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Review Article

Implications on visual apperception: Energy, duration, structure and synchronization

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ABSTRACT

Although primary visual cortex (V1 or striate) activity *per se* is not sufficient for visual apperception (normal conscious visual experiences and conscious functions such as detection, discrimination, and recognition), the same is also true for extrastriate visual areas (such as V2, V3, V4/V8/VO, V5/M5/MST, IT, and GF). In the lack of V1 area, visual signals can still reach several extrastriate parts but appear incapable of generating normal conscious visual experiences. It is scarcely emphasized in the scientific literature that conscious perceptions and representations must have also essential energetic conditions. These energetic conditions are achieved by spatiotemporal networks of dynamic mitochondrial distributions inside neurons. However, the highest density of neurons in neocortex (number of neurons per degree of visual angle) devoted to representing the visual field is found in retinotopic V1. It means that the highest mitochondrial (energetic) activity can be achieved in mitochondrial cytochrome oxidase-rich V1 areas. Thus, V1 bear the highest energy allocation for visual representation.

In addition, the conscious perceptions also demand structural conditions, presence of adequate duration of information representation, and synchronized neural processes and/or 'interactive hierarchical structuralism.' For visual apperception, various visual areas are involved depending on context such as stimulus characteristics such as color, form/shape, motion, and other features. Here, we focus primarily on V1 where specific mitochondrial-rich retinotopic structures are found; we will concisely discuss V2 where smaller riches of these structures are found. We also point out that residual brain states are not fully reflected in active neural patterns after visual perception. Namely, after visual perception, subliminal residual states are not being reflected in passive neural recording techniques, but require active stimulation to be revealed.

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1. Introduction

It is well known that the activities of the primary visual cortex (V1) and higher visual areas (such as V2, V3, V4/V8/VO, V5/M5/MST, IT, and GF) are linked to the visual apperception (normal conscious visual experiences and conscious functions such as detection, discrimination, and recognition) of visual stimuli depending on their characteristics and the context.¹ However, it is hardly emphasized in the scientific studies that the visual apperception and stimulus-representations must have essential energetic conditions. These energetic conditions are achieved by spatiotemporal networks of dynamic mitochondrial distributions inside neurons. The generation of action potentials as well as synaptic transmission fundamentally depends on dynamic mitochondrial energetic/redox/Ca²⁺ and mitochondrial membrane potential $\Delta\psi_m$, as well as mitochondrial distributions (Tong, 2007; Ly and Verstreken, 2006; Verstreken et al., 2005; Hollenbeck, 2005).

Here, we suggest that normal V1 retinotopic visual area is essential (in addition to extrastriate areas and the necessary ingredients wakefulness, working memory, attention, and re-entry (Vimal, 2009c)) for the occurrence of explicit visual consciousness (Vimal, 2009b, 2010b) during visual perception.² Namely, we point out that synchronized (coupled) mitochondrial processes, duration of visual representation, and specific mitochondrial-rich early retinotopic structures are elementary conditions for the explicit conscious visual perception. Although V1 activity is not sufficient for normal visual apperception and the same is also true for extrastriate visual areas (such as V2, V3, V4/V8/VO, V5/M5/MST, IT, and GF),³ specific mitochondrial-rich (energy-rich) retinotopic structures are supplied mainly by the primary visual cortex V1.

There are three entities, namely, structure, function, and experience, which must be linked appropriately. Here, we try to link structure and function using the energetic framework, where

¹ The color area 'V8/V4/VO' refers to visual area V8 of Tootell-group (Hadjikhani et al., 1998; Tootell et al., 2003), visual area V4 of Zeki-group (Bartels and Zeki, 2000), and VO of Wandell-group (Wandell, 1999); they are the same human color area (Tootell et al., 2003). VO is ventral-occipital cortex. V5 is visual area 5, MT is the middle temporal area, and MST is the middle superior temporal area; they are motion related area. IT is inferior temporal cortex related to object recognition. GF is fusiform gyrus face area.

² In this article, we do not deal with the 'hard' problem of consciousness. The 'hard' problem related to subjective experiences (SEs) aspect of consciousness is addressed in (Vimal, 2008a,b, 2009a,b,d,e, 2010a; Vimal and Davia, 2008) using the dual-aspect-dual-mode PE-SE framework, where PE is proto-experience.

³ It is controversial that we are aware of neural activity in primary visual cortex (Crick and Koch, 1995a,b; Pollen, 1995, 1999, 2004). According to (LaRock, 2007), "persons with blindsight—a visual disorder caused by damage to cells in V1—can still be conscious of certain visual features, such as motion (Printz, 2000). This is because the neuronal area that correlates with the awareness of motion receives a direct visual input that bypasses V1 (Zeki, 2003). Consequently, the evidence gathered thus far indicates that V1 might be necessary as a source of inputs to higher regions of the visual cortex, but could not be the neural correlate of a feature-unified object of visual consciousness (cf. (Crick and Koch, 1995a); see also (Printz, 2000))." The "explicit conscious visual perception" and "visual apperception" include visual subjective experiences and visual functions such as visual detection, discrimination, and recognition. These involve also extrastriate areas (such as V2, V3, V4/V8/VO, V5/M5/MST, IT, and GF) in addition to V1.

dynamic mitochondrial energetic/redox/Ca²⁺ and mitochondrial membrane potential, as well as mitochondrial distributions are incorporated.

2. Color neural-network involves V1, V2, V4/V8/VO, IT, and GF

First, we define a neural-network by taking color neural-network as an example. According to (Vimal, 2009c), "the neural correlate of color related subjective experiences is 'V4/V8/VO'-color-neural-network. One could hypothesize that this network consists of: (a) the main color processing network in the ventral pathway (retina → parvocellular layers of the LGN ↔ cytochrome oxidase-rich blobs (and also interblobs) of the layer 2/3 of V1 ↔ thin stripes of V2 ↔ 'V4/V8/VO') ↔ IT ↔ GF; (b) the attentional network such as [fast (retinotectal: retina → SC → pulvinar → intraparietal lobule (IPL)/parietal cortex) and slow (geniculostriate: retina → LGN → V1 → V2 → 'V5/MT/MST' → IPL/parietal cortex)] → frontal cortex/PFC (such as FEF) ↔ 'V4/V8/VO';⁴ (c) other auxiliary networks such as emotion, face, and color related network such amygdala system ↔ GF ↔ IT ↔ 'V4/V8/VO', location and color related dorsal network such as parietal cortex ↔ FEF ↔ 'V4/V8/VO', and so on; (d) the ARAS arousal system that sends projections to thalamocortical neural-networks to bring them to wakefulness (Wakefulness is a periodic natural brain state in which a person is conscious and can perform coherent cognitive and behavior responses to the external world such as communication, intake of food and ambulation, procreation) as a baseline for consciousness to occur; (e) the memory related areas such as PFC, parietal and visual areas (Lamme, 2003; Pasternak and Greenlee, 2005); and (f) Self related areas (Bruzzo and Vimal, 2007; Northoff et al., 2006). The areas up to V2 are involved in processing local aspects of color vision (Lennie et al., 1990). The visual area V4 is involved in more global processing such as contextual information in color constancy, color induction, and color discrimination (Hurvich and Jameson, 1957; Kaiser and Boynton, 1996; Wray and Edelman, 1996; Zeki, 1983a,b). The IT is involved in color vision (Komatsu et al., 1992), but its functional role is not clear."

3. Energy dependence of apperception

It is scarcely stressed in the scientific papers that apperception (conscious perception/representation/function) requires energetic conditions. The brain can perceive, detect, discriminate, and recognize consciously just those pieces of external information, which reach a critical intrinsic energetic level (guaranteed by neuronal mitochondrial activity), an adequate duration of information representation as well as an adequate coherence levels that is provided by complex neural structures. At the end, the brain can perceive these signals consciously.

⁴ See Section 2 and (Chambers et al., 2004; LaBerge, 1997; LaBerge et al., 2000; Rossi et al., 2009).

Nonlinear dynamic biochemical networks in living systems are far from thermal equilibrium (Qian and Beard, 2005) that make possible to pick up extreme weak different information from the outside world. The sensory systems, which are results of nonlinear biochemical processes of cells, have extreme sensitivity to pick up diverse information from the external world.

Blindsight is the classic example as sensory stimuli that can affect behavior without being consciously perceived (Ptito and Leh, 2007). However, there is evidence about analogous phenomena. For example, a rod cell in the eye can detect and transform a single photon of light into a neural signal (Baylor et al., 1979). However, under natural circumstances, one photon, if it is below threshold, does not lead to conscious function (*such as detection, discrimination, and recognition*) in the brain, but it enters the brain, and it activates the appropriate system to some extent. The conscious hearing is not a thermal process (Sheppard, 1995); rather, it is a nonlinear process of cells if the signal of the surroundings is strong enough. The ear can also detect weak signal if it is at or above threshold, which might not be enough for discrimination and recognition. The ear works as a mechanic oscillating system if it gets a suitably strong sound signal, but it can also perceive weak signals. How? Cells in the ear may cause continuously an own ultra-weak, electromagnetic oscillation, and the signals of the surroundings could superimpose on the cells' own oscillation. In case of sensing smells, there also exists a sort of non-conscious perception. It was discovered that the human brain could perceive ultra-weak signals of molecules (*pheromones*) just like other mammals including rats (Leinders-Zufall et al., 2000). Various behavioral signals relate to the fact that a "sexual nose" (not conscious olfactory perception) acts besides the "thinking nose" (*conscious smell perception*). This "sexual nose" can affect unconsciously the emotions and the behavior. However, even information lacks critical and adequate conditions, sensory stimuli can enter the brain and can affect oscillation, and the signals of the surroundings could superimpose on the cells' own oscillation.

The above mentioned processes are analogous: representation of various sensory information can become conscious (*or explicit*) in our mind, only if it reaches a threshold level of energy and duration (*in case of sight and hearing*), or concentration (*in the case of olfactory sensing*), and neurostructural conditions are assured.

4. Cytochrome oxidase activity corresponds to mitochondrial activity

To date, mitochondria are viewed as simple cellular energy sources in most of scientific literature. According to Aon et al. (2008), mitochondria act as metabolic and redox hubs as well as key integration centers of cellular signaling pathways in eukaryotic cells. *Cytochrome oxidase* (CO) is the last enzyme in the mitochondrial respiratory electron transport chain that is located in the mitochondrial membrane. The strict coupling between oxidative energy metabolism and *neuronal activity* is the basis for the use of CO as an endogenous metabolic marker for neurons (Wong-Riley, 1989). Because CO staining intensity correlates with neuronal functional activity, when we talk about *cytochrome oxidase* activity we also talk about mitochondrial activity. We should keep in mind that *cytochrome oxidase* activity may have direct link with mitochondrial activity, distributions, and processes (*as in neuronal activity*); this has an enormous importance if we want to understand neuronal processes.

5. Mitochondrial networks can reflect the sensory information within neurons during representation

In general, the mitochondrion is described as little roundest organelle of a size much smaller than that of the cell. However, cells

very often contain filamentous mitochondria (Skulachev, 2001). What is more, vertebrate mitochondria of muscular, connective, or neuronal tissue are mostly filamentous. It has been proven that mitochondrial networks can be electrically coupled and can coordinate and synchronize each other (Drachev and Zorov, 1986; Dedov and Roufogalis, 1999; Skulachev, 2001). Namely, mitochondria are functionally connected and constitute a dynamical network inside neuronal cells. Mitochondria frequently fuse and divide and their morphology and intracellular distribution are changed according to the energy demand of cells (Müller et al., 2005).

Mitochondria play elementary roles in cellular life such as redox homeostasis, ATP production, thermogenesis, free radical creation, Ca^{2+} homeostasis, cell growth, apoptosis, various cell signaling, iron metabolism, steroidogenesis, and *can take up* about 25% of cell volume of neurons (Kann and Kovács, 2007; Lemasters et al., 1999; Ly and Verstreken, 2006).

Mitochondria also take essential roles in the synthesis and secretion of neurotransmitters. Important steps in the metabolism of the excitatory glutamate and the inhibitory GABA neurotransmitters are located in the mitochondrial tricarboxylic acid cycle (Waagepetersen et al., 1999). In addition, monoamine oxidase (MAO) flavo-enzyme, which is localized to the outer mitochondrial membrane, plays a crucial metabolic role in the turnover of dopamine, serotonin, norepinephrine, and epinephrine in the central nervous system (Cohen and Kesler, 1999; Cohen, 2000).

Mitochondria and mitochondrial DNA play also critical roles in learning and memory and these processes occur in interaction of with nuclear DNA (Roubertoux et al., 2003; Battersby et al., 2003; Desler et al., 2007). During neuronal communication, mitochondrial DNA can modulate/regulate nuclear DNA and vice versa.

There is a direct coupling between mitochondrial organization-movement-activity and synaptic activity (Mattson, 2007). Information processing of different sensory experiences by the brain is reflected in dynamical changes of the electrical activity in time, frequency, and space. While the brain processes information from different perceptions, the energetic processes (*dynamic mitochondria networks and processes*) must reflect the perceived information processes because the energy demand of neuronal electrical activity is achieved essentially by mitochondrial processes and networks. Since sensory information processes are directly linked to mitochondrial energetic processes, it means that information that comes from the different perceptions have to be represented not only by structural processes (*such as neural networks*) and neuronal electrical activity, but also by spatiotemporal energetic/redox/ $\text{Ca}^{2+}/\Delta\psi_m$ processes of mitochondrial networks within neurons. Thus, spatiotemporal mitochondrial processes can also reflect representations within neurons during sensory experiences (Fig. 1).

Recently, Tong (2007) suggested that the spatiotemporal dynamic patterns of mitochondrial distribution can work as a "mitochondrial memory code" that dictates the potentiation of specific synapses and the plasticity of the neuronal network. However, spatiotemporal energetic/redox/ $\text{Ca}^{2+}/\Delta\psi_m$ patterns of mitochondrial distribution can perform an intrinsic representation patterns within neurons during various sensory experiences.

Since mitochondrial networks play essential regulating roles in the turnover of several neurotransmitters, Ca^{2+} buffering, energetic and redox processes, and mitochondria occupy up to 25% of cell volume in neurons, this suggests that mitochondrial networks may act as transient intrinsic representation systems (*transient "mitochondrial memory codes"*) inside neurons. However, mitochondria are not only simple cellular energy sources but also bear fundamental roles in cellular and neurocellular computational processes.

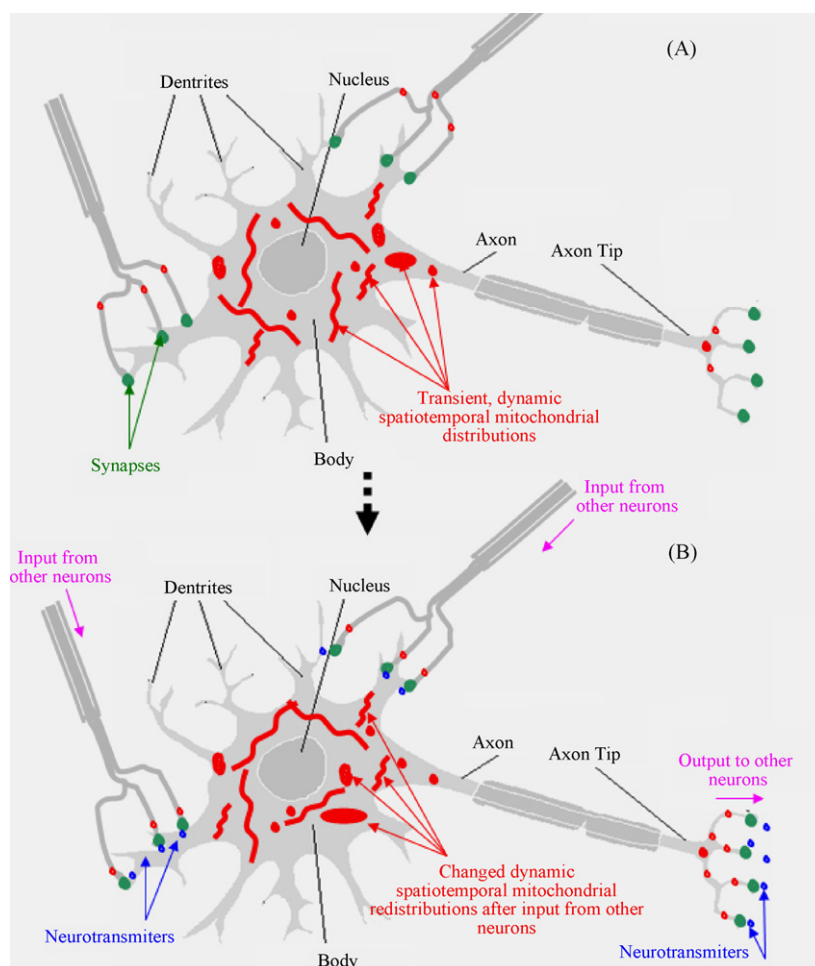


Fig. 1. Mitochondrial distributions create spatiotemporal energetic, $[Ca^{2+}]_m$, $\Delta\psi_m$, ROS distribution patterns (A). Synaptic sensory input from other neurons produces changes in spatiotemporal mitochondrial distributions. These new energetic/redox/calcium/ROS redistributions of mitochondrial networks in space and time can act as transient information representation systems within neurons during sensory representations (B).

6. Methylene blue, cytochrome oxidase activity, and memory retention

Mitochondrial cytochrome oxidase enzyme (*that is an endogenous metabolic marker of neuronal activity and oxidative metabolism*) is the terminal enzyme in the electron transport chain, and it catalyzes the utilization of molecular oxygen to form water and ATP during oxidative phosphorylation. Low-dose administration of methylene blue (MB) can enhance memory retention in normal rats by increasing brain cytochrome oxidase activity, thereby improving brain energy production MB serves as a redox compound acts as an alternative electron acceptor within mitochondria (Gonzalez-Lima and Bruchey, 2004; Wrubel et al., 2007). MB appears to work as a brain metabolic enhancer by increasing mitochondrial cytochrome oxidase activity. Since MB can enhance memory retention by the means of mitochondrial cytochrome oxidase activity, these experiments may also support our idea that mitochondrial processes can have essential roles in the representation of information inside neurons (Gonzalez-Lima and Bruchey, 2004; Wrubel et al., 2007).

7. Activity-dependent neurotransmitter release produces activity-dependent mitochondrial distributions within neurons

Chen et al. (2007, 2008) showed in *in vitro* hippocampal neurons that neurotransmitter dopamine and serotonin (5-HT) can reversibly control mitochondrial motility and distribution via the

Akt-GSK3beta signaling cascade. They found that dopamine displays a net inhibitory effect on mitochondrial movement, but serotonin has stimulatory effect on mitochondrial movement. They proposed that dopamine and 5-HT can determine the mitochondrial distribution as energy sources within neurons. However, Chen et al.'s experiments favor our hypothesis that during various perceptions, mitochondrial networks in space and time can act as representation networks inside neurons. In other words, during sensory representation processes, activity-dependent neurotransmitter release (*in our case dopamine and serotonin*) can produce activity-dependent mitochondrial distributions in neurons. Thus, external visual and other types of information can also be represented by spatiotemporal energetic/redox/ Ca^{2+} / $\Delta\psi_m$ patterns processes of mitochondrial networks within neurons. Moreover, mitochondria play crucial roles in the turnover of glutamate, GABA, dopamine, serotonin, norepinephrine, and epinephrine in the central nervous system; this means that mitochondrial distributions can also regulate neurotransmitter signal processes during sensory representation processes. It seems that there is a fundamental regulation between classic neurotransmitters and mitochondrial activity/distribution/functions in neurons.

In summary, mitochondrial distributions can be regulated by neurotransmitters. Coordinated energetic/redox/ Ca^{2+} / $\Delta\psi_m$ distribution processes of mitochondrial networks in space and time can act as transient representation systems (*transient "mitochondrial memory codes"*) in neurons during sensory representation. In other words, mitochondrial networks can reflect the sensory informa-

tion within neurons during representation. Mitochondria act as metabolic and redox hubs as well as fundamental integration centers of cellular signaling pathways in eukaryotic cells. We should not forget that neuronal activity (*neurobiological processes*) is fundamentally achieved by mitochondrial procedures. Finally, we should consider in the future that mitochondria are not only mere cellular energy sources but they also have essential roles in cellular and neurocellular computational processes.

8. Mitochondrial-rich retinotopic V1 areas

Retinotopy is a fundamental organizing principle of the visual cortex. The expanded neural representation of the fovea found in the retina and *lateral geniculate nucleus* (LGN) is maintained in the visual cortex. In primates, LGN, the striate cortex (V1) and several extrastriate visual cortical areas are organized in a retinotopic manner, respecting the topological distribution of photon stimuli on the retina (Martínez et al., 1999; Kaido et al., 2004).

The highest density of neurons in neocortex (*number of neurons per degree of visual angle*) (Rockel et al., 1980; O’Kusky and Colonnier, 1982) and the highest volume of gray matter of the retino-geniculo-striate pathway devoted to representing the visual field (Winter et al., 1969; Barlow, 1981; Perry and Cowey, 1985; Schein, 1988; Felleman and Van Essen, 1991) are found in V1. It is hardly accidental that the highest mitochondrial (*energetic*) activity can be achieved by mitochondrial cytochrome oxidase-rich V1 areas in the brain. Thus, V1 bear the highest energy allocation for the visual representation.

Since V1 is retinotopic and its input from LGN is monocular, all properties must be represented for each eye, except in binocular neurons of V1 (Cumming and Parker, 1999). Most cells in mitochondrial cytochrome oxidase-rich blobs are unoriented and selective for color, while most cells elsewhere are oriented and not selective for color (Lu and Roe, 2008). It was concluded that the mitochondrial cytochrome oxidase-rich blobs represent monocular sites of color processing in primate striate cortex. Since cytochrome oxidase is a mitochondrial respiratory chain (*complex IV*) enzyme, we also can use the term mitochondrial-rich blobs. Therefore, mitochondrial-rich blobs can represent monocular sites of color processing in primate striate cortex.

During visual perception, the high activity of cytochrome oxidase is connected to high mitochondrial activity because cytochrome oxidase is a mitochondrial respiratory chain enzyme. There is growing evidence that different CO compartments in V1 and V2 are connected in parallel and the projection from V1 cytochrome oxidase blobs (*or patches*) to V2 thin stripes is responsible for color. However, V1 and V2 may represent all submodalities of vision such as color, form, motion, and depth (Sincich and Horton, 2005). According to Sincich and Horton (2005), “now make it likely that the visual attributes of color, form, and motion are not neatly segregated by V1 into different stripe compartments in V2. Instead, there are just two main streams, originating from cytochrome oxidase patches and interpatches, that project to V2.”

9. Iterative/recursive processes during visual perception

During visual perception, the visual system may use iterative/recursive neurocomputation (Deco and Schürmann, 2000) between top-down and bottom-up processes as long as the perceived image and the activated long-term visual information have a similar convergence. V1 and V2 visual areas are not only processors of afferent information but also targets of feedback *circuits* of neurons from numerous extrastriate and high-level visual areas. Thus, iterative neurocomputation between recognition spaces and per-

ceptual spaces may be a basic requirement for visual apperception (Pollen, 1995, 2008). There are about 11,000 feedback neurons in V2 and 14,000 feedforward neurons in V1 (Rockland, 1997). According to recent findings, there is a very rapid effect of feedback connections on the visual responses of neurons in lower order areas (Hupé et al., 2001; Girard et al., 2001). Namely, the effects of feedback connections delay by less than 10 ms with respect to the beginning of the responses of neurons in low-order visual areas. The feedback and feedforward connections between V1 and V2 have comparable fast conduction velocities (around 3.5 m/s) (Girard et al., 2001). These fast iterative/recursive processes between V1 and V2 are also essential for that we can consciously identify an object during visual perception.

10. Blindsight

In humans, the primary visual cortex (V1, striate) is essential for conscious vision.⁵ However, in the lack of V1 and in the absence of awareness, some preserved ability to exactly respond to visual inputs has been proven (Boyer et al., 2005). This phenomenon is referred to as blindsight. The visual abilities of subjects without acknowledged awareness have been called Type I blindsight (*or attention blindsight*). Type I blindsight characterized by target detection and localization by saccadic eye movements, relative velocity discrimination, movement direction, and stimulus orientation detection (Pöppel et al., 1973; Barbur et al., 1980; Weiskrantz et al., 1995; Weiskrantz, 1986). Type II blindsight (*or impaired awareness*) includes remaining visual abilities with awareness i.e., semantic priming from words presented in the blind field or consciously detecting a fast-moving stimulus (Weiskrantz et al., 1995; Marcel, 1998). It was suggested that blindsight might be due to remaining function in the primary (*geniculostriate visual pathway: mediated by preserved “islands” in V1*) or a secondary (*retinotectal visual pathway: projections to the superior colliculus and pulvinar could provide indirect visual input to the extrastriate areas*) pathway (Fendrich et al., 1992).

However, hemispherectomized patients are good models for studying remaining visual abilities because entire occipital lobe has been removed or disconnected from the rest of the brain. In hemispherectomized subjects, visual signals cannot be executed by geniculostriate pathways. Thus, visual information from the blind visual field can only be achieved through the ipsilesional superior colliculus or the contralesional pulvinar pathway on to the intact hemisphere (Ptito and Leh, 2007). Recently, Yoshida et al. (2008) provided evidence that blindsight occurs because visual information is conveyed bypassing the primary visual cortex. However, the proposed visual processing mechanisms subserving these residual visual abilities have been controversial.

11. Blindsight and destruction of V1

The destruction (*removal*) of V1 cortical area abolishes the powerful energetic representations generated by mitochondrial-rich networks in retinotopically organized V1 visual neurons. *In other words*, without V1, visual information cannot be realized consciously during perception because it cannot reach an adequate high (*strong*) level of mitochondrial energy representation (*energy dependent conscious visual threshold*). Recently, Lau and Passingham (2007) suggested that blindsight patients might have conscious vision, but set their threshold for reporting awareness too high.

⁵ LaRock (2006) summarized the participation of V1 in visual consciousness as follows: “V1 may be necessary as a source of inputs to higher regions of the visual cortex, but could not be the neural correlate of feature-unified objects of visual consciousness (see Crick and Koch, 1995a; Printz, 2000).”

This suggestion can be in relationship with our notion about energy dependent conscious visual threshold.

Type II blindsight might due to the preserved “islands” in V1 and extrastriate areas which get visual information through sub-cortical pathways that escaped the cortical damage. However, these preserved “islands” could take a strong enough retinotopic mitochondrial energy representation.

In contrast, in Type I blindsight subjects, visual information cannot be conveyed by geniculostriate pathways; thus, visual information from the blind visual field can only be transported by the ipsilesional superior colliculus or the contralesional pulvinar on to the intact hemisphere. As a result, hemispherectomized patients cannot perform any residual visual awareness that is due to the total lack of retinotopic spatiotemporal mitochondrial-rich energy representation in V1. Thus, only some degraded visual information can emerge as target detection and localization by saccadic eye movements, detection of movement direction, etc., that can be achieved in the intact hemisphere.

According to Lamme (2001), “...unconscious visuo-motor transformations, as in blindsight, may be executed in an entirely feedforward processing cycle, while visual awareness is critically dependent on feedback connections to the primary visual cortex.” However, V1 is also essential for iterative/recursive neurocomputation between bottom-up and top-down processes, which is necessary for the conscious identification of an object during visual perception.

12. State-dependent phosphenes

Phosphenes can originate at different levels in the visual system (Bókkon and Vimal, 2009; Vimal and Pandey-Vimal, 2007) Cowey and Walsh, 2000. 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 s 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. 2). The negative afterimages lasted about 69 s. In these experiments, state-dependent phosphenes persisted for about 91 s, meaning that the information of perceived visual color (*after 30 s visual adaptation to a color*) was not consciously represented for 91 s in early visual areas. This subliminal temporary representation of a color became explicit/conscious information, for a moment, by TMS stimulation.

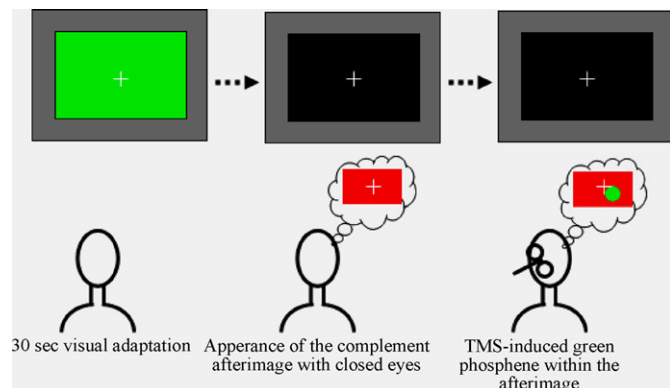


Fig. 2. A schematic drawing of TMS-induced phosphenes within the afterimage (see text for explanation)

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.

13. 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.

14. 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 see inevitably by the most modern neural recording procedures, but require active stimulation to be emerged.

15. Synchronized neural processes, synchronized mitochondrial energetic processes, and interactive hierarchical structuralism and binding problem

Synchronized neural processes, possibly, produce synchronized mitochondrial processes because mitochondria are the sources of most of neural processes. One could argue that there can be a differential synchronization rather than uniform synchronization during visual perception. Neural synchrony has been proposed to be dominant mechanism to address the binding problem (*how various features that are analyzed in various specific areas are bound together for unified consciousness, see also (Vimal, 2010a)*). However, it has been criticized by (LaRock, 2006, 2007).

The “neural synchrony hypothesis emphasize that the temporal correlation of neuronal firings (rather than physical interconnectivity) is the distinctive neural activity that underlies object feature binding in visual consciousness” (LaRock, 2006). Furthermore, (Crick and Koch, 1990) relate the temporal correlation of neuronal firings with ‘binding’ as follows: “in neural terms binding means the temporally correlated firing of the neurons involved. In other words, neurons in different parts of the cortex responding to the currently perceived object fire action potentials at about the same time” (p. 270). Moreover, neuronal synchronies are phase-locked and the feature ambiguity problem is addressed by the functional role of attention (Crick and Koch, 1990).

However, LaRock (2006) argues that neural synchrony fails to explain the unity of visual consciousness on both empirical and philosophical grounds: “First, neural synchrony probably cannot account for the enduring character of object representations in visual consciousness because of its fleeting nature. [...] Second, temporal synchrony could play a functional role other than binding an object’s attributes together. For example, it could be that neural synchrony fundamentally explains the flexibility of our cognitive architecture rather than its binding capacity.”

Third, neural synchrony results primarily from moving stimuli and is difficult to measure with stationary stimuli. In addition, Tovee and Rolls (1992) suggested that the absence of synchronized neuronal activity in inferior temporal cortex (IT) implies that a synchronization-based mechanism of feature binding should be rejected.

“Fourth, the experimental data used to confirm the temporal correlation hypothesis were obtained from both anaesthetized and awake animals, namely, cats and monkeys ... synchronized neuronal firings in the 40 Hz range occur in response to visually presented objects in the brains of both conscious and unconscious animals. ... the same neuronal mechanism (SNFs) allegedly explains both stimulus-related binding correlated with consciousness and stimulus-related binding correlated with unconsciousness” (LaRock, 2006).

Fifth, Crick and Koch (1990) try to address the feature ambiguity problem by invoking the attentional mechanism. This needs further elaboration.

“Finally, even if binding were to occur because of some yet to be discovered neural mechanism, one could argue that an explanatory gap would still remain between binding and experience.” In addition, “the research of (Luck and Beach, 1998) adds further reason to doubt that neural synchrony could suffice as the mechanism of object feature binding at intermediate/higher levels of the visual system. This is because the receptive fields of cells in these areas are too large, hence increasing the probability of the accidental synchronizations of output neurons that correlate with the attributes of different objects” (LaRock, 2007).

To address above problems LaRock (2007) proposes *interactive hierarchical structuralism* (IHS) in place of neural synchrony hypothesis: “This view suggests that a unified percept (i.e., a feature-unified object of visual consciousness) is *not* reducible to the activity of any cognitive capacity or to any localized neural area, but *emerges* out of the interaction of visual information organized by spatial structuring capacities correlated with lower, higher, and intermediate levels of the visual hierarchy.”

Furthermore, Searle (1992) proposes a weak emergentist view of consciousness called *biological naturalism*: “Consciousness emerges only if there are sufficiently organized neurons present to allow for suitable causal relations. [...] he defends emergentism merely on grounds of the *non-deducible* character of consciousness, rather than also appealing to ‘downwards causation’ in the sense described and defended by those who hold to a stronger notion of emergentism. [...] A stronger notion of emergentism is also ‘downwards causation.’ [...] Upwards causation leads to the production of novel features that have their own transient careers. Downwards causation refers to holistic emergent processes that control or constrain lower-level interactions (Varela and Thompson, 2003, p. 273). [...] for example, how the cognitive subject’s interpretations of ambiguous figures [such as Necker cube] supply implicit evidence for a stronger variety of emergentism” (LaRock, 2007).

LaRock (2007) argues that “IHS is compatible with this stronger notion of emergence in the sense that a unified percept (i.e., a feature-unified object of visual consciousness) emerges out of the interaction of information organized by spatial structuring capacities that correlate with lower, higher, and intermediate levels of the visual hierarchy. [...] *Lower-Level Spatial Structuring* the rela-

tion between the spatial properties of retinal images and the spatial properties laid out on the surface area of V1 is a relation of structural coherence [...] *Higher-Level Spatial Structuring*. Recent evidence suggests that structural information correlated with IT cortex contributes to object perception in the sense that what is stored in (or correlated with) IT are 3D structures whose *top-down interaction* with incoming information from striate cortex assists in establishing shape assignment ... Thus, the initial retinotopically organized V1 embodies information that operates as salient cues (e.g., shape from shading), causing feedback from 3D structures stored in IT ... The visual information that interacts between V1 and IT is organized by these spatial structuring capacities in order to assist in achieving shape assignment. ... neural activity in IT cannot be the sole mechanism that underlies visual consciousness of objects. [...] *Intermediate-Level Spatial Structuring* ... our ability to bind color [V4/V8/VO] to shape [IT] relies, in part, upon a spatial structuring capacity at the intermediate level. [...] IHS implies that visual consciousness depends upon feedforward to feedback interactions of information from lower areas to higher areas [...]. IHS holds that consciousness emerges in connection with information implemented upon suitably organized biological systems” (Bold mine).

From above, one could argue that processes related to *interactive hierarchical structuralism* might produce IHS related mitochondrial processes because mitochondria are the sources of most of neural processes.⁶ This could be the energetic basis of binding of various features, such as color, shape, motion and so on. This is because each cell has mitochondria for supplying energy to cell. V1 has specific mitochondrial-rich retinotopic structures. The relation between the spatial properties of retinal images, the spatial properties laid out on the surface area of V1, and mitochondrial-rich retinotopic structures in V1 is a relation of structural coherence. V2 has smaller riches of specific mitochondrial-rich retinotopic structures. Further extrastriate areas must have mitochondria for supplying energy. Retinotopic is the property of receptive fields (RF). RFs increase and retinotopy decreases as we go from V1 to V2 to V4 to IT (*shape recognition*) to GF. The face recognition area GF has almost no retinotopic because RFs are very large, but GF neurons must have mitochondria for supplying energy. In other words, both neural synchrony hypothesis and IHS may have mitochondrial energetic basis.

16. Summary

Our argument is concisely summarized as follows. Without V1 representation:

- There is the absence of synchronized (*coupled*) powerful mitochondrial energetic processes (the highest density of neurons – the highest mitochondrial (cytochrome oxidase) energetic activity – in neocortex is found in V1).
- There is the absence of adequate duration of (*subliminal*) information representation.
- There is the absence of feed forward and feedback (*from higher to lower order areas*) iterative/recursive processes that is essential for the conscious identification of an object.
- There is the absence of structural condition (*lack of well organized retinotopic V1, respecting the topological distribution of photon stimuli on the retina*).

In the lack of V1 area, visual signals can still reach several extrastriate parts but appear incapable of generating normal conscious visual experiences. Here, we pointed out that synchronized (*cou-*

⁶ IHS is based on the emergentism hypothesis that is materialism, and has a number of problems including not closing the explanatory gap between experiences and their respective neural correlates (Vimal, 2010b).

pled) mitochondrial processes, duration of visual representation (that is also needed to the feedforward and feedback iterative/recursive processes), and specific mitochondrial-rich retinotopic structures in V1 are elementary conditions for the emergence of explicit conscious visual perception. We presented several arguments and new point of view about that these fundamental demands could be guaranteed mainly by the primary visual cortex. However, it is hardly accidental that the highest density of neurons in neocortex (number of neurons per degree of visual angle) devoted to representing the visual field is found in V1. Namely, the highest mitochondrial (energetic) activity can be achieved in mitochondrial cytochrome oxidase-rich V1 areas.

In addition, since mitochondria are not only mere cellular energy sources but can act as metabolic and redox hubs as well as fundamental integration centers of cellular signaling pathways, and they have essential roles in cellular and neurocellular computational processes, we also suggested that mitochondrial networks could reflect the sensory information within neurons during representation processes.

We also pointed out that residual brain states of early visual areas are not fully reflected in active neural patterns after visual perception. That is, subliminal, residual states are not being reflected in passive neural recording techniques, but require active stimulation to be revealed. Consequently, mitochondrial-rich retinotopic V1 (early visual areas) structures are not only elementary conditions for the emergence of explicit conscious visual perception, but can also maintain subliminal visual representation for several seconds after visual perception.

Conflict of interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

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