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Better than sleep: Theta neurofeedback training accelerates memory consolidation

Miriam Reiner[a,*], Roman Rozengurt[b], Anat Barnea[c]

[a] *The Virtual Reality and NeuroCognition Lab, Technion Israel Institute of Technology, Israel*
[b] *Gonda Multidisciplinary Brain Research Center, Bar-Ilan University, Israel*
[c] *Bio Keshev – Private Practice for Neurofeedback, Givat Chaim Ichud 38935, Israel*

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ABSTRACT

Consistent empirical results showed that both night and day sleep enhanced memory consolidation. In this study we explore processes of consolidation of memory during awake hours. Since theta oscillations have been shown to play a central role in exchange of information, we hypothesized that elevated theta during awake hours will enhance memory consolidation.

We used a neurofeedback protocol, to enhance the relative power of theta or beta oscillations. Participants trained on a tapping task, were divided into three groups: neurofeedback theta; neurofeedback beta; control. We found a significant improvement in performance in the theta group, relative to the beta and control groups, immediately after neurofeedback. Performance was further improved after night sleep in all groups, with a significant advantage favoring the theta group. Theta power during training was correlated with the level of improvement, indicating a clear relationship between memory consolidation, and theta neurofeedback.

1. Introduction

Improving memory has been a long-time quest. A large body of evidence points to night sleep as playing a central role in consolidation of memory (e.g. Dudai, 2004; Rauchs, Desgranges, Foret, & Eustache, 2005; Stickgold, 2005). More recent evidence points to day-time-naps as supporting memory consolidation (Korman, Doyon, et al., 2007). The central question in this study is whether consolidation of memory occurs during awake hours, and if so, what conditions support consolidation without day sleep. We consider the potential role of theta rhythms engaged in the hippocampal/PFC (prefrontal cortex) interplay in consolidation of memory and report empirical results on the effect of enhanced theta oscillations on memory consolidation.

It is widely accepted that memory consolidation process happen off-line, after the initial hippocampus encoding event. Consolidation relies on the re-activation of neuronal circuits that were implicated in the initial encoding (Albouy et al., 1995). Recent accumulating research provides consistent support for the central role of sleep in memory consolidation, suggesting that some forms of declarative and hippocampus-mediated memories are consolidated across periods of sleep (Censor et al., 2006; Diekelmann & Born, 2010; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Stickgold, 2005; Walker, 2005). A meta-analysis of sleep and delayed procedural memory-consolidation, showed correlations of 0.56–0.95 between sleep and memory consolidation, "explaining an average across studies of 69% of the variance" (Stickgold, 2005, p. 1277). Another meta-analysis (Stickgold, 2005, p. 1273) of night sleep and memory consolidation across varying tasks showed T1ing improvement following night-sleep, and no similar effects during an equivalent period of being awake. These sleep-dependent processes of memory enhancement continue for at least 24–96 h (Stickgold, 2005).

Experimental evidence suggests that motor memory formation occurs in two subsequent phases (Albouy et al., 1995; Dudai, 2004; Karni et al., 1994; Luft & Buitrago, 2005). The first is initial encoding of experience during training that occurs within the first minutes-to-hours after training, and is characterized by rapid improvement in performance. This initial encoding occurs in all memory systems studied so far. The second phase is memory consolidation, and involves a series of systematic changes at the molecular level, that occur after training. This second phase requires longer time. During consolidation, memories are reorganized and hippocampus-dependent initial memories may become hippocampal-independent (Albouy et al., 1995; Maquet, 2008). Processes of reactivation of memories lead to renewed consolidation each time reactivations occur, enhancing the first consolidated memory representation, and converting it into a long-lasting stable

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* Corresponding author. Tel.: +972 48292166.
E-mail address: miriamr@technion.ac.il (M. Reiner).

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memory trace (Dudai, 2004). Delayed additional gains occur after the second phase, even without additional practice (Karni et al., 1994).

Of the two stages above, it is the delayed gains in memory consolidation, that have been found to be highly dependent on night sleep (Albouy et al., 1995; Fischer, Hallschmid, Elsner, & Born, 2002; Karni et al., 1994, 1998; Maquet, 2001; Stickgold & Walker, 2005; Stickgold, Hobson, Fosse, & Fosse, 2001; Walker & Stickgold, 2004). For instance, both speed and accuracy of sequential motor tasks such as the Finger Tapping Task (FTT) (e.g. Karni et al., 1994; Korman, Raz, Flash, & Karni, 2003), were significantly improved after night sleep. Short day sleep might be effective too (Mednick, Nakayama, & Stickgold, 2003). Just a 90-min day nap led to delayed gains of about 10% improvement in motor performance, followed by additional improvement of about 10% after a night sleep (Korman et al., 2007). Which unique sleep-specific processes contribute to memory consolidation, and which sleep stage/processes are responsible for motor memory consolidation, are still open questions. Overnight memory improvements showed a strong relationship with NREM sleep (Walker, Stickgold, et al., 2005) and with early sleep (Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Gais, Plihal, Wagner, & Born, 2000) Also, it seems that sleep spindles might have an important role in motor memory consolidation (Nishida & Walker, 2007; Schabus et al., 2004). Stage II NREM is characterized by slow (4–8 Hz) theta rhythm oscillations (Mizuseki et al., 2009), hinting at a potential role of theta oscillations in sleep-dependent motor memory consolidation.

Neural oscillations, in general, have been assumed to play a central role in cognitive processes. Specific oscillatory rhythms and synchronicity are correlated with changes in specific cognitive processes, (Herrmann, Munk, & Engel, 2004; Keizer, Verment, & Hommel, 2010; Zoefel, Huster, & Herrmann, 2011), and separate frequency bands have different roles in enhancement of distinctly different cognitive processes, such as mental rotation (Hanslmayr, Sauseng, Doppelmayr, Schabus, & Klimesch, 2005; Klimesch, Sauseng, & Gerloff, 2003), object detection (Engel, Fries, & Singer, 2001; Salari et al., 2012) mediating attention (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Schroeder & Lakatos, 2009), working memory and memory consolidation (Klimesch, 1999; Jaušovec & Jaušovec, 2012). States of phase synchronization are considered a mechanism of increased communication between regions (Fell & Axmacher, 2011; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Womelsdorf et al., 2007).

Several lines of evidence suggest that theta oscillations play an important role in formation of memory: theta oscillations are typical of hippocampal activity, upon memory encoding, generating oscillations which can propagate to other brain structures (even relatively distant), supporting memory consolidation and are thought to play a critical role in the induction of long-term plasticity, associated with memory consolidation (Chauvette, 2013; Kropotov, 2008). Theta rhythms are correlated with episodic and semantic memory (Buzsáki, 2005; Guderian & Duzel, 2005; Kahana, 2003) and are involved in learning and memory within the mPFC (medial prefrontal cortex) and hippocampal system (Anderson, Rajagovindan, Ghacibeh, Meador, & Ding, 2010, Benchenane et al., 2010; Steinvorth, Wang, Ulbert, Schomer, & Halgren, 2010). Frontal-midline theta seems to be correlated with processing of memory in general, and specifically with working memory and/or sustained attention (Mitchell et al., 2008); Theta coordination in the limbic system in mice is reported to influence inter-individual differences in memory consolidation of aversive experiences (Popa, Duvarci, Popescu, Léna, & Paré, 2010). Fear memory consolidation and retention in humans shows enhanced theta phase synchronization between the hippocampus and amygdala during the retrieval of the fear memory (Moses et al., 2007; Nishida, Pearsall, Buckner, & Walker, 2009). Theta synchronization between the hippocampus and remote areas must then happen, in the processes of memory consolidation depending on the type of memory.

Several studies point to theta synchronization as a mechanism underlying communication between the hippocampus, the ventromedial prefrontal cortex and remote memory areas, during consolidation. The underlying mechanism is still not clear. One attempt to explain the mechanism of memory consolidation is known as the "system-level memory consolidation theory" (Nieuwenhuis & Takashima, 2011). This model suggests that the hippocampus is strongly activated in the first stages of memory-related neocortical formations, but gradually new forms of memory become independent of hippocampal activations, and consolidation correlates with increased activation in the human subgenual ventromedial prefrontal cortex (vmPFC). The vmPFC, similar to the anterior cingulate cortex, seems to link the neocortical representational areas in remote memory (Maquet, 2008; Nieuwenhuis & Takashima, 2011). According to this approach, the hippocampus and vmPFC access distributed representations. Whether it is transferred from the hippocampus to the neocortex, or whether the trace is replicated repeatedly to consolidate the memory trace, is not clear (Battaglia, Benchenane, Sirota, Pennartz, & Wiener, 2011). The system-level memory consolidation view, implies exchange of information in a network of brain areas. The center is the hippocampus and the communicating areas include the neocortex and structures such as the amygdala and the striatum (Battaglia et al., 2011; Maquet, 2008) The interaction between the hippocampus and striatum resembles the interaction between the hippocampus and neocortex (Battaglia et al., 2011). This exchange is theorized to be linked to theta oscillations: hippocampal cells fire preferentially at a specific theta phase (Mizuseki et al., 2009; Klausberger et al., 2003), and so do areas in the medial temporal lobe and other areas that exchange information with the hippocampus. Thus theta is assumed to regulate information exchange between the hippocampus and striatum (for a review see Battaglia et al., 2011). This exchange of information extends to relatively distant sensory and associative areas of parietal cortex, which are also entrained by theta (and gamma) oscillations (Sirota et al., 2008). Exchange of information is based on a dynamical evolving schema, in which synchronized discharge of cell assemblies across brain structures are orchestrated by theta to encode information. Recent results further support the central role of the hippocampus–striatum exchange in motor memory consolidation, and suggest that the interplay between the striatum and the hippocampus during motor training conditions subsequent motor sequence memory consolidation, which is further supported by reorganization of cerebral activity in hippocampo-neocortical networks after sleep (Albouy et al., 2013). The ventral striatum is involved in learning beyond memory consolidation and was found to be related to individual variations in learning performance (Vink, Pas, Bijleveld, Custers, & Gladwin, 2013). Note that the results cited here are based mainly on human studies, simply since in animals, theta can reliably be measured from the hippocampus, but in humans it cannot, and the relation between animal theta originating from the hippocampus and human theta recorded at the scalp is not obvious.

Following these findings, we adopt a system-level memory consolidation view, suggesting a two level process of memory: first formation in the hippocampus, then formation of neocortical structures that are hippocampus independent. Theta is suggested to regulate exchange of information between the hippocampus and the neocortical areas for memory consolidation. We hypothesize that enhanced theta supports exchange of information between the hippocampus and neocortical areas during consolidation of memory, hence will be reflected in indicators of memory consolidation. In the current study we used a neurofeedback paradigm for training subjects to manipulate the power of theta and compare with two control groups: one manipulating beta (instead of theta)