



## Two brakes are better than one: The neural bases of inhibitory control of motor memory traces

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### ABSTRACT

Inhibitory control of actions is one important aspect in daily life to warrant adequate context related behavior. Alpha activity (oscillatory brain activity around 10 Hz) has been suggested to play a major role for the implementation of inhibitory control. In the present study electrophysiological correlates of voluntary suppression of acquired, memorized motor actions have been compared to the suppression of novel motor actions. Multichannel EEG analyses of alpha power and alpha phase coherence were used. Healthy subjects were asked to inhibit the execution of either well-trained, memorized or untrained, novel sequential finger movements depending on the respective context. An increase of focal upper alpha activity at bilateral sensorimotor cortices was found during suppression of movements independent of whether these were memorized or novel. This represents a memory unspecific mechanism of motor cortical inhibition. In contrast, interregional phase synchronization between frontal and (left) central recording sites showed a differential effect with decoupling during suppression of memorized movements which was not the case with novel ones. Increase of fronto-central coupling at upper alpha frequency during retrieval of the memory trace and decrease during suppression of retrieval were obtained. This further supports the view of the functional relevance of upper alpha oscillations as a mechanism of context-dependent sustained inhibition of memory contents.

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### Introduction

To act successfully in daily life the execution of well-trained motor skills has to be persistently withheld under certain circumstances. There are situations in which relatively complex sequential movements have to be performed due to a cue in the regular context. However, if the context has changed the movement might have to be voluntarily suppressed for at least a few seconds to act successfully, although the respective cue has appeared. For instance, while dining in a restaurant usually a guest takes the spoon and starts eating (motor program) after the waiter has put the soup (cue) on the table in front of the guest. If, however, the waiter tells the guest who has got intolerance to shellfish that the soup contains shrimps (changed context) the person has to inhibit starting to eat to prevent negative aftermath. During sustained voluntary inhibition of complex motor programs, i.e. the suppression of movements without any time constraints, a pattern of increased rhythmical brain activity around 10 Hz (so called alpha activity) was demonstrated in the human electroencephalogram

(EEG) at recording sites overlying the motor cortex (Hummel et al., 2002). Increased alpha activity was associated with attenuated corticospinal excitability determined directly by transcranial magnetic stimulation (Hummel et al., 2002; Sauseng et al., 2009a, 2009b) and with a negative blood oxygenation level-dependent signal compared to unconstrained rest at motor areas (Hummel et al., 2004). These findings are well in line with the idea that high EEG alpha amplitudes are rather the neural signature of deactivation/inhibition of a cortical area (Klimesch et al., 2007) beyond simple nil-working or idling (Pfurtscheller et al., 1996).

An important question which still has remained open is whether increased EEG alpha activity during voluntary suppression of actions is restricted to acquired, memorized actions. Or in other words, is increased rhythmical brain activity in the alpha frequency range a neural correlate of action suppression in general or solely involved in the control of well-trained motor programs, i.e. actions that are stored in long-term memory? Following Keele et al. (1995) there are two different coding systems for movement sequences: an effector-based system in which muscle combinations are selected to code for sequences and an effector-free spatial coding system (or motor vs. cognitive coding scheme; Shea et al., 2011). Complex, novel actions which have not been performed before are likely to be coded effector-based. Well-trained movements, on the other hand, seem to be coded by an effector-free spatial representation system in addition to effector-based coding. So, if these two different types

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of actions (novel vs. well trained) are likely to be coded differently, it is also plausible that inhibitory control of these actions is implemented in two different ways. Whereas well-trained movements are most likely prepared as a complete and effector-free spatial representation which then is inhibited, for a novel motor program each digit of the sequential movement is effector-based represented and needs to be inhibited separately.

There is sound evidence for the assumption that inhibition of a motor memory trace (which would be an effector-free spatial representation) is associated with increased alpha activity (Hummel et al., 2002). It has been suggested that for instance during encoding and retention of information in working memory increased alpha activity can be found (Jensen et al., 2002; Klimesch et al., 1999; Sauseng et al., 2009a, 2009b). This indicates inhibition of task irrelevant brain areas (Jensen et al., 2002; Jokisch and Jensen, 2007; Klimesch et al., 1999; Sauseng et al., 2009a, 2009b) preventing the processing of distracting sensory information. It has also been discussed that high alpha activity reflects the top-down control of memory processes (Klimesch et al., 2007; Palva and Palva, 2007; Sauseng et al., 2005). Since this type of inhibitory activation is predominately found during memory processes inhibition of motor-related brain activity by the means of increased EEG alpha amplitude is expected particularly when there is a memory representation of a movement which has to be suppressed.

On the other hand, a recent study suggests that the voluntary suppression of a memory trace is associated with decreased distributed interregional coherence in the alpha frequency range (Bäumel et al., 2008). Bäumel et al. (2008) demonstrated a decrease of mainly temporal phase coherence at alpha frequency when participants attempted to deliberately inhibit information from episodic long-term memory. Moreover, interregional phase coherence might more likely reflect motor memory components of complex finger movements than local amplitude estimates (Sauseng et al., 2007). Thus, it is expected that interregional phase coherence at alpha frequency can dissociate between inhibition of memorized, well-trained movements and inhibition of novel motor programs.

To test whether the suppression of a motor memory trace is specifically reflected by focal increases of alpha power or decreases of interregional alpha phase coherence, multichannel EEG was recorded while subjects either had to perform or suppress well-trained or novel complex finger sequences depending on the respective context. Brain oscillatory activity was analyzed with an emphasis on amplitude estimate and phase coherence differences between the experimental conditions.

## Material and methods

Twelve healthy volunteers participated in the study (7 female). Mean age was  $26.6 \pm 2.9$  years (mean  $\pm$  SD). Only volunteers who did not regularly play the piano were included in this protocol as musical (piano) education might possibly alter the way subjects learn complex finger movements. All subjects were right-handed according to the Edinburgh-Handedness-Scale and gave written informed consent according to the declaration of Helsinki (World Medical Association, 1996). The study protocol was approved by the review board of the University of Tuebingen Medical School where the experiment was carried out (this is a re-analysis of EEG data which has been published by Hummel et al., 2002).

The experiment consisted of two parts: an initial training session and a subsequent testing session the following day. During the training session a motor sequence consisting of 16 consecutive finger movements (key presses on an electronic four key response pad) had to be practiced until the subjects were able to perform the motor sequences 10 times in a row without errors (Gerloff et al., 1998; Hummel et al., 2002; Hummel et al., 2003; Hummel et al., 2004). After each attempt participants were informed verbally whether the

sequence was performed correctly or not. If incorrect, they, however, were not told what exactly the error was. On average it took 17.7 min (standard error of mean 3.2) of training for the participants to meet this criterion. The complex finger movement sequence was 5-3-2-4-3-4-2-5-4-4-2-3-5-2-4-3, where the labels 2–5 represent index, middle, ring and little finger of the right hand. No EEG was recorded during the training session.

During the testing session, subjects sat in front of a video screen with the right arm relaxed and resting on a pillow. The right hand was positioned palm down so that the response keys could be pressed easily and without any wrist movements. At the beginning and the end of the testing session EEG was acquired during unconstrained rest (REST) in which participants were asked to solely fixate the centre of the monitor for 5 min.

During the experiment four tasks were performed: The memorized or novel sequences with comparable complexity had to be played on a four key response pad or these movement sequences had not to be executed. Each trial started with a screen indicating whether the memorized, well-trained sequence (MEMORIZED) or a novel sequence (NOVEL) was required. This was followed by the instruction displayed on the screen whether to execute or not to execute the respective sequence. Thereafter 16 cues were presented at a rate of 1 Hz to externally pace the finger movements during MEMORIZED and NOVEL at the same rate. When a novel sequence was required the respective cues were the numbers 2–5 corresponding to the four fingers as explained above. When the novel sequence had to be executed subjects had to tap the respective finger as indicated on the screen. When the sequence had not to be executed subjects were instructed not to move their fingers, i.e. not to enter the sequence, but to attentively watch the visual cues. When the memorized sequence had to be executed/not executed meaningless visual cues (e.g., %, #, \$, &) with similar complexity as the numbers 2–5 were shown at a 1 Hz rate on the screen. However, the order of meaningless cues was not associated with the sequence what so ever; i.e., it was not possible for participants to relate the meaningless cues with the memorized sequence. Participants were asked to either enter the memorized sequence paced by the meaningless visual cues (1 Hz) or not to move the fingers while attending these meaningless cues. The purpose of the cues only was to pace the rhythm of entering the sequence. For further details on the experimental setup please see also (Hummel et al., 2002).

EEG was recorded with a SynAmps 32-channel amplifier (NeuroScan Inc., Herndon, VA, USA) at a sampling rate of 250 Hz from 28 Ag-AgCl scalp electrodes arranged according to the extended international 10-20-System and mounted in a flexible cap (Electro-Cap International, Inc., Eaton, OH, USA). As reference during recording linked earlobes were used, impedance was kept below 5 kOhm, upper filter cutoff was 50 Hz and the time constant was set to DC.

Data from the 16 s intervals in which sequences had to be executed or suppressed were segmented into epochs of 1000 ms duration around cue onset (data were resampled at a rate of 256 Hz using spline fit interpolation) for each experimental condition separately. For REST data from the baseline recording pre and post experiment were collapsed. There was no statistically significant difference in amplitude or phase coherence for any frequency band or recording site/electrode pair between the pre and post measurement (all  $t < 2.201$ ,  $p > .05$  uncorrected). Segments containing blinks or muscular artifacts were manually rejected from further analysis after visual inspection. On average the number of artifact-free trials (standard error of mean) submitted to further analyses was 189.8 (10.4), 198.5 (8.8), 182.7 (11.9), 195.3 (8.1) and 158.5 (7.5) for the conditions MEMORIZED<sub>suppress</sub>, MEMORIZED<sub>execute</sub>, NOVEL<sub>suppress</sub>, NOVEL<sub>execute</sub>, and REST. Laplacian current source density was applied to attenuate effects of volume conduction (this is particularly important for the analysis of interregional phase coherence, see e.g. Srinivasan et al., 2007). Using BESA 5.1 (MEGIS Software Inc., Munich, Germany), complex demodulation (Hochstetter et al., 2004; Papp and Ktonas, 1977) of EEG signals was

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