Activation of retinotopic visual areas is central to REM sleep associated dreams: Visual dreams and visual imagery possibly co-emerged in evolution

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Abstract

The latest experimental results support that multiple retinotopic visual systems play a central role not only in the processing of visual signals but also in the integration and processing of internally represented auditory and tactile information. These retinotopic maps have access to higher levels of cognitive processing, performed by the frontal lobes, for example. The occipital cortex may have a special role in multisensory integration. There is a functional basis for the development and maturation of visual memory in association of rapid eye movement sleep (REMS) which is linked to dreams and visual imagery. Physiological and psychological processes of REMS are similar to waking visual imagery. Furthermore, visual imagery during REMS utilizes a common visual neural pathway similar to that used in wakefulness and during dreams expressed during REMS. This pathway subserves visual processes accompanied with auditory experiences and intrinsic feelings. We argue that the activation of the retinotopic visual areas is central to REM sleep associated dreams and that REMS associated dreaming and visual imagery may have co-evolved in homeothermic animals during evolution. We also suggest that protoconscious state during REM sleep, as introduced by Hobson many years ago, may be a basic visual process.

Introduction

It is well known that numerous retinotopic visual pathways are activated during visual perception and imagery. We argue and propose that such a pathway is retraced during visual component of dreams associated to REMS (rapid eye movement sleep) in particular. We also propose that activation of visual areas, V1 in particular, may play a central role in processing and integrating internally represented information with higher level of cognitive processes.

Our arguments support the broad notion that essentially the development and maturation of visual system and visual memory have co-evolved in association with REMS associated visual dreams and associated with REMs (rapid eye movements). We also point out that protoconscious state during REM sleep, proposed by Hobson, may be essentially a visual process.

Additionally, we think, that consequent upon development of vivid replay of visuals (dreams) during sleep, the atonia of the antigravity muscles associated to REMS has followed the development of REMs in evolution to provide protection from physical injury to the dreamer at least.

Finally, we dispute that while children and people are watching TV their eye movement variability is significantly reduced (gaze), which can increase the latency of subliminal visual representation in visual areas and which may increase the appearance of colors in REM dream pictures.

Brief description of neural basis of REMS regulation

The group led by Hobson (Hobson, McCarley, & Wyzinski, 1975; McCarley & Hobson, 1971) first proposed the existence of reciprocal inhibitory interactions between monoaminergic REM-OFF and cholinergic REM-ON neurons in the pontine brainstem for the regulation of REMS (reviewed by Pal & Mallick, 2007). However, this idea of direct inputs from the cholinergic REM-ON neurons on to the adrenergic REM-OFF neurons was questioned because acetylcholine did not inhibit the latter (Egan & North, 1985; Mallick, Kaur, & Saxena, 2001). Mallick's group finally showed the involvement of GABA in inhibiting the REM-OFF neurons for the generation of REMS (Mallick, Kaur, & Saxena, 2001; Jha & Mallick, 2011). Pal, Madan, and Mallick (2005) have proposed that cessation of REM-OFF neurons is a pre-requisite for REMS regulation. In addition, REMS may be controlled by several means including activation of kainate receptors in the brain stem pedunculopontine tegmentum (PPT) of the cat and rat (Datta, 2000) and modulation of pontine nucleus oralis (Lydic, Douglas, & Baghdoyan, 2002).

On the other hand, aminergic and GABA-ergic modulation of cholinergic REM-ON neurons in the PPT and their interactions have been shown in recent years (Pal & Mallick, 2006; Pal & Mallick, 2009). Notwithstanding, these REMS related neurons may be modulated by several regions in the brain including wakefulness as well as non-REMS generating areas in the brainstem and in the basal forebrain using varieties of neurotransmitters including serotonin, noradrenalin, acetylcholine, GABA, glutamate, orexin and so on, which have been reviewed and discussed in detail recently (Saper et al., 2010; Lu, Sherman, Devor, & Saper, 2006; Mallick, Pandi-Perumal, McCarley, & Morrison, 2011). Based on current knowledge, Figure 1a shows the REM sleep initiation via activation of brain stem processes.

Retinotopic visual representation

About 90% of the fibers from the optic tract reach the visual cortex via the retinotopic lateral geniculate nucleus (LGN) whereas, the rest about 10% of the fibers project to the retinotopic superior colliculus and pretectal areas (Chan et al., 2011; Chen, Zhu, Thulborn, & Ugurbil, 1999). In the visual system there are many retinotopically organized areas such as V1 (striate), V2, V3, V4, V5/MT+, V7, V8, VO, LO1, and LO2 (Larsson & Heeger, 2006; Gardner, Merriam, Movshon, & Heeger, 2008). Recently, Slotnick (2010) provided evidence for the existence of retinotopic areas in frontal- and parietal- cortex during spatial attention and working memory. In addition, retinotopic fMRI activity was localized in the frontal cortex eye fields (Slotnick, 2010). These retinotopic visual projections are likely to perform some important function during visual perception and imagery which is reenacted during visual component of dreams associated to REMS in particular.

According to Slotnick (2010), "*The existence of retinotopic maps in higher cortical regions, particularly in the frontal cortex, during spatial attention and working memory, challenges the long held view that only visual sensory regions have retinotopic organization and suggests other tasks might also produce comparable retinotopic maps in frontal- and parietal- cortex.*"

Based on their recent fMRI results Golomb and Kanwisher (2011) state that "*..despite our subjective impression that visual information is spatiotopic, even in higher level visual cortex, object location continues to be represented in retinotopic coordinates*". They also argued that there is a no explicit, hard-wired spatiotopic representation in the brain and the spatiotopic object position can be computed not directly and continually reconstructed by each eye movement.

Special role of the occipital cortex in the multisensory integration

Traditionally, perception has been considered as a modular function with different sensory modalities operating basically as independent process and multisensory integration have been assigned to higher-order brain areas (Jones & Powell, 1970). However, recent experiments provided evidence that visual, auditory and somatosensory integrations occur concurrently at several levels along brain pathways (Giard & Peronnet, 1999; Macaluso & Frith, 2000; Calvert, Spence, & Stein, 2004; Budinger, Heil, Hess, & Scheich, 2006). According to Vasconcelos et al. (2011), "*Neurons with cross-modal responses in primary sensory areas probably act as information hubs that regulate multisensory cortical recruitment under various regimes of sensory stimulation*". This view may be strongly supported by the latest findings that many visual areas including V1 can be activated by tactile and auditory inputs in blind as well as individuals with normal-vision (Calvert, Spence, & Stein, 2004; Burton, Sinclair, & McLaren, 2004; Voss et al., 2008). Muckli (2010), in his recent review, based on latest fMRI findings claimed that V1 region could be involved in higher cognitive functions. These findings support the notion that activation of visual areas may play a fundamental role in processing of visual, auditory and tactile information that are linked to higher level of cognitive functions and the visual experiences are most common fundamental property associated to dream (Nir & Tononi, 2010). Therefore, we argue that the visual activation of retinotopic areas is likely to be a fundamental associated factor for dreaming.

Activation of retinotopic V1 area during visual imagery and dreams associated to REMS

There is a long-standing dispute in cognitive science regarding visual imagery between Kosslyn's pictorial theory (1994) and Pylyshyn's (2003) tacit knowledge explanation. Kosslyn's pictorial concept argues that visual mental imagery exploits top-down neural pathways to generate visual imagery in the retinotopic striate and extrastriate parts. The visual system processes these representations as if they were visual percepts. Pylyshyn claimed (2003) that the activation of early visual areas is an epiphenomena during visual mental imagery. Namely, mental imagery may be explained by language-like representations and reduced to the tacit knowledge used in general thinking. Explicitly, we represent objects more abstractly in a symbolic/propositional format compared with the analog or depictive format suggested by pictorial theory. Notwithstanding, although increasing evidence indicates that visual perception and imagery share very similar neural substrates, and that both visual perception and imagery induce activation in retinotopically organized striate and extrastriate areas (Cichy, Heinzle, & Haynes, 2011; Broggin, Savazzi, & Marzi, 2011; Lewis, Borst, & Kosslyn, 2011; Stokes, Thompson, Cusack, & Duncan, 2009), the imagery dispute is still unsolved.

Visual cortex has been reported to be activated during REMS, however, there are some inconsistencies among the findings in the literature about whether there is activation of V1 during REMS (Braun et al., 1998; Peigneux et al., 2001; Igawa et al., 2001). The controversy about the activation of V1 during REMS associated dreams may be due to difference in tasks, baseline conditions and methods of analysis used in various studies. However, REMS visual imagery uses very similar neural systems as those used in wakefulness (Nir & Tononi, 2010; Sprenger et al., 2010). Nevertheless, recent event-related fMRI showed activation of V1 during REMS (Hong et al., 2009; Miyauchi et al., 2009) and the findings that REMS associated visual imagery uses very similar neural systems as those used in wakefulness (Nir & Tononi, 2010; Sprenger et al., 2010) support our contention.

Visual imagery and visual REM dream without V1?

It is well known that early visual stimulation, during critical period, is essential for normal development of visual function and imagery as well as for visual REM dream (Kozma, Kovács, & Benedek, 2001).

One may argue, for example, that subjects with lesions in the visual association cortex experience loss of visual imagery during dreams and loss of capacity to conjure up visual imagery in the awake state (Solms, 1995; 1997), but patients with lesions in the striate cortex have reported to preserve visual imagery in dreams and wakefulness (Stoerig, 2001; Kleiser et al., 2001; Silvanto & Rees, 2011; Bridge et al., 2011). However, we should emphasize that our presented notions in this paper are related to normal healthy subjects with intact V1 and not to the many exceptional subjects with very diverse V1 damages, lesions, excisions, and malfunctions, which still need confirmation.

In addition, it is possible that it is not the most important issue if V1 can be activated during visual imagery or during visual REM dream, because in exceptional V1 cases, there are many possible mechanisms bypassing or helping V1 such as compensation, neural reorganization, preserved "islands" in V1 (geniculostriate visual pathway), projections to the superior colliculus and pulvinar that can provide indirect visual input to the extrastriate areas (retinotectal visual pathway) (Fendrich, Wessinger, & Gazzaniga, 1992; Danckert & Rossetti, 2005), and at present still unknown V1 bypassing visual pathways.

The retinotopic superior colliculus and the pretectum may be important in determining the onset of NREMS, REMS, and wakefulness in mammals

The optic tectum (or tectum) is a paired structure that is one of the major components of the vertebrate midbrain. In mammals, optic tectum is usually called the superior colliculus (SC). The SC is a subcortical laminar structure in the mammalian midbrain that projects to numerous brain regions, including periaqueductal gray, thalamus, cortex, brainstem and spinal cord (Albers, 1990). As a result, the midbrain tectum is in a key position to initiate behavioral responses to sensory stimuli. The SC performs complex multisensory integrations (Alvarado et al., 2009) and transforms both visual and non-visual sensory signals into motor commands that control orienting behaviors. The upper layers of the SC are visual and in the deeper layers most of the cells respond to combinations of visual, auditory and tactile stimuli. Its superficial layers obtain visual signals from the retina in the precise retinotopic/topological manner (Chan et al., 2011). The single major afferents to the SC are visual, which however, originate from two sources one from the retina and the other from the V1; interestingly both the retina and the retinotopic SC project to the retinotopic LGN.

The eyes scan dream images during REMS

It has been proposed that the visuals (images) during the dream stage possibly originate from long-term visual memories following the pathway, which helped visual information processing, however, in a reverse order than that of image processing for memory formation (Cantero, Atienza, Salas, & Gómez, 1999; Ogawa, Nittono, & Hori, 2006). According to Braun et al. (1998), the brain mechanisms underlying REMS are visual association cortices and their paralimbic projections, operating as a closed system dissociated from the regions of the visual hierarchy, which mediate interactions with the external world. During REMS associated dreams appearance of REMs may reflect replaying visual information (Leclair-Visonneau et al., 2010). This relationship between the REMs and dream imagery of REMS has been known as the scanning hypothesis (Eiser, 2005).

Recently, Hong et al. (2009) confirmed the REM-locked activation in the striate cortices. According to Hong et al. (2009), "*Our findings suggest that the sharing in waking* *and dreaming goes beyond the expected visual scanning mechanism; it extends to the distributed sensory-perceptual processing of the visual information obtained by the scanning. These findings are consistent with the revised scanning hypothesis which implies that REMs are visually targeted saccades and proposes that REMs scan what we 'see' when dreaming".*

Solms writes (2007) in a recent book: "*The prevailing view is that imagery of all kinds (including dream imagery) is generated by `projecting information backward in the system' (Kosslyn, 1994, p. 75). Accordingly, dreaming is conceptualized as `internally generated images which are fed backwards into the cortex as if they were coming from the outside' (Zeki, 1993, p. 326).*"

According to Dement and Kleitman (1957), the REMs during REMS are binocularly synchronous and are similar to waking fixational eye movements. The differences in the eye movements during REMS and wakefulness (Aserinsky et al., 1985), suggest that their neural mechanism(s) of generation may be different.

However, REM-associated activation of the SC suggests that REMs are visually targeted (Leigh & Zee, 2006). In addition, precise retinotopic upper layers in the SC may be necessary to scan intrinsic visual dream images because visual dream images are also emerged in retinotopic visual areas during REMs.

The PGO waves

The PGO waves appear seconds before and during REMS. These waves are phasic neural electrical bursts that start in the pons and progress to the LGN and terminate in the V1. Recently, Miyauchi et al. (2009) presented evidence for the existence of PGO waves in human REMS and demonstrated that activity in the pontine tegmentum, ventroposterior thalamus, and V1 took place in the few seconds prior to REM saccades. They proposed that REM saccades may be in response to PGO-initiated dreamed visual imagery, because V1 activation is arisen some seconds before REM saccades. It seems that one of the most important events during REMS is activation of retinotopic visual areas and REMS associated dreams are primarily accompanied with visual replay (Hobson, 1988).

Activation of retinotopic areas as a central function of REMS associated with dream

Dream reports include various sensations across different sensory modalities. According to dream reports the most common sensory modality experienced during dreams is vision. Practically all dreams invariably contain at least one visual component, audition is associated with 40–60% of dreams, movements and tactile sensations appears with 15–30% of dreams, while smell and taste are hardly associated with dreams (1%) (Calkins, 1893; Strauch, Meier, & Foulkes, 1996). So, dreams expressed during REMS are first and foremost intrinsic visual processes accompanied with intrinsic auditory experiences and intrinsic feelings (Nir & Tononi, 2010), and all these intrinsic experiences originate from the long-term memories.

It seems that visual imagery during REMS utilizes, to a certain extent, common visual neural pathway as those used in wakefulness (Cantero, Atienza, Salas, & Gómez, 2000; Hong et al., 1995; Nir & Tononi, 2010). However, complex retinotopic visual can serve some special function not only during visual perception and imagery but also during REMS associated visual dreams. Since, it appears that numerous retinotopic visual areas are activated during REMS (Igawa et al., 2001; Peigneux et al., 2001; Hong et al., 2009; Miyauchi et al., 2009), it suggests that one of the major aims of REMS is to activate visual imagery directed via subconscious processes. Based on present knowledge, the neuro-anatomo-chemical substrates in the brain for activation of REMS-associated expression of visual imagery may be supported by the diagram shown in Figure 1a and 1b.

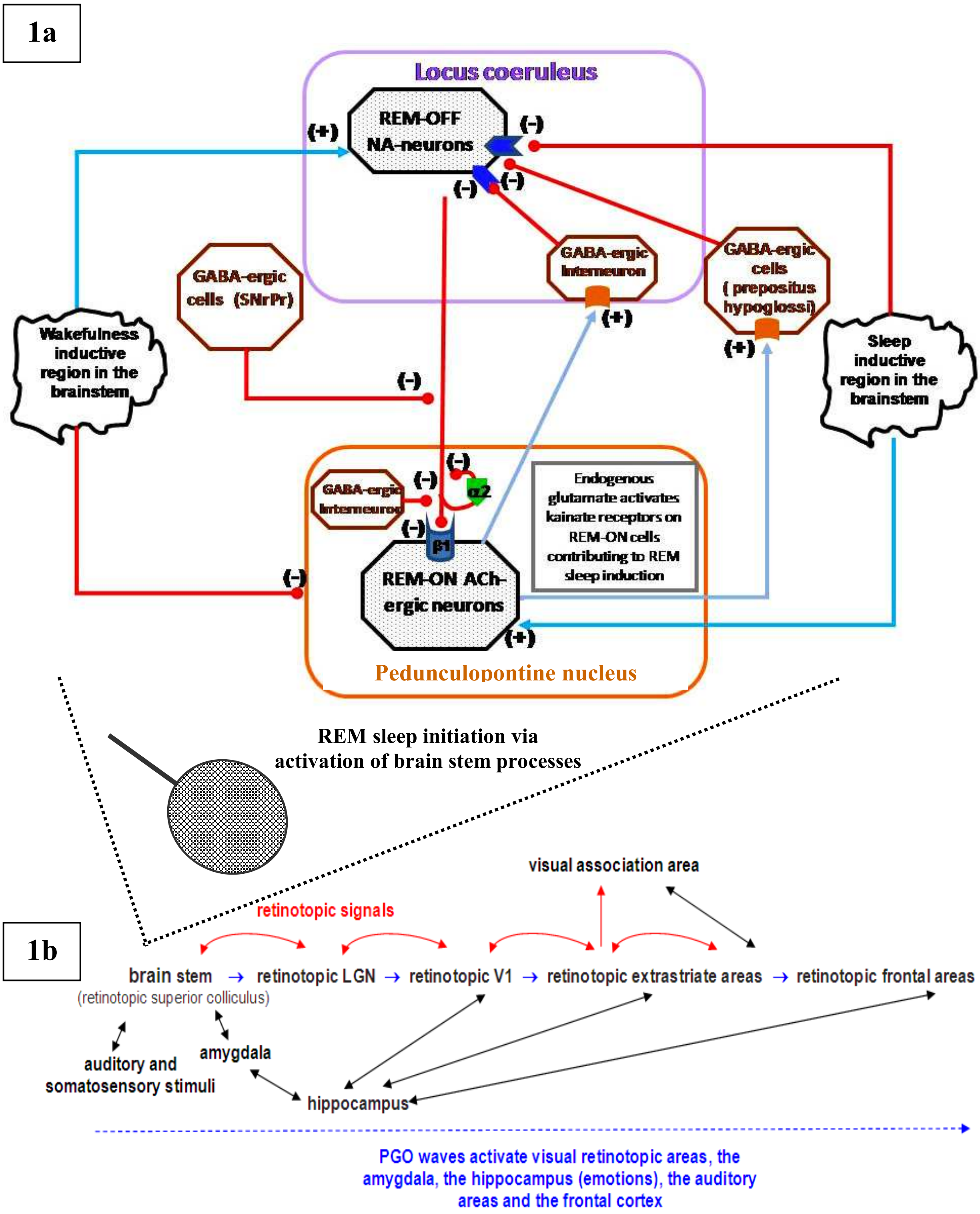

Figure 1. a. REM sleep initiation via activation of brain stem processes.
b. The activation of retinotopic areas as a central function of REM dream.

Kubota et al. (2011) reported that activation of the dorsolateral prefrontal cortex closely coincided with the onset of the REMS. The authors suggested that this can play a role in cognitive processes associated to REMS at least in humans. Recent findings from fMRI experiments proved that not only extrastriate but also primary visual cortex (V1) can be activated in relation to REMS (Hong et al., 2009; Miyauchi et al., 2009). In addition, Muckli (2010) based on latest fMRI findings suggested that V1 can be involved in higher cognitive functions. Because both the low level V1 and higher prefrontal areas may perform higher cognitive functions, and there are retinotopic areas not only in V1 and in extrastriate areas but also some retinotopic areas in the prefrontal cortex (Muckli, 2010; Slotnick, 2010), it is plausible that higher level retinotopic areas cooperate with lower level retinotopic visual activity.

During postnatal critical period in the development of the visual system, external sensory signal robustly affect the maturation of synaptic connectivity. Latest experiments by Shaffery et al. (2012) support that both endogenous REMS-generated activation of the visual system and exogenous sensory stimulation of visual system are necessary for normal termination of critical period synaptic plasticity.

The visual cortex in normal-sighted persons can also be activated by auditory signals or during tactile discrimination tasks. Hall and Lomber (2008) recently identified direct projections from tonotopically organized auditory cortex to the retinotopic visual V1 and V2 in adult cats.

All these together may imply that retinotopic visual areas play fundamental roles in the multisensory integration. Since the visual imagery and visual dreams originate from the long-term visual memory, activated visual retinotopic areas in association with visual REMS may also play a central role in processing and integration of represented visual, auditory and tactile information, while these are linked to superior level cortical functions.

Superior colliculus may play an essential role in integrating as well as reviewing the visual information and the generation of PGO waves in REMS

In a few non-mammalian vertebrates, for example, fish and birds, the tectum is one of the largest areas in the brain. In mammals (particularly in primates) the substantial expansion of the cerebral cortex may be linked to significant decrease in the size of the tectum, the seat of SC. Although the size of the tectum decreased along with evolution, the SC retained several functions. Therefore, in higher species it possibly acquired new roles including multisensory integration (Alvarado et al., 2009) for example and visual information processing is most important function of this area. The visual system, particularly the retinotopic SC-circuit (Chan et al., 2011), is intensely activated during REMS (Cohen & Castro-Alamancos, 2010), and all dreams essentially have visual experiences (Nir & Tononi, 2010).

Sprenger et al. (2010) recently studied kinematic parameters of REMs during REMS and suggested that REMs may be related to exploratory saccadic behavior during awake to remember visual stimuli. They also mentioned that "*..we cannot exclude that the oculomotor system and the PGO wave system are activated in parallel inducing simultaneous eye movements and limbic and cortical activations*". In addition, Miller, Obermeyer, Behan, and Benca (1998) proposed that the (retinotopic) pretectum and the (retinotopic) SC may be important in determining the onset of NREMS, REMS and wakefulness in mammals.

Based on the findings mentioned above, especially with reference to SC, it is possible that it plays an essential role in integrating as well as reviewing the visual information and the generation of PGO waves may be an associated phenomenon. Since, this process is expressed during REMS, REMs and PGO waves are associated to REMS.

REMS dream and visual imagery may have co-evolved in evolution

REMS and NREMS states are not clearly separated processes in human embryos, and typical REMS appears only in 1-2 month after birth (Karlsson & Blumberg, 2003). It is probable that adult-like consciousness dream can be emerged and linked to REMS when brain maturity and language acquisition make conscious narrative reports possible about dreamed subjective experiences in REMS (Hobson, 2009).

It is unlikely accidental that parallels may be drawn between development of REMS associated visual dream and visual imagery in children. Preschool children's dreams have a static nature and they also have an absence of movement during visual imagery (Domhoff, 2001). It seems that visual imagination may develop progressively and be required cognitive prerequisite for dreaming (Domhoff, 2001). There are also no autobiographic, episodic memories in preschool children. Preschool children can make naturalistic pictures, draw figures that have distinct phosphene and form constant-like characters. Verbal and linguistic abilities do not play a role until dreaming is wholly developed (Foulkes, 1999). According to Lehmkuhl and Frölich (2004), "*…dreams being complex cognitive processes which* *differentiate increasingly and are not only automatic perception which is found in sleep laboratory studies conducted with children*."

In the mental rotation task (Shepard & Cooper, 1982), reaction time of adult subjects increased linearly with the degree of rotation, but children did not demonstrate this relationship and they could not mentally imagine movement by means of visuo-spatial imagery. This is essentially similar to children's dream reports without movements (Foulkes, 1999). According to Nir and Tononi (2010), "*Overall, dreaming appears to be a gradual cognitive development that is tightly linked to the development of visual imagination*."

People who went blind around the age of 5–7 generally have visual imagination and visual dreams throughout life (Hollins, 1985; Büchel, Price, Frackowiak, & Friston, 1998). In contrast, for people who went blind before the age of 5, usually there is absence of visualization in waking and dreaming. In addition, because color representation originates from the long-term visual memory and that congenital blind people are unable to dream in color, it suggests that the long-term visual memory is the common source of dreams pictures as well as visual imagery in normal individuals.

Recent fMRI results showed that V1 striate cortex is activated in association with REMS (Hong et al., 2009; Miyauchi et al., 2009). Besides, the visual imagery that we see in our dreams can help stimulate our visual system for that it can develop properly and visual imagery utilizes very similar neural systems as those used in wakefulness during REMS (Cantero, Atienza, Salas, & Gómez, 2000; Hong et al., 1995; Nir & Tononi, 2010).

REMS associated dreams have a high amount of narrative and dream imagery is not generated by random activation of the forebrain, but rather by forebrain mechanisms with dreams and complex cognitive processes (Solms, 2000). We can see our dreams from first-person perspective, indicating that dreams are a feature of consciousness.

According to Hobson (2009), "*...REM sleep may constitute a protoconscious state, providing a virtual reality model of the world that is of functional use to the development and maintenance of waking consciousness*". Since the activation of retinotopic visual areas may be one of the most important functions of REMS that can stimulate our visual system development, the protoconscious state may be essentially linked to retinotopic visual areas in evolution. Our notion, that the protoconscious state may be necessarily linked to retinotopic visual areas, can be supported by new results, i.e., the low level V1, V2 areas may achieve higher cognitive functions, and there are some retinotopic areas in the prefrontal cortex

(Muckli, 2010; Slotnick, 2010). As a result, the protoconscious state (Hobson, 2009) may be essentially visual process.

Recently, we have suggested that characteristics of homeothermic state (*homeotherm animals are from birds to mammals with constant and relatively high body temperature*) make the development of explicit memory possible (Bókkon, 2005). Both REM phase of sleep and the homeothermic state probably co-developed in evolution (Jouvet, 1992). Unlike in homeotherms, the brain cells continuously divide throughout life in poikilotherms (*poikilotherm organism, such as a fish or reptile, having a body temperature that varies with the temperature of its surroundings*) (Jouvet, 1992; Paton & Notthebohm, 1984) however, in exchange complex everlasting neuronal connections are developed in the former. A structured and restricted neuronal network is necessary to develop long-term explicit memory, because it can guarantee specificity as well as distinct oriented recruitment of neurons which also give rise to a strong synchronization (coupled) of neural signals resulting in increased signal/noise ratio in the brain. It is probably therefore, explicit memory has emerged first in homeotherms (Bókkon, 2005). For example, a Gabonese grey parrot could memorize 1200 words similar to a five-year old child (Griffin, 1982; Pepperberg 1999). Emergence of REMS is particularly important in humans, because it could guarantee a functional connection between implicit and explicit information of the brain (Bókkon, 2005). According to Fischer et al. (2011), "*.. sleep does not benefit the forgetting of unwanted memories but, on the contrary, REM sleep might even counteract the voluntary suppression of memories making them more accessible for retrieval".* However, it is probable that protoconscious state, suggested by Hobson (2009), may be emerged from implicit memory (Bókkon, 2005) in homeotherms during evolution of REMS and this state may be basically visual process.

Finally, physiological and psychological processes of REMS are similar to waking visual imagery (Cantero, Atienza, Salas, & Gómez, 2000; Ogawa, Nittono, & Hori, 2006; Lliná & Ribary, 1993; Gottesmann & Gottesman, 2007). All these together support our contention that there is essentially functional basis for the development and maturation of visual memory in association of REMS associated dreams and visual imagery. This suggests that possibly REMS associated dreams and visual imagery may co-evolved in homeothermic animals in evolution.

REMS associated muscle atonia

The classical REMS associated muscle atonia possibly has evolved to prevent the subject enacting physical activities during visual experience of dreams associated to REMS. Interestingly, although atonia is experienced by the antigravity muscles, the muscles responsible for REMs during REMS are not paralyzed. Although we do not know the precise reason for development of such inverse relationship between muscle activities in evolution, based on our hypothesis it may be safe to propose that the REMs probably play an important physiological role and that could be visual memory consolidation. This view may be supported by the fact that during REMS ponto-geniculo-occipital (PGO) waves are expressed in association with REMs (Conduit, Crewther, & Coleman, 2004) and expressions of PGO waves have been correlated with memory processing (Datta, 2000; Datta, Li, & Auerbach, 2008). However, Pontine-waves (P-waves) (the pontine component of ponto-geniculo-occipital waves) can be involved in numerous significant brain functions, such as memory consolidation as well as development of the hippocampus, amygdala and visual system (Dang-Vu, Desseilles, Peigneux, & Maquet, 2006; Frank, Issa, & Stryker, 2001; Datta, 2006; Guzman-Marin & McGinty, 2006). Based on these views we propose (pending confirmation) that REMs associated to dream experience is likely to have evolved first which was followed by evolution of REMS associated muscle atonia in antigravity muscles as a complementary mechanism to prevent personal injury to the subject in case of enactment of physical behavior during dreams; the latter is due to replaying of visual imagery for memory consolidation. This view may be supported by the fact that muscle atonia is the only peripheral signs expressed associated unlike EEG, EOG, PGO, hippocampal waves, which are controlled by the central nervous system.

Colors in dreams

The appearance of colors in dreams also indicates the importance of the visual processes in REMS. However, there are inconsistent reports on colored dreams (Schwitzgebel, 2002). It is questioned that differences in the reported color of dreams can be attributed to the influence of black and white/or color media, or to methodological issues. However, recently, British psychologist Eva Murzyn (2008) concluded that people, who watched only black-and-white TV as children and those older than 55 years of age during study period, reported dreaming in gray-scale more often than children raised watching color television. One may argue that people use their ocular inputs for things other than just TV. Children and people don't watch TV all day, a higher percentage of their awake time is spent viewing the world around them which is in color. However, this argument is not convincing because while children and people are watching TV their eye movements variability (gaze) are reduced that can increase the latency of subliminal visual representation (*i.e. early retinotopic areas able to sustain rich detailed, subliminal visual information for several seconds after visual perception*) (Bókkon et al., 2011; Bókkon & Vimal, 2012 submitted).

This increased latency of subliminal visual representation by gaze can be supported by Silvanto, Muggleton, Cowey, & Walsh (2007) experiments. Recently, Silvanto et al. (2007) induced phosphenes into afterimages (*Creating a vivid negative afterimage requires a steady gaze on the external object or on the computer/TV monitor.*). Explicitly, after 30 sec visual adaptation to a homogeneous color, Transcranial magnetic stimulation (TMS) was applied on the occipital cortex that could elicit phosphenes that took on the color qualities of the adapting color. For example, if voluntaries were adapted to a green color, they perceived a red negative afterimage into which the TMS could induce green phosphenes. The negative afterimages lasted about 69 sec. However, phosphenes induced into afterimages persisted for 91 sec, meaning that the information of perceived visual color (*after 30 sec visual adaptation to a homogeneous color*) was not consciously (subliminal) represented for 91 sec in early visual areas. These findings may support that during watching TV (or computer monitor), the gaze can increase the latency of not consciously (subliminal) visual representation in early visual areas and as a result, color representation may get more pronounced role in the short-term as well as in the long-term visual memories, which may produce an enhanced color appearance in dreams.

According to Hoss (2010), "*The natural waking experience certainly appears to influence the natural colors making up a dream scene (grass is typically seen as green, and sky is typically seen as blue for example). Many elements of the dream however, such as cars, clothes and such, have no pre-determined color assignment from our waking environment and can be almost any color, and sometimes it can be quite un-natural (a blue dog for example)". "The conclusion from the observed data was that the specific colors recalled from a dream is not dominated by the waking visual experience nor by personal preferences, but rather dream color appears to align with neurological mechanisms involved in the perception of color as well as psychological factors including the human emotional response to color."*

In brief, natural viewing the surrounding color world is not the same neural process as the gaze during watching TV. Thus, the increased appearance of colors in dreams may be attributed to the influence of color media on visual perception as well as visual representation.

However, several elements of the dream are not pre-determined color assignment from our waking environment.

Summary and Conclusions

We should emphasize again that our presented notions in this paper are based on findings on healthy subjects with intact V1 and not on findings from exceptional (including diseased) cases, which are controversial and still need confirmation.

Briefly summarized important thoughts as shown below may have highlighted an essential relationship between the REM visual dream and the visual imagery:

- There is multiple retinotopic visual system in the brain.
- Occipital cortex may have a special role in the multisensory integration processes in the brain.
- Recent fMRI experiments proved that not only extrastriate but also primary visual cortex (V1) is activated in relation to REMS.
- The retinotopic PT and the SC areas may be important in determining the onset of NREMS, REMS, and wakefulness in mammals.
- SC may play an essential role in integrating as well as reviewing the visual information and the generation of PGO waves.
- The revised scanning hypothesis implies that REMs are visually targeted saccades and proposes that REMs scan what we ‘see’ when dreaming”.
- The precise retinotopic upper layers of the SC may be necessary to scan intrinsic visual dream images because visual dream images are also emerged in retinotopic visual areas during REMs.
- Dreams expressed during REMS are first and foremost intrinsic visual processes accompanied with intrinsic auditory experiences and intrinsic feelings.
- Visual imagery during REMS utilizes, to a certain extent, common visual neural pathway as those used in wakefulness.
- Latest experiments support that both endogenous REMS-generated activation of the visual system and exogenous sensory stimulation of visual system are necessary for normal termination of synaptic plasticity in postnatal critical period.
- There are parallels between development of REMS associated visual dream and visual imagery in children.
- Physiological and psychological processes of REMS are similar to waking visual imagery.
- Since the activation of retinotopic visual areas may be one of the most important functions of REMS that can stimulate our visual system development, the protoconscious state may be essentially linked to retinotopic visual areas in evolution.
- Emergence of REMS in homeotherms is particularly important in humans, because it could guarantee a functional connection between implicit and explicit information of the brain.

- Protoconscious state, suggested by Hobson, may be emerged form implicit memory in homeotherms during evolution of REMs.

We have presented numerous experimental and theoretical results to support that the multiple retinotopic visual system may play essential roles not only in the processing of visual signals but also in the integration and process of represented auditory and tactile information, among them, which are connected to the higher level of cognitive mechanism through the visual system. Namely, the occipital cortex may bear a particular role in the multisensory integration processes in the brain.

The visual information is not routed through the brainstem reticular formation, which is active during waking while it is largely inactivated during sleep. Nevertheless, a specific group of neurons, the REM-ON neurons in the brainstem (among them neurons in the retinotopic superior colliculus (SC) and the pretectum (PT)), are active during rapid eye movement (REM) sleep (REMS). It seems that the retinotopic PT and the SC areas may be important in determining the onset of NREMS, REMS, and wakefulness in mammals.

Considering these, here we proposed that multiple retinotopic visual areas in the brain may perform some special function not only in visual perception and imagery but also associated with visual experiences of dreams during REMS. We argued that the primary purpose of dreams associated to REMS especially appearance of REMs could be due to activation of retinotopic visual areas in the brain, because those inputs/signals would not be retrained otherwise because those inputs are not routed through the reticular formation.

Activation of the retinotopic lateral geniculate nucleus (LGN) can have a considerable role in processing and integrating of visual information, especially which are linked to higher level of cognitive functions. Since other sensory (e.g. auditory, smell and tactile) inputs/areas are not directly linked to visual inputs they are not prominently associated with dreams; however, association of these signals could be due to their indirect association. In addition, mostly the visual experiences are associated to dreams and there are parallels between development of REMS associated visual dream and visual imagery in children. As a consequence we proposed that development of REMs associated with dream in general and visual experiences in particular might have co-evolved for effective memory consolidation especially in relation to visual image processing.

Recently, 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 from implicit memory in homeotherms during evolution of REMS. We also suggested that REM protoconscious state may be essentially visual-based process.

The classical REMS associated muscle atonia was considered as a protection from physical injury of subject during visual experience of dreams associated to REMS.

Finally, we argued that during watching TV (or computer monitor), the gaze can increase the latency of not conscious (subliminal) visual representation in early visual areas and as a result, color representation may get more pronounced role in the short-term as well as in the long-term visual memories, which may produce an enhanced color appearance in visual REM dreams.

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Declaration of interest

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

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