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Aging reduces experience-induced sensorimotor plasticity. A magnetoencephalographic study

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ABSTRACT

Modulation of the mu-alpha and mu-beta spontaneous rhythms reflects plastic neural changes within the primary sensorimotor cortex (SM1). Using magnetoencephalography (MEG), we investigated how aging modifies experience-induced plasticity after learning a motor sequence, looking at post- vs. pre-learning changes in the modulation of mu rhythms during the execution of simple hand movements. Fifteen young (18–30 years) and fourteen older (65–75 years) right-handed healthy participants performed auditory-cued key presses using all four left fingers simultaneously (Simple Movement task — SMT) during two separate sessions. Following both SMT sessions, they repeatedly practiced a 5-elements sequential finger-tapping task (FTT). Mu power calculated during SMT was averaged across 18 gradiometers covering the right sensorimotor region and compared before vs. after sequence learning in the alpha (9/10/11 Hz) and the beta (18/20/22 Hz) bands separately. Source power maps in the mu-alpha and mu-beta bands were localized using Dynamic Statistical Parametric Mapping (dSPM). The FTT sequence was performed faster at retest than at the end of the learning session, indicating an offline boost in performance. Analyses conducted on SMT sessions revealed enhanced rebound after learning in the right SM1, 3000–3500 ms after the initiation of movement, in young as compared to older participants. Source reconstruction indicated that mu-beta is located in the precentral gyrus (motor processes) and mu-alpha is located in the postcentral gyrus (somatosensory processes) in both groups. The enhanced post-movement rebound in young subjects potentially reflects post-training plastic changes in SM1. Age-related decreases in post-training modulatory effects suggest reduced experience-dependent plasticity in the aging brain.

Introduction

The ability to learn complex sequences of movements is a necessary requisite for many everyday motor activities. In addition, motor skills acquired during training continue to develop offline after practice has ended, while awake or asleep. Offline processes taking place after the end of the training period participate in memory consolidation, allowing newly acquired abilities to become increasingly stable and resistant to interference through the passage of time (Dudai, 2004; Frankland and Bontempi, 2005; McGaugh, 2000; Walker and Stickgold, 2006). Learning and consolidation of motor skills are accompanied by functional and structural reorganization within specific cerebral regions (Peigneux et al., 2006), especially in the primary motor cortex (M1) known to be involved in motor learning (Censor et al., 2010; Karni et al., 1995; Muellbacher et al., 2002; Robertson et al., 2005). The functional role of M1 in motor sequence learning can be defined as the storage site for new motor memories, where representations of the sequence are progressively strengthened in specific networks of neurons, supporting practice-related plastic changes in motor maps (Penhune and Steele, 2012). Besides M1, several other brain regions are involved in the acquisition and consolidation of motor sequence learning. Motor skill learning is supported by cortico-cerebellar and cortico-striatal systems (e.g., Doyon et al., 2009; Penhune and Steele, 2012). The cerebellum has been hypothesized to participate to sensorimotor integration and error correction that facilitate the first phases of learning (Penhune and Steele, 2012). Activity in the cerebellum decreases with practice of the motor sequence. By contrast, the striatum and associated motor cortical regions remain activated when the sequence of movement is well learned, supporting their role in long-term consolidation (Doyon et al., 2009). The striatum might play an important

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role for learning associations between individual movements in the sequence (e.g. motor chunks) (Penhune and Steele, 2012).

Young participants trained on a motor sequence exhibit a strong but transient offline improvement of motor performance after an inactivity period of 5–30 min following training (Albouy et al., 2006; Hotermans et al., 2006, 2008; Schmitz et al., 2009), which is not present anymore after 4 h of inactivity or during uninterrupted practice (Hotermans et al., 2006). The amplitude of the performance boost predicts the size of the performance gains observed 48 h after learning, suggesting a functional implication of the boost phenomenon in motor memory processes (Hotermans et al., 2006). However, repetitive transcranial magnetic stimulation (rTMS) applied over M1 immediately after the end of learning, and before the motor sequence test, reduces the boost effect but does not impact delayed, overnight gains in performance (Hotermans et al., 2008). Similarly, TMS applied over M1 immediately after practice hinders improvements in motor memory over the day, but not overnight (Robertson et al., 2005). Altogether, these results suggest that M1 plays a critical role during the motor training phase and during the immediately ensuing post-learning wake period, but that different neural networks are already involved in longer-term motor memory consolidation processes (Hotermans et al., 2008; Robertson et al., 2005), indicating that the boost effect reflects a temporary activated state of motor memory (Hotermans et al., 2008). This temporary improvement in motor performance is independent of the practiced material as it generalizes also to untrained sequences (Schmitz et al., 2009), suggesting that the motor boost subtends the optimization of general features of motor learning, rather than consolidating specific sequential components of the material to be learned.

Memory and plasticity processes are crucial players in the maintenance and optimization of cognitive functioning in aging (Lupien and Wan, 2004; Walker, 2005). Several studies evidenced a decline in M1 plasticity with aging, which might be responsible for motor deficits (Freitas et al., 2011; Sawaki et al., 2003; Todd et al., 2010). However, recent studies suggest that older adults are as efficient as young adults at the initial encoding phase of motor learning, and that potential difficulties may appear later on during the offline memory consolidation phase (Brown et al., 2009; Spencer et al., 2007; Wilson et al., 2012). The boost and memory consolidation phases are distinctive in that the former is transiently present after only a few minutes, whereas the latter sustains and takes hours to days to achieve (Press et al., 2005). To the best of our knowledge, the potential impact of aging on the boost of motor performance following a 5–30 min offline resting period has never been investigated. As well, how reorganization processes take place in M1 following learning in young and older participants has not been specifically studied either.

Activity in the primary sensorimotor cortex (SM1) can be assessed by measuring changes in the rolandic mu rhythm with dominant frequencies in alpha (~10 Hz) and beta (~20 Hz) frequency bands (Cheyne, 2012; Hari and Salmelin, 1997; Jones et al., 2009). Mu-alpha and mu-beta may involve distinct functional networks (Hari and Salmelin, 1997; Hari, 2006; Ritter et al., 2009). The beta rhythm would originate in the pre-central gyrus, responsible for motor functions, whereas the alpha rhythm would be generated more posteriorly, in the post-central gyrus, responsible for somatosensory processes. Power decrease or increase in the ongoing mu rhythm is known as event-related desynchronization (ERD) or synchronization (ERS), respectively (Pfurtscheller and Lopes da Silva, 1999). The mu rhythm observed at rest is transiently reduced during movement execution, observation, imagination and preparation (Chatrian et al., 1959; Cheyne et al., 2003; Hari, 2006; Hari and Salmelin, 1997; Neuper et al., 2006; Pineda, 2005), and then enhanced after movement termination (Jurkiewicz et al., 2006; Neuper et al., 2006; Pfurtscheller et al., 1996). This post-movement mu rebound overtakes pre-movement levels and lasts a few seconds before returning to baseline (Pfurtscheller et al., 1996). The mu ERD is believed to represent an active state of motor and/or sensory networks during movement preparation and execution (Jurkiewicz et al., 2006), whereas the mu ERS would reflect active cortical inhibition (Gaetz et al., 2010; Klimesch et al., 2007), cortical stabilization (Caetano et al., 2007) or active immobilization (Erbil and Ungan, 2007; Salmelin et al., 1995) of the SM1. More recently, it has also been suggested that ERS may represent an active process in SM1 that promotes the maintenance of the current movement, i.e. the "*status quo*" hypothesis (Engel and Fries, 2010). Theta burst stimulation over M1 induces an increased beta power that may represent Long-Term Depression (LTD) plasticity mechanisms (McAllister et al., 2013; Noh, et al., 2012). Importantly, developing expertise in a motor task may also require modulation of the cortical mu rhythm to integrate the new motor ability. Enhanced modulation of the mu rhythm was evidenced during motor skill acquisition (Boonstra et al., 2007), with a stronger decrease in beta power and improved proficiency in bimanual sequence execution (Andres et al., 1999), a greater decrease in alpha power during repetitive sensory stimulation associated with subsequent perceptual learning improvement (Freyer et al., 2013), and a progressive decrease in the 10-Hz power coupled with increased explicit knowledge of the motor sequence (Zhuang et al., 1997). These changes in the modulation of the mu rhythm might reflect plasticity processes taking place in M1 during the course of motor learning. However, to the best of our knowledge, there is nowadays no study evidencing a role of mu ERD/S in the motor plastic changes that take place after a specific and complex motor learning.

In the present study, we hypothesized that modulation of mu rhythms over M1 during simple movements would be influenced by a prior, complex motor sequence learning experience, in line with studies suggesting an involvement of M1 within the first minutes (Hotermans et al., 2008) or hours (Robertson et al., 2005) after learning. Supporting this hypothesis, previously published MEG investigations disclosed increased beta modulation in M1 (i.e. increased beta ERD and ERS) during motor learning positively correlated with motor performance, suggesting that increased modulation may reflect M1 functional reorganization during the time course of motor learning (Boonstra et al., 2007). In line with these findings, increased modulation of the mu rhythm following motor sequence learning during the execution of simple movements may reflect a practice-dependent sensorimotor reorganization. However, mere movement repetition may result in a progressive ERD decrease, more directly related to an habituation effect reducing attentional demands directed towards the motor task (Dirnberger et al., 2004; Erbil and Ungan, 2007). Experience-dependent modulation of the cortical mu rhythm following learning might be diminished with aging, in line with studies suggesting an age-related decline in M1 plasticity following motor learning (Freitas et al., 2011; Sawaki et al., 2003; Todd et al., 2010). To test these predictions, we investigated the modulation of mu rhythms using magnetoencephalography (MEG) during the execution of simple hand movements (Simple Movement Task, SMT) after learning a motor sequence of finger movements (Finger Tapping task, FTT; Karni et al., 1995).

Materials and methods

Participants

Fifteen young (7 females; range 18–30 years; 24.26 ± 3.33) and fourteen older (8 females; range 65–75 years; 69.1 ± 1.46) right-handed healthy participants gave their written agreement to participate in this MEG study approved by the ULB-Hospital Erasme Ethics Committee. Participants had no history of neuropsychiatric disease or movement disorders and were right-handed according to the Edinburgh handedness inventory (Oldfield, 1971). Participants were screened for depression using the Shortened version of the Beck Depression Inventory (BDI, Beck et al., 1974; French adaptation by Collet and Cottraux, 1986). Sleep habits were assessed using the Pittsburgh Sleep Quality Index (PSQI, Buysse et al., 1989) and the scores were similar in both groups ($t(27) = 0.86$; $p = 0.4$; young: 4.2 ± 2.98; older: 3.36 ± 2.24).