal lines were presented to the left and right of fixation. During the retrieval phase, old shapes and new shapes were presented at fixation and participants classified each item as "old-left", "old-right", or "new". The contrast of spatial memory-hits>spatial memory-misses (with accurate item memory) produced activity in BA17/18. During the encoding phase of Experiment 2, abstract shapes with colored and oriented internal lines were presented at fixation. During the retrieval phase, old shapes, changed shapes (with the same outline but different colored and oriented internal lines), and new shapes were presented at fixation and participants made an old-new classification during runs with a specific retrieval orientation or a non-specific retrieval orientation. Critically, the contrast of old-hits>old-misses during specific retrieval orientation produced activity in BA17/18. **The results of the present experiments support the hypothesis that conscious processing during retrieval can occur in BA17/18.**

[Proc Natl Acad Sci U S A.](#) 2013 Aug 27;110(35):14196-201. doi: 10.1073/pnas.1303312110. Epub 2013 Aug 12.

Language can boost otherwise unseen objects into visual awareness.

[Lupyan G¹](#), [Ward EJ](#).

Author information

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Abstract

Linguistic labels (e.g., "chair") seem to activate visual properties of the objects to which they refer. Here we investigated whether language-based activation of visual representations can affect the ability to simply detect the presence of an object. We used continuous flash suppression to suppress visual awareness of familiar objects while they were continuously presented to one eye. Participants made simple detection decisions, indicating whether they saw any image. Hearing a verbal label before the simple detection task changed performance relative to an uninformative cue baseline. Valid labels improved performance relative to no-label baseline trials. Invalid labels decreased performance. Labels affected both sensitivity (d') and response times. In addition, we found that the effectiveness of labels varied predictably as a function of the match between the shape of the stimulus and the shape denoted by the label. Together, the findings suggest that facilitated detection of invisible objects due to language occurs at a perceptual rather than semantic locus. **We hypothesize that when information associated with verbal labels matches stimulus-driven activity, language can provide a boost to perception, propelling an otherwise invisible image into awareness.**

[J Vis.](#) 2011 Oct 21;11(12):17. doi: 10.1167/11.12.17.

Viewed actions are mapped in retinotopic coordinates in the human visual pathways.

[Porat Y¹](#), [Pertzov Y](#), [Zohary E](#).

Author information

- ¹Department of Neurobiology, Hebrew University, Jerusalem, Israel. yporat@gmail.com

Abstract

Viewed object-oriented actions elicit widespread fMRI activation in the dorsal and ventral visual pathways. This activation is typically stronger in the hemisphere contralateral to the visual field in

which action is seen. However, since in previous studies participants kept fixation at the same screen position throughout the scan, it was impossible to infer if the viewed actions are represented in retina-based coordinates or in a more elaborated coordinate system. Here, participants changed their gaze between experimental conditions, such that some conditions shared the same retinotopic coordinates (but differed in their screen position), while other pairs of conditions shared the opposite trait. The degree of similarity between the patterns of activation elicited by the various conditions was assessed using multivoxel pattern analysis methods. Regions of interest, showing robust overall activation, included the intraparietal sulcus (IPS) and the occipitotemporal cortex. In these areas, the correlation between activation patterns for conditions sharing the same retinotopic coordinates was significantly higher than that of those having different retinotopic coordinates. In contrast, the correlations between activation patterns for conditions with the same spatiotopic coordinates were not significantly greater than for non-spatiotopic conditions. **These results suggest that viewed object-oriented actions are likely to be maintained in retinotopic-framed coordinates.**

[PLoS One](#). 2013 Jul 17;8(7):e68560. doi: 10.1371/journal.pone.0068560. Print 2013.

Iterative fragmentation of cognitive maps in a visual imagery task.

[Fourtassi M](#), [Hajjioui A](#), [Urquizar C](#), [Rossetti Y](#), [Rode G](#), [Pisella L](#). laure.pisella@inserm.fr

Source

INSERM, U1028; CNRS, UMR5292; Lyon Neuroscience Research Center, ImpAct team, Lyon, France ; Université Lyon 1, Biologie Humaine, Lyon, France ; Hospices Civils de Lyon, Mouvement et Handicap, Hôpital Henry Gabrielle, St-Genis-Laval, France ; Mouvement et Handicap, Hôpital Neurologique, Lyon, France ; Faculté de Médecine et de pharmacie, Université Mohamed Premier, Oujda, Morocco.

Abstract

It remains unclear whether spontaneous eye movements during visual imagery reflect the mental generation of a visual image (i.e. the arrangement of the component parts of a mental representation). To address this specificity, we recorded eye movements in an imagery task and in a phonological fluency (non-imagery) task, both consisting in naming French towns from long-term memory. Only in the condition of visual imagery the spontaneous eye positions reflected the geographic position of the towns evoked by the subjects. This demonstrates that eye positions closely reflect the mapping of mental images. Advanced analysis of gaze positions using the bi-dimensional regression model confirmed the spatial correlation of gaze and towns' locations in every single individual in the visual imagery task and in none of the individuals when no imagery accompanied memory retrieval. In addition, the evolution of the bi-dimensional regression's coefficient of determination revealed, in each individual, a process of generating several iterative series of a limited number of towns mapped with the same spatial distortion, despite different individual order of towns' evocation and different individual mappings. Such consistency across subjects revealed by gaze (the mind's eye) gives empirical support to theories postulating that visual imagery, like visual sampling, is an iterative fragmented processing.

[PLoS One](#). 2013 Jun 5;8(6):e65161. doi: 10.1371/journal.pone.0065161. Print 2013.

Refractive errors affect the vividness of visual mental images.

[Palermo L](#), [Nori R](#), [Piccardi L](#), [Zeri F](#), [Babino A](#), [Giusberti F](#), [Guariglia C](#).

Source

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Abstract

The hypothesis that visual perception and mental imagery are equivalent has never been explored in individuals with vision defects not preventing the visual perception of the world, such as refractive errors. Refractive error (i.e., myopia, hyperopia or astigmatism) is a condition where the refracting system of the eye fails to focus objects sharply on the retina. As a consequence refractive errors cause blurred vision. We subdivided 84 individuals according to their spherical equivalent refraction into Emmetropes (control individuals without refractive errors) and Ametropes (individuals with refractive errors). Participants performed a vividness task and completed a questionnaire that explored their cognitive style of thinking before their vision was checked by an ophthalmologist. Although results showed that Ametropes had less vivid mental images than Emmetropes this did not affect the development of their cognitive style of thinking; in fact, Ametropes were able to use both verbal and visual strategies to acquire and retrieve information. **Present data are consistent with the hypothesis of equivalence between imagery and perception.**

Science. 2013 May 3;340(6132):639-42. doi: 10.1126/science.1234330. Epub 2013 Apr 4.

Neural decoding of visual imagery during sleep.

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Source

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Abstract

Visual imagery during sleep has long been a topic of persistent speculation, but its private nature has hampered objective analysis. Here we present a neural decoding approach in which machine-learning models predict the contents of visual imagery during the sleep-onset period, given measured brain activity, by discovering links between human functional magnetic resonance imaging patterns and verbal reports with the assistance of lexical and image databases. Decoding models trained on stimulus-induced brain activity in visual cortical areas showed accurate classification, detection, and identification of contents. **Our findings demonstrate that specific visual experience during sleep is represented by brain activity patterns shared by stimulus perception, providing a means to uncover subjective contents of dreaming using objective neural measurement.**

Front Psychol. 2013 May 28;4:200. doi: 10.3389/fpsyg.2013.00200. eCollection 2013.

Global workspace dynamics: cortical "binding and propagation" enables conscious contents.

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Abstract

A global workspace (GW) is a functional hub of binding and propagation in a population of loosely coupled signaling elements. In computational applications, GW architectures recruit many distributed, specialized agents to cooperate in resolving focal ambiguities. In the brain, conscious experiences may reflect a GW function. For animals, the natural world is full of unpredictable dangers and opportunities, suggesting a general adaptive pressure for brains to resolve focal ambiguities quickly and accurately. GW theory aims to understand the differences between conscious and unconscious brain events. In humans and related species the cortico-thalamic (C-T) core is believed to underlie conscious aspects of perception, thinking, learning, feelings of knowing (FOK), felt emotions, visual

imagery, working memory, and executive control. Alternative theoretical perspectives are also discussed. The C-T core has many anatomical hubs, but conscious percepts are unitary and internally consistent at any given moment. Over time, conscious contents constitute a very large, open set. This suggests that a brain-based GW capacity cannot be localized in a single anatomical hub. Rather, it should be sought in a functional hub - a dynamic capacity for binding and propagation of neural signals over multiple task-related networks, a kind of neuronal cloud computing. In this view, conscious contents can arise in any region of the C-T core when multiple input streams settle on a winner-take-all equilibrium. The resulting conscious gestalt may ignite an any-to-many broadcast, lasting ~100-200 ms, and trigger widespread adaptation in previously established networks. To account for the great range of conscious contents over time, the theory suggests an open repertoire of binding coalitions that can broadcast via theta/gamma or alpha/gamma phase coupling, like radio channels competing for a narrow frequency band. Conscious moments are thought to hold only 1-4 unrelated items; this small focal capacity may be the biological price to pay for global access.

Visuotopic maps in cortex specialize in features like color, retinal size, motion, object identity, and egocentric/allocentric framing, so that a binding coalition for the sight of a rolling billiard ball in nearby space may resonate among activity maps of LGN, V1-V4, MT, IT, as well as the dorsal stream. Spatiotopic activity maps can bind into coherent gestalts using adaptive resonance (reentry). Single neurons can join a dominant coalition by phase tuning to regional oscillations in the 4-12 Hz range. Sensory percepts may bind and broadcast from posterior cortex, while non-sensory FOKs may involve prefrontal and frontotemporal areas. The anatomy and physiology of the hippocampal complex suggest a GW architecture as well. In the intact brain the hippocampal complex may support conscious event organization as well as episodic memory storage.

Curr Biol. 2013 Jul 16. pii: S0960-9822(13)00690-8. doi: 10.1016/j.cub.2013.05.065. [Epub ahead of print]

Shared Representations for Working Memory and Mental Imagery in Early Visual Cortex.

Albers AM, Kok P, Toni I, Dijkerman HC, de Lange FP. floris.delange@donders.ru.nl

Source

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Abstract

Early visual areas contain specific information about visual items maintained in working memory, suggesting a role for early visual cortex in more complex cognitive functions [1-4]. It is an open question, however, whether these areas also underlie the ability to internally generate images de novo (i.e., mental imagery). Research on mental imagery has to this point focused mostly on whether mental images activate early sensory areas, with mixed results [5-7]. Recent studies suggest that multivariate pattern analysis of neural activity patterns in visual regions can reveal content-specific representations during cognitive processes, even though overall activation levels are low [1-4]. Here, we used this approach [8, 9] to study item-specific activity patterns in early visual areas (V1-V3) when these items are internally generated. We could reliably decode stimulus identity from neural activity patterns in early visual cortex during both working memory and mental imagery. Crucially, these activity patterns resembled those evoked by bottom-up visual stimulation, suggesting that mental images are indeed "perception-like" in nature. **These findings suggest that the visual cortex serves as a dynamic "blackboard" [10, 11] that is used during both bottom-up stimulus processing and top-down internal generation of mental content.**

Cereb Cortex. 2013 May 21. [Epub ahead of print]

Subjective Characteristics of TMS-Induced Phosphenes Originating in Human V1 and V2.

[Salminen-Vaparanta N](#), [Vanni S](#), [Noreika V](#), [Valiulis V](#), [Móró L](#), [Revonsuo A](#).

Source

Centre for Cognitive Neuroscience.

Abstract

One way to study the neural correlates of visual consciousness is to localize the cortical areas whose stimulation generates subjective visual sensations, called phosphenes. While there is support for the view that the stimulation of several different visual areas in the occipital lobe may produce phosphenes, it is not clear what the contribution of each area is. Here, we studied the roles of the primary visual cortex (V1) and the adjacent area V2 in eliciting phosphenes by using functional magnetic resonance imaging-guided transcranial magnetic stimulation (TMS) combined with spherical modeling of the TMS-induced electric field. Reports of the subjective visual features of phosphenes were systematically collected and analyzed. We found that selective stimulation of V1 and V2 are equally capable of generating phosphenes, as demonstrated by comparable phosphene thresholds and similar characteristics of phosphene shape, color, and texture. However, the phosphenes induced by V1 stimulation were systematically perceived as brighter than the phosphenes induced by the stimulation of V2. Thus, these results suggest that V1 and V2 have a similar capability to produce conscious percepts. Nevertheless, V1 and V2 contribute differently to brightness: **neural activation originating in V1 generates a more intense sensation of brightness than similar activation originating in V2.**

[Neuroimage](#). 2012 Feb 1;59(3):3015-20. doi: 10.1016/j.neuroimage.2011.10.022. Epub 2011 Oct 17.

Cross-adaptation combined with TMS reveals a functional overlap between vision and imagery in the early visual cortex.

[Cattaneo Z](#), [Bona S](#), [Silvanto J](#).

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Abstract

The extent to which the generation of mental images draws on the neuronal representations involved in visual perception has been the subject of much debate. To investigate this overlap, we assessed whether adaptation to visual stimuli affects the ability to generate visual mental images; such cross-adaptation would indicate shared neural representations between visual perception and imagery. Mental imagery was tested using a modified version of the clock task, in which subjects are presented with a digital time (e.g. "2.15") and are asked to generate a mental image of the clock hands displaying this time on an empty clock face. Participants were adapted to oriented lines either on the upper or lower side of the clock face prior to the mental image generation. The results showed that mental imagery was impaired when the mental image had to be generated in the adapted region of visual space (Experiment 1). In Experiment 2, we used TMS to determine whether this adaptation effect occurs in the early visual cortex (EVC; V1/V2). Relative to control conditions (No TMS and Vertex TMS), EVC TMS facilitated mental imagery generation when the mental image spatially overlapped with the adapter. **Our results thus show that neuronal representations in the EVC which encode (and are suppressed by) visual input play a causal role in visual mental imagery.**

[Artif Organs](#). 2013 Apr;37(4):401-8. doi: 10.1111/aor.12005. Epub 2013 Mar 13.

Phosphene object perception employs holistic processing during early visual processing stage.

[Guo H](#), [Yang Y](#), [Gu G](#), [Zhu Y](#), [Qiu Y](#).

Source

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Abstract

Psychophysical studies have verified the possibility of recovering the visual ability by the form of low-resolution format of images, that is, phosphene-based representations. Our previous study has found that early visual processing for phosphene patterns is configuration based. This study further investigated the configural processing mechanisms of prosthetic vision by analyzing the event-related potential components (P1 and N170) in response to phosphene face and non-face stimuli. **The results reveal that the coarse processing of phosphenes involves phosphene-specific holistic processing that recovers separated phosphenes into a gestalt; low-level feature processing of phosphenes is also enhanced compared with that of normal stimuli due to increased contrast borders introduced by phosphenes**; while fine processing of phosphene stimuli is impaired reflected by reduced N170 amplitude because of the degraded detailed features in the low-resolution format representations. Therefore, we suggest that strategies that can facilitate the specific holistic processing stages of prosthetic vision should be considered in order to improve the performance when designing the visual prosthesis system.

[J Cogn Neurosci](#). 2013 May;25(5):685-96. doi: 10.1162/jocn_a_00347. Epub 2012 Dec 18.

Neuromodulation of early multisensory interactions in the visual cortex.

[Convento S](#), [Vallar G](#), [Galantini C](#), [Bolognini N](#).

Source

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Abstract

Merging information derived from different sensory channels allows the brain to amplify minimal signals to reduce their ambiguity, thereby improving the ability of orienting to, detecting, and identifying environmental events. Although multisensory interactions have been mostly ascribed to the activity of higher-order heteromodal areas, multisensory convergence may arise even in primary sensory-specific areas located very early along the cortical processing stream. In three experiments, we investigated early multisensory interactions in lower-level visual areas, by using a novel approach, based on the coupling of behavioral stimulation with two noninvasive brain stimulation techniques, namely, TMS and transcranial direct current stimulation (tDCS). First, we showed that redundant multisensory stimuli can increase visual cortical excitability, as measured by means of phosphene induction by occipital TMS; such physiological enhancement is followed by a behavioral facilitation through the amplification of signal intensity in sensory-specific visual areas. The more sensory inputs are combined (i.e., trimodal vs. bimodal stimuli), the greater are the benefits on phosphene perception. Second, neuroelectrical activity changes induced by tDCS in the temporal and in the parietal cortices, but not in the occipital cortex, can further boost the multisensory enhancement of visual cortical excitability, by increasing the auditory and tactile inputs from temporal and parietal regions, respectively, to lower-level visual areas.

[Exp Eye Res](#). 2012 May;98:88-96.

Preservation of retinotopic map in retinal degeneration.

[Xie J](#), [Wang GJ](#), [Yow L](#), [Humayun MS](#), [Weiland JD](#), [Cela CJ](#), [Jadvar H](#), [Lazzi G](#), [Dhrami-Gavazi E](#), [Tsang SH](#).

Source

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Abstract

Retinal degenerations trigger the loss of photoreceptors and cause the remaining de-afferented neural retina to undergo remodeling. Concerns over this potential retinal synaptic reorganization following visual loss have raised questions regarding the usefulness of visual restoration via retinal electrical stimulation. We have used quantitative positron emission tomography (PET) and 2-deoxy-2-[¹⁸F]fluoro-d-glucose (FDG) to objectively evaluate the connection between the retina and the primary visual cortex under both light and transcorneal electrical stimulation (TcES) in five subjects with retinal degeneration (RD) who have had more than ten years of light-perception-only best visual acuity and five age-matched normal-sighted controls. All subjects underwent quantitative PET with FDG as the metabolic tracer during stimulation of the right eye under both light stimulation condition and transcorneal electrical stimulation (TcES) using ERG-Jet contact lens electrode. Cortical activation maps from each stimulation condition were obtained using statistical parametric mapping. TcES phosphene threshold current and qualitative visual cortex activation from both stimulation conditions were compared between the two subject groups. Average phosphene threshold current was 0.72 ± 0.18 mA for the five normal-sighted controls and 3.08 ± 2.01 mA for the retinal degenerative subjects. Phosphene threshold current was significantly higher in retinal degenerative subjects compared to normal-sighted controls ($p < 0.05$). We found both light stimulation and TcES resulted in retinotopically mapped primary visual cortex activation in both groups. In addition, the patterns of early visual area activation between the two subject groups are more similar during TcES than light stimulation. **Our findings suggest primary visual cortex continues to maintain its retinotopy in RD subjects despite prolonged visual loss.**

[Psychol Bull.](#) 2012 Jul;138(4):744-74. doi: 10.1037/a0027580. Epub 2012 Mar 26.

Elementary visual hallucinations and their relationships to neural pattern-forming mechanisms.

[Billock VA](#), [Tsou BH](#).

Source

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Abstract

An extraordinary variety of experimental (e.g., flicker, magnetic fields) and clinical (epilepsy, migraine) conditions give rise to a surprisingly common set of elementary hallucinations, including spots, geometric patterns, and jagged lines, some of which also have color, depth, motion, and texture. Many of these simple hallucinations fall into a small number of perceptual geometries-the **Klüver forms-that (via a nonlinear mapping from retina to cortex) correspond to even simpler sets of oriented stripes of cortical activity (and their superpositions). Other simple hallucinations (phosphenes and fortification auras) are linked to the Klüver forms and to pattern-forming cortical mechanisms by their spatial and temporal scales.** The Klüver cortical activity patterns are examples of self-organized pattern formation that arise from nonlinear dynamic interactions between excitatory and inhibitory cortical neurons; with reasonable modifications, this model accounts for a wide range of hallucinated patterns. The Klüver cortical activity patterns are a subset of autonomous spatiotemporal cortical patterns, some of which have been studied with functional imaging techniques. Understanding the interaction of these intrinsic patterns with stimulus-driven cortical activity is an important problem in neuroscience. In line with this, hallucinatory pattern formation interacts with physical stimuli, and many conditions that induce hallucinations show interesting interactions with one another. Both types of interactions are predictable from neural and psychophysical principles such as localized processing, excitatory-inhibitory neural circuits, lateral inhibition, simultaneous and sequential

contrast, saccadic suppression, and perceptual opponency. Elementary hallucinations arise from familiar mechanisms stimulated in unusual ways.

[J Headache Pain](#). 2012 Jan;13(1):83-9. doi: 10.1007/s10194-011-0401-x. Epub 2011 Nov 17.

Beta-blocker migraine prophylaxis affects the excitability of the visual cortex as revealed by transcranial magnetic stimulation.

[Gerwig M](#), [Niehaus L](#), [Stude P](#), [Katsarava Z](#), [Diener HC](#).

Source

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Abstract

The objective of this study is to assess effects of beta-blocker migraine prophylaxis on cortical excitability determined by transcranial magnetic stimulation (TMS). Phosphene and motor thresholds (PT, MT) were investigated in 29 patients with migraine, in 15 of them prior to and following preventive medication with metoprolol and in 14 patients without prophylaxis. Following prophylaxis headache frequency significantly decreased ($p = 0.005$) and mean PT were significantly increased (51.5 ± 7.5 vs. $63.6 \pm 8.4\%$) compared to patients without preventive treatment (53.7 ± 5.3 vs. $52.3 \pm 6.3\%$; $p = 0.040$). Mean MT did not significantly differ either between groups or due to treatment. In the group of all patients, a significant inverse correlation between headache frequency and the level of PT was found ($R = -0.629$; $p < 0.01$). There was, however, no significant correlation in the subgroups of patients. We conclude that (a) clinical efficacy of beta-blocker treatment in migraine could be (at least partly) linked to its ability to modulate the excitability of the visual cortex and (b) the PT determined by TMS appears suitable to assess the effects of prophylaxis on cortical excitability in the individual patient. This may be useful in clinical trials investigating migraine preventive drugs.

[Exp Brain Res](#). 2011 Sep;213(2-3):193-201. doi: 10.1007/s00221-011-2742-8. Epub 2011 Jun 4.

Looming sounds enhance orientation sensitivity for visual stimuli on the same side as such sounds.

[Leo F](#), [Romei V](#), [Freeman E](#), [Ladavas E](#), [Driver J](#).

Source

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Abstract

Several recent multisensory studies show that sounds can influence visual processing. Some visual judgments can be enhanced for visual stimuli near a sound occurring around the same time. A recent TMS study (Romei et al. 2009) indicates looming sounds might influence visual cortex particularly strongly. But unlike most previous behavioral studies of possible audio-visual exogenous effects, TMS phosphene thresholds rather than judgments of external visual stimuli were measured. Moreover, the visual hemifield assessed relative to the hemifield of the sound was not varied. Here, we compared the impact of looming sounds to receding or "static" sounds, using auditory stimuli adapted from Romei et al. (2009), but now assessing any influence on visual orientation discrimination for Gabor patches (well-known to involve early visual cortex) when appearing in the same hemifield as the sound or on the opposite side. The looming sounds that were effective in Romei et al. (2009) enhanced visual orientation sensitivity (d') here on the side of the sound, but not for the opposite hemifield. This crossmodal, spatially specific effect was stronger for looming than receding or static sounds. Similarly to Romei et al. (2009), the differential effect for looming sounds was eliminated when using white

noise rather than structured sounds. **Our new results show that looming structured sounds can specifically benefit visual orientation sensitivity in the hemifield of the sound, even when the sound provides no information about visual orientation itself.**

[Neuroimage](#). 2012 Jan 2;59(1):840-5. doi: 10.1016/j.neuroimage.2011.07.062. Epub 2011 Aug 2.

Causal evidence for subliminal percept-to-memory interference in early visual cortex.

[Silvanto J](#), [Soto D](#).

Source

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Abstract

There has been recent interest in the neural correlates of visual short-term memory (VSTM) interference by irrelevant perceptual input. These studies, however, presented distracters that were subjected to conscious scrutiny by participants thus strongly involving attentional control mechanisms. In order to minimize the role of attentional control and to investigate interference occurring at the level of sensory representations, we developed a paradigm in which a subliminal visual distracter is presented during the delay period of a visual short-term memory task requiring the maintenance of stimulus orientation. This subliminal distracter could be either congruent or incongruent with the orientation of the memory item. Behavioral results showed that the intervening distracter affected the fidelity of VSTM when it was incongruent with the memory cue. We then assessed the causal role of the early visual cortex in this interaction by using transcranial magnetic stimulation (TMS). We found that occipital TMS impaired the fidelity VSTM content in the absence of the memory mask. Interestingly, TMS facilitated VSTM performance in the presence of a subliminal memory mask that was incongruent with the memory content. Signal detection analyses indicated that TMS did not modulate perceptual sensitivity of the masked distracter. That the impact of TMS on the precision of VSTM was dissociated by the presence vs. absence of a subliminal perceptual distracter and its congruency with the VSTM content provides causal evidence for the view that **competitive interactions between memory and perception can occur at the earliest cortical stages of visual processing.**

[Front Hum Neurosci](#). 2014 Jul 30;8:506. doi: 10.3389/fnhum.2014.00506. eCollection 2014.

Parallel processing in the brain's visual form system: an fMRI study.

[Shigihara Y](#), [Zeki S](#).

Author information

- Wellcome Laboratory of Neurobiology, University College London London, UK.

Abstract

We here extend and complement our earlier time-based, magneto-encephalographic (MEG), study of the processing of forms by the visual brain (Shigihara and Zeki, 2013) with a functional magnetic resonance imaging (fMRI) study, in order to better localize the activity produced in early visual areas when subjects view simple geometric stimuli of increasing perceptual complexity (lines, angles, rhombuses) constituted from the same elements (lines). **Our results show that all three categories of form activate all three visual areas with which we were principally concerned (V1-V3),** with angles producing the strongest and rhombuses the weakest activity in all three. The difference between the activity produced by angles and rhombuses was significant, that between lines and

rhombuses was trend significant while that between lines and angles was not. **Taken together with our earlier MEG results, the present ones suggest that a parallel strategy is used in processing forms, in addition to the well-documented hierarchical strategy.**

[Cereb Cortex](#). 2014 Aug 6. pii: bhu168. [Epub ahead of print]

Neural Anatomy of Primary Visual Cortex Limits Visual Working Memory.

[Bergmann J](#)¹, [Genç E](#)², [Kohler A](#)³, [Singer W](#)⁴, [Pearson J](#)⁵.

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- ³Department of Neurophysiology, Max-Planck-Institute for Brain Research, 60528 Frankfurt am Main, Germany Brain Imaging Center Frankfurt, 60528 Frankfurt am Main, Germany Institute of Cognitive Science, University of Osnabrück, 49076 Osnabrück, Germany.
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Abstract

Despite the immense processing power of the human brain, working memory storage is severely limited, and the neuroanatomical basis of these limitations has remained elusive. Here, we show that the stable storage limits of visual working memory for over 9 s are bound by the precise gray matter volume of primary visual cortex (V1), defined by fMRI retinotopic mapping. Individuals with a bigger V1 tended to have greater visual working memory storage. This relationship was present independently for both surface size and thickness of V1 but absent in V2, V3 and for non-visual working memory measures. Additional whole-brain analyses confirmed the specificity of the relationship to V1. **Our findings indicate that the size of primary visual cortex plays a critical role in limiting what we can hold in mind, acting like a gatekeeper in constraining the richness of working mental function.**

[Brain Struct Funct](#). 2014 Jun 19. [Epub ahead of print]

Eye position modulates retinotopic responses in early visual areas: a bias for the straight-ahead direction.

[Strappini F](#)¹, [Pitzalis S](#), [Snyder AZ](#), [McAvoy MP](#), [Sereno MI](#), [Corbetta M](#), [Shulman GL](#).

Author information

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Abstract

Even though the eyes constantly change position, the location of a stimulus can be accurately represented by a population of neurons with retinotopic receptive fields modulated by eye position gain fields. Recent electrophysiological studies, however, indicate that eye position gain fields may serve an additional function since they have a non-uniform spatial distribution that increases the neural response to stimuli in the straight-ahead direction. We used functional magnetic resonance imaging and a wide-field stimulus display to determine whether gaze modulations in early human visual cortex enhance the blood-oxygenation-level dependent (BOLD) response to stimuli that are straight-ahead. Subjects viewed rotating polar angle wedge stimuli centered straight-ahead or vertically displaced by $\pm 20^\circ$ eccentricity. Gaze position did not affect the topography of polar phase-angle maps, confirming that coding was retinotopic, but did affect the amplitude of the BOLD response, consistent with a gain field. In agreement with recent electrophysiological studies, BOLD responses in V1 and V2 to a wedge stimulus at a fixed retinal locus decreased when the wedge location in head-centered coordinates was farther from the straight-ahead direction. We conclude that stimulus-evoked BOLD signals are modulated by a systematic, non-uniform distribution of eye-position gain fields.

[PLoS One](#). 2014 Apr 11;9(4):e94633. doi: 10.1371/journal.pone.0094633. eCollection 2014.

Repetitive and retinotopically restricted activation of the dorsal lateral geniculate nucleus with optogenetics.

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Abstract

Optogenetics allows the control of cellular activity using focused delivery of light pulses. In neuroscience, optogenetic protocols have been shown to efficiently inhibit or stimulate neuronal activity with a high temporal resolution. Among the technical challenges associated with the use of optogenetics, one is the ability to target a spatially specific population of neurons in a given brain structure. To address this issue, we developed a side-illuminating optical fiber capable of delivering light to specific sites in a target nucleus with added flexibility through rotation and translation of the fiber and by varying the output light power. The designed optical fiber was tested in vivo in visual structures of ChR2-expressing transgenic mice. To assess the spatial extent of neuronal activity modulation, we took advantage of the hallmark of the visual system: its retinotopic organization. Indeed, the relative position of ganglion cells in the retina is transposed in the cellular topography of both the dorsal lateral geniculate nucleus (LGN) in the thalamus and the primary visual cortex (V1). The optical fiber was inserted in the LGN and by rotating it with a motor, it was possible to sequentially activate different neuronal populations within this structure. The activation of V1 neurons by LGN projections was recorded using intrinsic optical imaging. Increasing light intensity (from 1.4 to 8.9 mW/mm²) led to increasing activation surfaces in V1. Optogenetic stimulation of the LGN at different translational and rotational positions was associated with different activation maps in V1. The position and/or orientation of the fiber inevitably varied across experiments, thus limiting the capacity to pool data. With the optogenetic design presented here, we demonstrate for the first time a transitory and spatially-concise activation of a deep neuronal structure. The optogenetic design presented here thus opens a promising avenue for studying the function of deep brain structures.

[J Vis](#). 2014 Mar 19;14(3):22. doi: 10.1167/14.3.22.

Spatial specificity of working memory representations in the early visual cortex.

[Pratte MS¹](#), [Tong F.](#)

Author information

- ¹Psychology Department and Vanderbilt Vision Research Center, Vanderbilt University, Nashville, TN, USA.

Abstract

Recent fMRI decoding studies have demonstrated that early retinotopic visual areas exhibit similar patterns of activity during the perception of a stimulus and during the maintenance of that stimulus in working memory. These findings provide support for the sensory recruitment hypothesis that the mechanisms underlying perception serve as a foundation for visual working memory. However, a recent study by Ester, Serences, and Awh (2009) found that the orientation of a peripheral grating maintained in working memory could be classified from both the contralateral and ipsilateral regions of the primary visual cortex (V1), implying that, unlike perception, feature-specific information was maintained in a nonretinotopic manner. Here, we evaluated the hypothesis that early visual areas can maintain information in a spatially specific manner and will do so if the task encourages the binding of feature information to a specific location. To encourage reliance on spatially specific memory, our experiment required observers to retain the orientations of two laterally presented gratings. Multivariate pattern analysis revealed that the orientation of each remembered grating was classified more accurately based on activity patterns in the contralateral than in the ipsilateral regions of V1 and V2. In contrast, higher extrastriate areas exhibited similar levels of performance across the two hemispheres. A time-resolved analysis further indicated that the retinotopic specificity of the working memory representation in V1 and V2 was maintained throughout the retention interval. **Our results suggest that early visual areas provide a cortical basis for actively maintaining information about the features and locations of stimuli in visual working memory.**

[Neuroimage](#). 2014 May 1;91:336-43. doi: 10.1016/j.neuroimage.2014.01.016. Epub 2014 Jan 17.

Neural basis of non-conscious visual working memory.

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Abstract

Recent research indicates that human observers can perform high-level cognitive tasks typically associated with working memory processes (e.g. learning of complex item sequences, reading, arithmetic or delayed visual discrimination) independently of conscious awareness of the relevant information. However, the neural basis of this phenomenon is not known. Here we show neuroimaging and neurostimulation evidence that the dorsolateral and anterior prefrontal cortex can operate on non-conscious information in a manner that goes beyond automatic forms of sensorimotor priming and which may support implicit working memory processes and higher-level cognitive function.

[Neuroimage](#). 2012 Feb 1;59(3):3015-20. doi: 10.1016/j.neuroimage.2011.10.022. Epub 2011 Oct 17.

Cross-adaptation combined with TMS reveals a functional overlap between vision and imagery in the early visual cortex.

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Abstract

The extent to which the generation of mental images draws on the neuronal representations involved in visual perception has been the subject of much debate. To investigate this overlap, we assessed whether adaptation to visual stimuli affects the ability to generate visual mental images; such cross-adaptation would indicate shared neural representations between visual perception and imagery. Mental imagery was tested using a modified version of the clock task, in which subjects are presented with a digital time (e.g. "2.15") and are asked to generate a mental image of the clock hands displaying this time on an empty clock face. Participants were adapted to oriented lines either on the upper or lower side of the clock face prior to the mental image generation. The results showed that mental imagery was impaired when the mental image had to be generated in the adapted region of visual space (Experiment 1). In Experiment 2, we used TMS to determine whether this adaptation effect occurs in the early visual cortex (EVC; V1/V2). Relative to control conditions (No TMS and Vertex TMS), EVC TMS facilitated mental imagery generation when the mental image spatially overlapped with the adapter. Our results thus show that neuronal representations in the EVC which encode (and are suppressed by) visual input play a causal role in visual mental imagery.

[Neuroimage](#). 2014 Jan 1;84:765-74. doi: 10.1016/j.neuroimage.2013.09.051. Epub 2013 Sep 29.

Overlapping activity periods in early visual cortex and posterior intraparietal area in conscious visual shape perception: a TMS study.

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Abstract

Parietal cortex is often activated in brain imaging studies on conscious visual processing, but its causal role and timing in conscious and nonconscious perception are poorly understood. We studied the role of posterior intraparietal sulcus (IPS) and early visual areas (V1/V2) in conscious and nonconscious vision by interfering with their functioning with MRI-guided transcranial magnetic stimulation (TMS). The observers made binary forced-choice decisions concerning the shape or color of the metacontrast masked targets and rated the quality of their conscious perception. TMS was applied 30, 60, 90, or 120ms after stimulus-onset. In the shape discrimination task, TMS of V1/V2 impaired conscious perception at 60, 90, and 120ms and nonconscious perception at 90ms. TMS of IPS impaired only conscious shape perception, also around 90ms. Conscious color perception was facilitated or suppressed depending on the strength of the TMS-induced electric field in V1/V2 at 90ms. The results suggest that simultaneous activity in V1/V2 and IPS around 90ms is necessary for visual awareness of shape but not for nonconscious perception. The overlapping activity periods of

IPS and V1/V2 may reflect recurrent interaction between parietal cortex and V1 in conscious shape perception.