



Location specific sleep spindle activity in the early visual areas and perceptual learning



Ji Won Bang^a, Omid Khalilzadeh^c, Matti Hämäläinen^b, Takeo Watanabe^a, Yuka Sasaki^{a,*}

^aLaboratory for Cognitive and Perceptual Learning, Department of Cognitive, Linguistic & Psychological Sciences, Brown University, 190 Thayer St, Providence, RI 02912, USA

^bAthinoula A. Martinos Center for Biomedical Imaging, 149 13th St, Charlestown, MA 02129, USA

^cDepartment of Radiology, Massachusetts General Hospital and Harvard Medical School, 55 Fruit St, Boston, MA 02114, USA

ARTICLE INFO

Article history:

Received 10 August 2013

Received in revised form 27 November 2013

Accepted 20 December 2013

Available online 29 December 2013

Keywords:

Visual perceptual learning

Consolidation

Sleep

Reactivation

Sleep spindle

Magnetoencephalography (MEG)

ABSTRACT

Visual perceptual learning (VPL) is consolidated during sleep. However, the underlying neuronal mechanisms of consolidation are not yet fully understood. It has been suggested that the spontaneous brain oscillations that characterize sleep stages are indicative of the consolidation of learning and memory. We investigated whether sleep spindles and/or slow-waves are associated with consolidation of VPL during non-rapid eye movement (NREM) sleep during the first sleep cycle, using magnetoencephalography (MEG), magnetic resonance imaging (MRI), and polysomnography (PSG). We hypothesized that after training, early visual areas will show an increase in slow sigma, fast sigma and/or delta activity, corresponding to slow/fast sleep spindles and slow-waves, respectively. We found that during sleep stage 2, but not during slow-wave sleep, the slow sigma power within the trained region of early visual areas was larger after training compared to baseline, and that the increase was larger in the trained region than in the untrained region. However, neither fast sigma nor delta band power increased significantly after training in either sleep stage. Importantly, performance gains for the trained task were correlated with the difference of power increases in slow sigma activity between the trained and untrained regions. This finding suggests that slow sigma activity plays a critical role in the consolidation of VPL, at least in sleep stage 2 during the first sleep cycle.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Our visual system remains plastic even after early postnatal development. This plasticity manifests itself, e.g., in visual perceptual learning (VPL), which is defined as a long-term performance improvement on a visual task after repeated experience (Sasaki, Nanez, & Watanabe, 2010). VPL is highly specific to the visual location of the trained stimulus (Crist et al., 1997; Fahle & Edelman, 1993; Fiorentini & Berardi, 1980; Karni & Sagi, 1991; McKee & Westheimer, 1978; Poggio, Fahle, & Edelman, 1992; Sagi & Tanne, 1994; Shiu & Pashler, 1992) and features of the stimulus (Ball & Sekuler, 1987; Fiorentini & Berardi, 1980; Koyama, Harner, & Watanabe, 2004; Poggio, Fahle, & Edelman, 1992; Schoups et al., 2001; Vaina et al., 1998; Watanabe et al., 2002). These perceptual specificities suggest that neuronal changes associated with VPL occur within visual areas, which are highly organized with respect to

location and feature. Previous studies have investigated the possible cortical sites of VPL and reported neuronal changes in the lowest areas of visual cortex, such as V1 (Hua et al., 2010; Li, Piech, & Gilbert, 2004; Schoups et al., 2001; Schwartz, Maquet, & Frith, 2002; Shibata et al., 2011) or higher-level visual cortical areas such as V4 (Adab & Vogels, 2011; Raiguel et al., 2006; Yang & Maunsell, 2004) and MT (Gu et al., 2010; Zohary et al., 1994). It should be noted, however, that the location specificity in VPL has become controversial in some cases (Xiao et al., 2008; Zhang et al., 2010a, 2010b) and sensory adaptation plays a critical role in location specificity (Harris, Glikberg, & Sagi, 2012).

It has been shown that consolidation of VPL occurs during sleep (Gais et al., 2000; Karni & Sagi, 1993; Stickgold, James, & Hobson, 2000; Stickgold et al., 2000; Yotsumoto et al., 2009). Karni and Sagi (1993) have demonstrated that learning of a texture discrimination task (TDT) does not improve after as much as 8 h of wakeful rest, but improves significantly after a full night sleep. Notably, research has shown that sleep must occur within 30 h of practice in order for subsequent performance improvements to develop (Stickgold, James, & Hobson, 2000). Sleep is a multifaceted process with distinct neuronal activity patterns nested within each sleep stage. Thus, it has been assumed that each sleep stage plays a different role in the consolidation of VPL (Stickgold et al., 2000).

* Corresponding author. Address: BOX 1821, Department of Cognitive, Linguistic & Psychological Sciences, Brown University, 190 Thayer St, Providence, RI 02912, USA.

E-mail addresses: ji_won_bang@brown.edu (J.W. Bang), o.khalilzadeh@gmail.com (O. Khalilzadeh), msh@nmr.mgh.harvard.edu (M. Hämäläinen), takeo_watanabe@brown.edu (T. Watanabe), yuka_sasaki@brown.edu (Y. Sasaki).

Sleep can be broadly categorized into non-rapid eye movement (NREM) sleep and rapid eye movement (REM) sleep: NREM sleep can be further divided into stage 2 and slow-wave sleep (SWS). According to Gais et al. (2000), the neuronal processes related to the early sleep period, which contains an abundance of NREM sleep and very little REM sleep, facilitate consolidation of VPL, whereas the later sleep period, which has abundant REM sleep, does not facilitate consolidation, if the later sleep period alone occurs. In addition, Yotsumoto et al. (2009) has shown that brain activity in the trained region of V1 during NREM sleep is significantly greater after training compared to before training. Interestingly, the brain activity within the trained region of V1 observed during NREM sleep was highly correlated with later performance improvements on the trained task. These studies suggest that NREM sleep plays a crucial role in the development of performance improvements. Notably, the latter study indicates that the consolidation processes of NREM sleep occur specifically within trained region of early visual areas.

However, the results so far obtained do not reveal which specific neuronal activities are specifically involved in the consolidation of VPL. There are two leading models which attempt to explain the neuronal mechanism of consolidation during sleep: an active system consolidation model (Born, Rasch, & Gais, 2006; Born & Wilhelm, 2012; Hasselmo, 1999; Rasch et al., 2007) and a synaptic homeostasis model (Tononi & Cirelli, 2003; Tononi & Cirelli, 2006). The active system consolidation model assumes that memory traces that are involved in learning are reactivated and redistributed during subsequent NREM sleep, so that synaptic connections in the neocortex are strengthened (Born, Rasch, & Gais, 2006; Born & Wilhelm, 2012; Hasselmo, 1999; Rasch et al., 2007). According to this model, the reactivation and redistribution processes are mediated by sleep spindle and slow-wave activity, which are the most prominent features of sleep stage 2 and SWS, respectively (Born, Rasch, & Gais, 2006; Born & Wilhelm, 2012). Sleep spindles are generated from the thalamic nucleus reticularis and spread to the entire neocortex (Steriade, McCormick, & Sejnowski, 1993), whereas slow-waves are primarily generated in the neocortex and extend to other areas such as the hippocampus and thalamus (Buzsaki & Draguhn, 2004; Steriade, 1999). Experiments have demonstrated that spike trains similar to spindle activity induce long-term potentiation (LTP) in cortical neurons (Rosanova & Ulrich, 2005). Research in humans has shown that spindle activity increases after intense learning of a declarative word pair task (Gais et al., 2002; Molle et al., 2009; Schabus et al., 2004; Schmidt et al., 2006) and a procedural motor task (Fogel & Smith, 2006; Morin et al., 2008). In addition, it has been shown that performance improvements on a trained task correlate with spindle activity in cortical areas primarily associated with the task: for example, the parietal cortex and a visuospatial task (Clemens, Fabo, & Halasz, 2006), the prefrontal cortex and a word pair task (Clemens, Fabo, & Halasz, 2005), and the motor cortex after a finger tapping task (Nishida & Walker, 2007). Slow-wave activity is also thought of as a signature of consolidation during sleep. Slow-waves temporally bind neuronal activity, including sleep spindles and ripples into depolarizing up-states during which neurons' firing rates increase to a level similar to a waking state (Steriade, 2006). Previous studies have shown that ripples and spindles nested in depolarizing up-states of slow-waves support LTP (Buzsaki, Haas, & Anderson, 1987; King et al., 1999; Rosanova & Ulrich, 2005). However, it should be noted that the role of slow-waves is still controversial; it has been shown that slow-waves with T-type Ca^{2+} influx lead to long-term depression (LTD) (Czarnecki, Birtoli, & Ulrich, 2007).

On the other hand, the synaptic homeostasis model proposes that global synaptic downscaling, which occurs during sleep, generates performance improvements after sleep as a by-product, and

does not necessarily support the existence of specific consolidation processes during sleep (Tononi & Cirelli, 2003; Tononi & Cirelli, 2006). According to this theory, synapses become potentiated as information is encoded in the brain during the waking state. Sleep then globally down-scales synaptic strength to an energetically sustainable level. As a result, weak synaptic connections are removed, and the remaining relatively strong synaptic connections are preserved. This process improves the signal-to-noise ratio of the encoded information and leads to memory enhancement. Slow-waves are assumed to be related to synaptic downscaling because slow-waves associated with Ca^{2+} channel activation induce LTD (Czarnecki, Birtoli, & Ulrich, 2007). There is some evidence to support the synaptic homeostasis model. A local increase in slow wave activity was found in cortical motor areas during sleep after a motor learning task, and this activity was correlated with performance gain (Huber et al., 2004). Subsequent research showed that slow wave activity was reduced when information encoding was prevented (Huber et al., 2006). This indicates that changes in synaptic strength are directly related to slow wave activity: greater synaptic strength is associated with greater downscaling.

It remains to be seen whether sleep spindles and/or slow-waves are involved in the consolidation of VPL, which is thought to involve early visual areas (Hua et al., 2010; Li, Piech, & Gilbert, 2004; Schoups et al., 2001; Schwartz, Maquet, & Frith, 2002; Shibata et al., 2011). Based on the aforementioned findings, this study aims to investigate which oscillatory activity plays a role in the consolidation of VPL, specifically within the first cycle of NREM sleep. To address this question, we trained subjects to perform a texture discrimination task (TDT) in one specific quadrant of the visual field, a paradigm that is well-known to induce location-specific learning (Karni & Sagi, 1993; Yotsumoto, Watanabe, & Sasaki, 2008; Yotsumoto et al., 2009). The location specificity of the task allows us to examine activity in the corresponding retinotopic area on the cortex, as well as a control area. We recorded brain activity during sleep using magnetoencephalography (MEG) and polysomnography (PSG). In order to source-localize the spontaneous brain oscillations measured by MEG to individuals' cortical space, we also collected the subjects' brain structures using magnetic resonance imaging (MRI). The combination of MEG and MRI provides fine spatio-temporal resolution (Ahveninen et al., 2007; Lin et al., 2004). Using a retinotopic mapping technique (Choi et al., 2012; Engel et al., 1994; Fize et al., 2003; Sereno et al., 1995; Shibata et al., 2011; Shibata et al., 2012; Yotsumoto, Watanabe, & Sasaki, 2008; Yotsumoto et al., 2009), we localized two different regions of the early visual areas which retinotopically correspond to trained and untrained visual field quadrants. A systemic frequency analysis was used to calculate power for oscillations from these identified cortical regions. Since we were interested in slow-waves and sleep spindles only, we selected the delta (0.5–4 Hz), slow sigma (11.5–12.5 Hz), and fast sigma (13.5–14.5 Hz) bands. The delta activity corresponds to the frequency of slow-waves, and each sigma to slow and fast sleep spindles. The separation of slow and fast sigma activity (faster or slower than 13 Hz) is based on results from previous studies (Anderer et al., 2001; Schabus et al., 2007; Schabus et al., 2008; Tamaki et al., 2009; Werth et al., 1997; Zeitlhofer et al., 1997; Zygierevic et al., 1999).

If neuronal activity in the sigma or delta bands is involved in the consolidation of TDT during NREM sleep, changes in those activities should fit the following three criteria. First, due to the location specificity of TDT learning, the power increase in the involved frequency band should be higher in the trained region compared to the untrained region. Second, due to the consolidation process, the power of the involved frequency band within the trained region of early visual areas should be higher during post-training sleep compared to pre-training sleep. Third, the difference in the

Download English Version:

<https://daneshyari.com/en/article/6203446>

Download Persian Version:

<https://daneshyari.com/article/6203446>

[Daneshyari.com](https://daneshyari.com)