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CHANGES OF MOTOR-CORTICAL OSCILLATIONS ASSOCIATED WITH MOTOR LEARNING

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Abstract—Motor learning results from practice but also between practice sessions. After skill acquisition early consolidation results in less interference with other motor tasks and even improved performance of the newly learned skill. A specific significance of the primary motor cortex (M1) for early consolidation has been suggested. Since synchronized oscillatory activity is assumed to facilitate neuronal plasticity, we here investigate alterations of motor-cortical oscillations by means of event-related desynchronization (ERD) at alpha (8–12 Hz) and beta (13–30 Hz) frequencies in healthy humans. Neuromagnetic activity was recorded using a 306-channel whole-head magnetoencephalography (MEG) system. ERD was investigated in 15 subjects during training on a *serial reaction time task* and 10 min after initial training. The data were compared with performance during a randomly varying sequence serving as control condition. The data reveal a stepwise decline of alpha-band ERD associated with faster reaction times replicating previous findings. The amount of beta-band suppression was significantly correlated with reduction of reaction times. While changes of alpha power have been related to lower cognitive control after initial skill acquisition, the present data suggest that the amount of beta suppression represents a neurophysiological marker of early cortical reorganization associated with motor learning. © 2014 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: event related desynchronization (ERD), humans, magnetoencephalography, serial reaction time task.

INTRODUCTION

Motor skills are acquired during practice but often even continue to develop after practice sessions during so-called offline periods (Karni et al., 1998; Walker et al., 2002; Robertson et al., 2005; Hallgato et al., 2013). There is converging evidence that such consolidation requires a critical period after initial learning which varies between 1 and 6 h (Brashers-Krug et al., 1996; Shadmehr and Brashers-Krug, 1997; Shadmehr and Holcomb, 1997; Robertson et al., 2005; Janacsek and Nemeth, 2012). Nevertheless, a few studies reveal evidence for the assumption that improvement may occur even after a brief interval of 15 min (Denny et al., 1955; Rachman and Grassi, 1965) for a review see Halsband and Lange (2006) suggesting that newly learned motor skills become rapidly stabilized being less susceptible for interference with other motor skills (Muellbacher et al., 2002; Krakauer and Shadmehr, 2006).

The pivotal role of the primary motor cortex (M1) for stabilization of newly learned skills has been evidenced in animal studies (Nudo et al., 1996; Kleim et al., 1998; Plautz et al., 2000) as well as in humans using transcranial magnetic stimulation (TMS) (Pascual-Leone et al., 1994; Classen et al., 1998; Muellbacher et al., 2002; Robertson et al., 2005) and continuous theta-burst stimulation (Krakauer and Shadmehr, 2006; Iezzi et al., 2010). These data indicate that disrupting M1 excitability within a time period up to 2 h after initial learning deteriorates consolidation and blocks offline improvement over day (Robertson et al., 2005). M1 seems to be particularly relevant for learning of repetitive movements (Muellbacher et al., 2001; Baraduc et al., 2004; Censor and Cohen, 2011). Mapping of the motor cortex by TMS during motor learning revealed that the motor cortical output maps become progressively larger during implicit learning and return to baseline, when knowledge becomes explicit (Pascual-Leone et al., 1994) supporting the significance of M1 particularly for implicit learning (for reviews see (Ashe et al., 2006; Halsband and Lange, 2006)). Functional reorganization associated with motor learning is most likely due to long-term potentiation (LTP)-like effects as shown in animals (Rioult-Pedotti et al., 1998, 2000; Hodgson et al., 2005) and humans (Ziemann et al., 2004; Jung and Ziemann, 2009).

Motor learning is additionally associated with changes of oscillatory activity in the alpha (8–12 Hz) (Zhuang et al., 1997) and beta (13–30 Hz) frequency range (Boonstra et al., 2007; Houweling et al., 2008). Synchronized oscillatory activity represents a pivotal mechanism for neuronal

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Abbreviations: ERD, event-related desynchronization; ITI, inter-tap intervals; LTP, long-term potentiation; M1, primary motor cortex; MEG, magnetoencephalography; PMC, premotor cortex; SRTT, serial reaction time task; S1/M1, primary sensorimotor cortex; TMS, transcranial magnetic stimulation.

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communication (Buzsaki and Draguhn, 2004; Fries, 2005). By temporally linking neurons in functional assemblies synchronized oscillatory activity facilitates neuronal plasticity and therefore plays an important role for consolidation of skills and knowledge.

TMS as well as behavioral studies suggest that consolidation of a newly learned movement requires at least 1 h. The neurophysiological changes within this interval have not been addressed so far. Therefore, the present study aims at investigating changes of motor cortical oscillations during acquisition and early consolidation of a motor sequence using magnetoencephalography (MEG).

EXPERIMENTAL PROCEDURES

Subjects and paradigm

Fifteen healthy subjects (seven male) participated in this study which was approved by the local ethics committee and complies with the Declaration of Helsinki. Data from one subject were excluded from the analysis due to poor quality of the MEG data. All participants gave their written informed consent prior to data acquisition. Mean age was 28.0 ± 2.3 years (mean ± standard error of the mean, s.e.m.). Subjects were naïve regarding the exact purpose of the study. The Edinburgh Handedness Inventory (Oldfield, 1971) revealed a mean lateralization ratio of 93.2 ± 1.5 indicating that all participants were right-handed.

Subjects performed a *serial reaction time task* (SRTT) that is commonly used for the investigation of motor learning (Nissen and Bullemer, 1987). It was introduced to the participants as a measure of reaction times. Four response keys of a nonmagnetic custom made response-box anatomically aligned to the right hand were spatially mapped with respect to four horizontally aligned bars presented on a back projection screen (Fig. 1) by a Panasonic PT-D7700E DLP projector (Panasonic Europe Ltd., Bracknell, U.K.). Subjects were instructed to react as quickly as possible as soon as one of the four bars changed from dark blue to light blue. The correct response triggered the presentation of the next bar after a time interval of 2 s in order to keep the overall movement rate constant. In case subjects did not press the correct button the bar remained light blue until subjects responded correctly.

Visual stimuli were presented on a back projection screen. The stimulus was presented at 3.9° of angle of vision (width 16 cm, height 11 cm, distance 160 cm).

Stimulus presentation and recording of reaction times were controlled with the help of Eprime® software (Psychology Software Tools, Sharpsburg, PA, USA) installed on a standard windows computer. Reaction times were determined by measuring each button press onset. Each subject performed three runs. In the *random* condition, presentation of the bars was completely randomized. Bars were presented 200 times. During *sequential 1* and *sequential 2* a cyclically repeating sequence of eight stimuli requiring a sequence of eight button presses was presented 25 times resulting in additional 200 button presses for each sequential run. The sequence was *thumb*, *middle*, *ring*, *index*, *middle*, *index*, *ring*, *middle*, *index*. The order of *sequential 1* and *random* was counterbalanced across subjects. Both runs always followed immediately after each other. *Sequential 2* always followed *sequential 1* after a break of 10 min. During the break subjects remained in the magnetically shielded room without any specific task. Response times that were two standard deviations below or above mean individual reaction times were defined as outliers and excluded from further analysis.

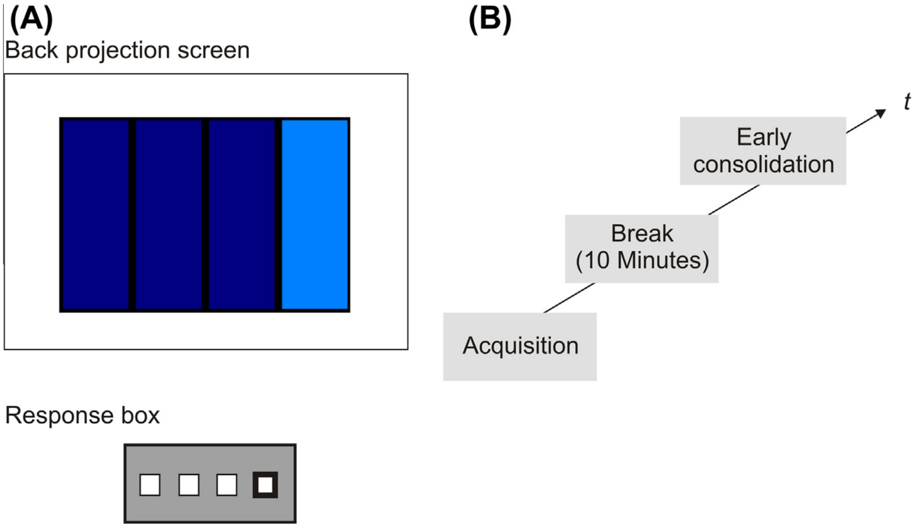

Fig. 1. Experimental setting. (A) The four response keys of a button box were spatially mapped with respect to four horizontally aligned bars presented on the back projection screen. Subjects were instructed to press the appropriate button as soon as the associate bar turned from dark to light blue. (B) MEG was recorded during presentation of a randomly varying sequence (*random*) and two sequential runs. Please note that *random* and *sequential 1* were counterbalanced across subjects and were conducted immediately after each other while *sequential 2* always followed sequential 1 with a break of 10 min. *Sequential 1* indicates motor learning and *sequential 2* serves as a measure of early motor consolidation.