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## Multivariate time–frequency analysis of electromagnetic brain activity during bimanual motor learning

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Although the relationship between brain activity and motor performance is reasonably well established, the manner in which this relationship changes with motor learning remains incompletely understood. This paper presents a study of cortical modulations of event-related beta activity when participants learned to perform a complex bimanual motor task: 151 channel MEG data were acquired from nine healthy adults whilst learning a bimanual 3:5 polyrhythm. Sources of MEG activity were determined by means of synthetic aperture magnetometry that yielded locations and time courses of beta activities. The relationship between changes in performance and corresponding changes in event-related power were assessed using partial least squares. Behavioral data revealed that participants successfully learned to perform the 3:5 polyrhythm and that performance improvement was mainly achieved through the proper timing of the finger producing the slow rhythm. We found event-related modulation of beta power in the contralateral motor cortex that was inversely related to force output. The degree of beta modulation increased during the experiment – although the force level remained constant – and was positively correlated with motor performance, in particular for the motor cortex contralateral to the slow hand. These electrophysiological findings support the view that activity in motor cortex co-varies closely with behavioral changes over the course of learning.

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**Keywords:** Motor learning; Polyrhythm; MEG; ERD; ERS; Source analysis; SAM; PCA; PLS; Wavelet analysis

### Introduction

Motor performance typically improves with repetition and practice. One would expect that the proficiency in a motor task requires a modulation of cortical motor outputs to accommodate

the newly acquired ability. For the modulation of cortex outputs, the plasticity of the brain appears vital as it enables the neural system to reorganize and adapt to improve motor control. Changes in metabolism related to skill acquisition have indeed been shown using functional imaging techniques (Schlaug et al., 1994; Karni et al., 1998; Toni et al., 1998), primarily indicating a reorganization of motor areas. Although the reorganization of cortical structures is generally thought to depend on, or caused by, changes in electromagnetic neural activity, relatively little is known about specific changes in neural activity during motor learning.

Locally synchronized behavior of neural assemblies yields fluctuations in local field potentials that can be measured using electro- and magneto-encephalography (EEG and MEG, respectively) (Lopes da Silva, 1991; Nunez, 1995). Using these techniques, motor performance is usually found to be accompanied by beta activity, i.e., oscillatory encephalographic signal in a frequency range of about 15 to 30 Hz. Above contralateral motor areas the amplitude of this beta activity, here abbreviated as beta amplitude, decreases during motor performance and increases after movement termination, referred to as event-related desynchronization (ERD) and synchronization (ERS), respectively<sup>1</sup> (Pfurtscheller, 1981; Feige et al., 1996; Pfurtscheller et al., 1996, 1998; Crone et al., 1998; Gerloff et al., 1998; Doyle et al., 2005). The significance of beta activity in motor performance has been further underscored by studies on cortico-muscular synchronization in the beta band recorded during constant force production (Conway et al., 1995; Salenius et al., 1997; Gross et al., 2000; Kilner et al., 2000; Mima et al., 2000). Apart from submitting a central role of beta activity per se, these results suggest that beta (de-) synchronization can serve as an effective mechanism of motor control, or in the least provides a direct index of such a mechanism (cf. Farmer, 1998; Schoffelen et al., 2005).

In the present study we examined changes in cortical activity during the acquisition of a new, demanding motor skill: a bimanual

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<sup>1</sup> There is an inference concerning the coherence of neurons which we do not measure here. We are aware of this, but prefer to follow convention for the purpose of relating the findings to the established literature.

3:5 polyrhythm. Polyrhythmic or multi-frequency performances are particularly useful for studying motor learning as the degree of difficulty can be easily manipulated by altering task demands (Peters, 1985; Summers et al., 1993a; Peper et al., 1995; Monno et al., 2000). When examining the accompanying brain activity, polyrhythmic performance allows for an immediate separation of activity originating from the bilateral motor cortices due to the obvious difference in movement frequency between fingers or hands (Daffertshofer et al., 2000). As with motor performance in general, rhythmic movements are also accompanied by changes in cortical beta amplitude (Toma et al., 2002; Boonstra et al., 2006; Daffertshofer et al., in press). Hence we used this amplitude modulation to localize sources and reconstruct their time-dependent signals using synthetic aperture magnetometry (SAM) (cf. Cheyne et al., 2006; Houweling et al., in press). SAM is a so-called beamformer technique that stresses signals originating from a certain region while suppressing residual activity from all other locations. In the present study SAM enhanced our focus on motor-related activity by suppressing activity related to other processes, e.g., activity caused by auditory pacing. The resulting signals were further studied via their event-related power (Boonstra et al., 2006) in order to identify learning-specific spectral changes in cortical activity. To achieve this, we employed principal component analysis (PCA) in the form of partial least squares (PLS) (McIntosh and Lobaugh, 2004) to quantify the co-variation between cortical activity and motor performance during motor learning.

## Methods

Nine participants (mean age: 28.5 years, range: 23–44, 7 male, 2 female) with no previous musical education took part in the experiment. Eight participants were self-reported right-handers. The experiment was conducted in full compliance with the guidelines of the medical ethical committee of the VU University medical center. All participants signed an informed consent form prior to participation.

Participants were instructed to produce isometric forces by flexing left and right index fingers at a frequency ratio of 3:5 (cf. Fig. 1). To assist this difficult bimanual performance both hands were paced by auditory stimuli presented ipsilaterally using earphones (50 ms duration; pitch: 600 Hz fast finger, 400 Hz slow finger; EARTone 3A, Cabot Safety Corporation). The inter-stimulus interval of the pacing signal was 0.9 s for the fast and 1.5 s for the

slow finger (or 1.11 and 0.67 Hz, respectively). Participants performed two blocks of six trials each: in one block the right finger produced the fast and the left finger the slow frequency and in the other block frequencies were swapped from left to right. The order of blocks was counterbalanced over participants. To optimize performance, a block always started with a trial in which participants were only required to listen passively to the rhythm. This was followed by five trials in which they were instructed to perform the polyrhythm to the best of their ability. Each trial lasted 45 s and consisted of 10 complete rhythmical cycles, yielding a total of 50 and 30 stimuli for the fast and slow finger, respectively. Trials were interspersed by 15 s breaks during which participants received visual feedback about their performance. To achieve this, the produced force pattern averaged over the 10 cycles was displayed in combination with the auditory pacing signal.

Brain activity was recorded using a 151-channel MEG (CTF Systems Inc., Vancouver, Canada) with 3rd-order synthetic gradiometers. One channel was not operational so that, effectively, 150 MEG signals were analyzed. The surface electromyogram (EMG) was recorded from the flexor digitorum superficialis of both arms; electrodes (Ag–AgCl; Ø 1 cm) were placed in a bipolar montage with an inter-electrode distance of approximately 1 cm. The voltages of both MEG-compatible force transducers (Boonstra et al., 2005a) and acoustic stimuli were simultaneously sampled. All signals were low-pass filtered at 415 Hz prior to digitization at a rate of 1250 Hz.

Motor performance was assessed by the frequency relationship between the force productions of both fingers. For this sake we determined the power spectra of the force signals using Welch's periodogram method with Hamming windows of 13.5 s, i.e., the first cycle of each trial was omitted to eliminate transient behavior and the next nine cycles were divided into three consecutive segments of three movement cycles. The frequency relationship was determined using a rescaled cross-spectral overlap (Daffertshofer et al., 2000) measuring the common spectral characteristics of fast and slow fingers after rescaling the frequency axis of the slow finger. More specifically, the overlap of the power spectra at a scaling factor of 3:5=0.6 was used to quantify the extent to which participants were performing the proper polyrhythm. The rescaled cross-spectral overlap was computed for each individual segment for scaling factors ranging from 0.1 to 2 in steps of 0.003.

EMG signals were high-pass filtered using a second order Butterworth filter to eliminate movement artifacts (cut-off

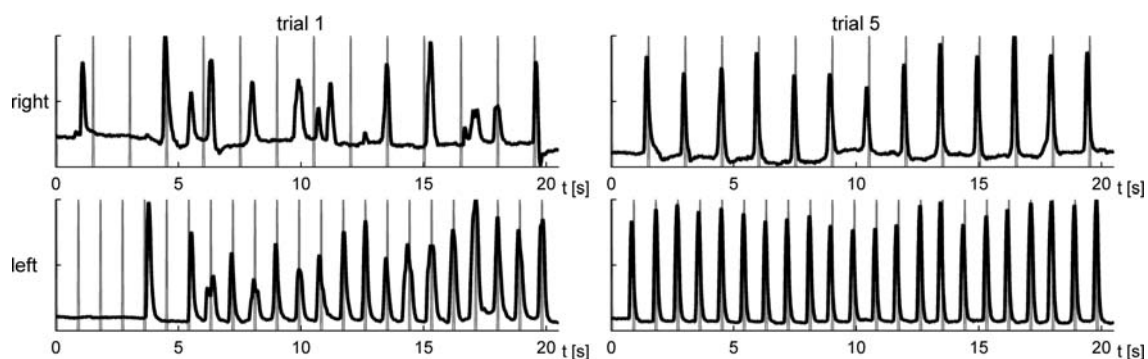


Fig. 1. Force traces of a single participant performing the 3:5 polyrhythm with the fast rhythm on the left side. Left panels show the first 20 s of the initial trial, i.e., the first encounter with the 3:5 polyrhythm. The upper panel shows the force of the right finger (black line) and the auditory pacing signal (grey line); lower panel is identical but displays the left side. Clearly this participant did not perform the proper polyrhythm during trial 1 (see the slow, right hand). Right panels show the first 20 s of trial 5 after the participant had successfully learned the polyrhythmic performance.

frequency, 20 Hz) and normalized to unit variance to correct for individual differences in signal strength. Next, EMGs were full-wave rectified using the Hilbert transform (Myers et al., 2003).

Sources of cortical activity were defined from the MEG data by means of SAM, a spatial filtering technique based on a nonlinearly constrained minimum-variance beamformer (Vrba and Robinson, 2001; Gaetz and Cheyne, 2006). Volumetric source images were generated by applying SAM to each voxel in the region of interest (5 mm voxel resolution) defined via an average MRI (International Consortium of Brain Mapping, ICBM). Focusing on beta ERS/ERD, we filtered the signals (band-pass frequency, 15–30 Hz) prior to computing covariance matrices (cf. Taniguchi et al., 2000). The SAM analysis was based on a comparison of beta activity between active and control states. Because cortical beta activity decreases during force production and increases afterwards, the active state was defined as the time interval of –200 to 200 ms relative to maximally produced force and the control state as the interval of 200 to 600 ms. Using the pseudo- $T$  differences, a statistical parametric image was computed and single-trial time series (virtual sensor) were reconstructed for the peak location of activity in these images, enabling analysis of source activity as a function of time. Event-related power of these reconstructed source data and the EMG data were determined using a continuous wavelet transform that was applied to single trial data. We used complex Morlet wavelets<sup>2</sup> at 1 Hz intervals in the 5 to 45 Hz range (cf. Duzel et al., 2003). The SAM source data were normalized to unit variance. The wavelet transform yielded complex wavelet coefficients whose squared modulus specified the signals' time-dependent power at distinct frequencies. Power values were averaged with respect to the motor output, i.e., force maxima, separately for different data segments, trials, participants and sides, resulting in  $3 \times 5 \times 9 \times 2 = 270$  time-resolved power spectra for each of the four channels ( $2 \times \text{EMG}$  and  $2 \times \text{MEG}$ ).

Statistical analyses of the frequency coupling of motor output and time–frequency decompositions of EMG and MEG data were realized with PCA in its capacity to extract major components from multivariate signals (see Daffertshofer et al., 2004 and references therein, cf., Boonstra et al., 2005b; Boonstra et al., 2006). Notice that PCA can be seen as the basis of several other multivariate data analysis methods such as PLS (McIntosh et al., 1996; Lobaugh et al., 2001), whereby it is restricted to the brain–behavior covariate matrix. In these terms, our application of PCA matched McIntosh and Lobaugh's spatiotemporal task PLS with mean centering (McIntosh and Lobaugh, 2004). In detail, we combined data of different conditions into a single matrix with (*number of observations*)  $\times$  (*number of conditions*) rows and (*number of signals*)  $\times$  (*number of samples*) columns. In all analyses, the number of observations was 3 (consecutive segments) and the number of conditions was (*trial*)  $\times$  (*side*)  $\times$  (*participants*) =  $5 \times 2 \times 9 = 90$ . The performance-related signals of the fast and slow hands were pair-wise combined in order to compare the time–frequency signals of both left and right conditions. The number of elements and samples differed across analyses: for the rescaled cross-spectra there were 634 samples and 1 signal, whereas for the wavelet spectra there were 16875 samples (13.5 s at 1250 Hz) and 41 signals (frequencies). Singular values of all seven

matrices ( $2 \times \text{EMG}$ ,  $2 \times \text{MEG}$ ,  $3 \times \text{cross-spectra}$ ) were computed, yielding 90 eigenvalues and eigenvectors for each matrix. Apart from the first eigenvector all other eigenvalues were rather small so that we could restrict the subsequent analyses to the first mode in all PCAs. That is, we projected the data onto the first eigenvector to determine the time–frequency changes that were covered by the first principal mode. Finally, multiplying these projections with the data yielded a matrix of so-called *brain scores* that were used to indicate the variation of task effects across observations, conditions, and participants (McIntosh and Lobaugh, 2004).

For the subsequent statistical assessment of the so obtained principal modes we used a repeated measure ANOVA. Instead of testing for significance of principal modes against a null distribution with, e.g., permutation testing, jackknife, or bootstrapping estimates, we tested whether the variance of test effects was significantly different ( $P < 0.05$ ) between conditions. In other words, we compared eigenvector coefficients of the first modes by performing a two-way ANOVA (*trial*  $\times$  *side* =  $5 \times 2$ ) with repeated measures. To address possible transfer effects of learning between sides, we added a between-subject variable *order* denoting whether a participant started the experiment either in the right or left side condition. Finally, to test whether changes in motor performance

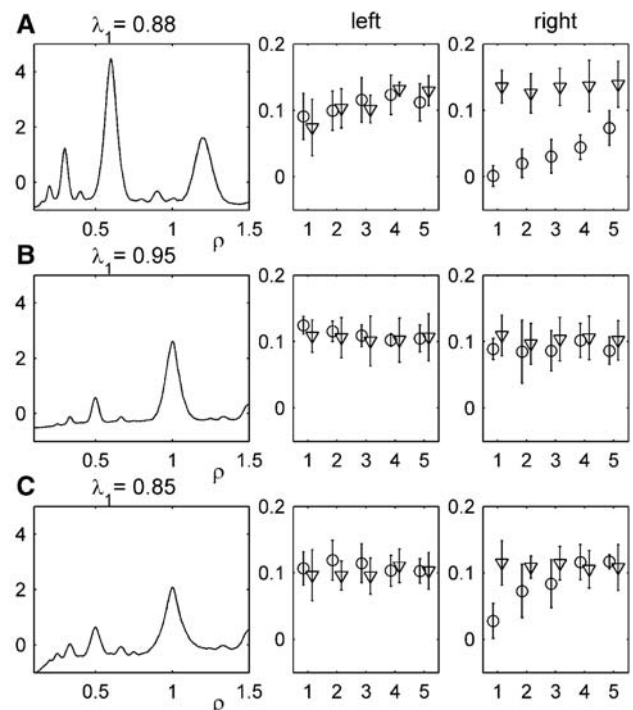


Fig. 2. Projections and eigenvectors of the first mode of PLS analyses of the frequency locking spectra: (A) First PLS mode of frequency-locking between the force production of the left and right side. Left panel: projection of the first mode revealing a peak in the frequency locking at 0.6 (3:5); the first mode explained 88% of the total variance. Right panels: eigenvector coefficients for trial 1 to 5 in both conditions (left: fast rhythm on left side; right: fast rhythm on right side). Circles refer to participants that started with the fast frequency on the right hand and triangles to participants that started with the fast frequency on the left side (error bars indicate the between-subject standard deviation). (B) First PLS mode of frequency-locking between force production of the fast hand and the fast pacing signal explaining 95% of the variance. (C) First PLS mode of frequency-locking between force production of the slow hand and the slow pacing signal explaining 85% of the variance.

<sup>2</sup> Similar to the more common Gabor transform, a complex Morlet wavelet includes a sliding Gaussian window of width  $a$ , which defines time scales or a certain frequency band around a central frequency  $f_0$ . It reads  $w(t, a) = \sqrt{\frac{1}{\pi a}} \exp\left\{-\frac{t^2}{a}\right\} e^{2\pi i f_0 t}$  in which  $t$  is time and  $i$  denotes complex unit.

were directly related to changes in event-related power, we compared the *brain scores* of the frequency coupling of the force signals with those of the time-frequency power of the SAM channels by means of conventional Pearson correlations for individual participants. For subsequent group analysis, the correlation coefficients were Fisher-transformed and tested for significance using a one-sample *T*-test.

## Results

### Analysis of motor behavior

Participants clearly learned the desired motor task (cf. Fig. 1). Their performance improved as signified by the convergence of the frequency locking between the force productions of both fingers towards the 3:5 polyrhythm. PLS analysis of rescaled cross-spectral overlaps extracted the 3:5 frequency locking in the first mode, which represented 88% of the variance (Fig. 2A, left panel). Apart from a peak at 3:5=0.6, the analysis also revealed small peaks at 0.3 (=3:10) and 1.2 (=6:5), i.e., at a higher harmonic and a subharmonic, presumably because the signals were not perfectly sinusoidal. As is evident from the right panels of Fig. 2A, the coefficients of the first eigenvector showed a significant increase in 3:5 frequency locking strength over trials ( $F(4,28)=11.9$ ,  $P=0.000$ ). The coefficients further revealed that participants who initiated the protocol with the fast frequency on the right side displayed a weaker frequency locking during that condition (Fig. 2A, most right panel), which was confirmed by a significant effect of *side* ( $F(1,7)=9.96$ ,  $P=0.016$ ) and a significant *side*×*order* interaction ( $F(1,7)=44.1$ ,  $P=0.000$ ). In that condition, the improvement in performance over trials was stronger than in the other conditions ( $F(4,28)=3.90$ ,  $P=0.012$ ). The improvement in performance was mainly due to improved timing of the slow finger, that is, the fast hand followed the fast pacing signal almost correctly from the start of the experiment (cf. Fig. 1 and Summers

et al., 1993b). The frequency locking between the fast finger and the fast pacing signal revealed a 1:1 frequency locking (Fig. 2B, left panel), and the strength of this frequency locking remained by and large constant during the experiment (see eigenvector coefficients in Fig. 2B, right panels). The steady performance of the fast finger was also underscored by the absence of any significant effect in the ANOVA. The slow finger, on the other hand, showed an obvious change in performance over trials as revealed by the frequency locking strength with the slow pacing signal: frequencies were locked at a 1:1 ratio throughout the experiment, but the locking strength increased over trials (Fig. 2C). The ANOVA of the corresponding eigenvector coefficients showed a significant effect of *trial* ( $F(4,28)=3.15$ ,  $P=0.029$ ) and a significant *trial*×*order* interaction ( $F(4,28)=2.92$ ,  $P=0.039$ ), implying a stronger increase over trials for participants starting with the right finger at the fast frequency. Finally, a significant three-way interaction between *trial*, *side*, and *order* ( $F(4,28)=6.24$ ,  $P=0.001$ ) demonstrated that the strongest increase in performance occurred in the right side condition of participants that started with the fast frequency for the right side (cf. Fig. 2C, right panel, circles).

### Analysis of brain data

SAM analysis revealed a clear event-related decrease in beta power originating from the contralateral motor cortex. The maximal pseudo-*T* values averaged over participants were 10.6 and 11.1 for the left and right motor cortex, respectively (Fig. 3).

As displayed in the time–frequency plots of Figs. 4C and D, the wavelet power of the rectified EMG showed a broadband increase peaking about 100 ms before the maximum force output. Neither the force trajectories nor the change in EMG power changed across conditions as revealed by the corresponding eigenvector coefficients (Fig. 4A–D, right panels). The event-related wavelet power of the reconstructed source data of both motor cortices revealed a clear modulation of power in the beta band with the maximum

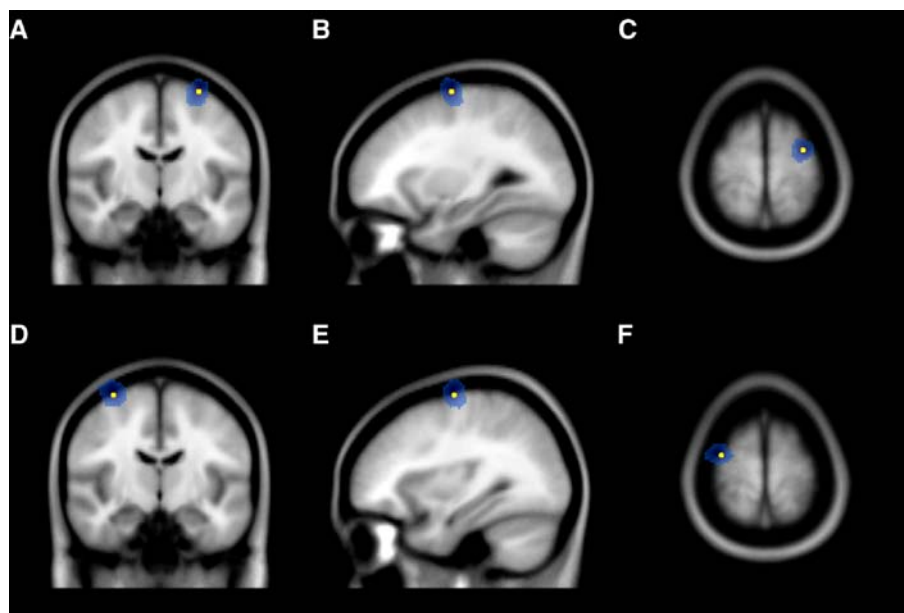


Fig. 3. Results of the SAM analysis: upper panels show the most prominent virtual channel (average pseudo-*T*, 11.1) when subjects produced forces with their left index finger in coronal image A, sagittal image B, and axial image C; lower panels display the same information for the right index finger (average pseudo-*T*, 10.6). Coronal and axial views show left on left.

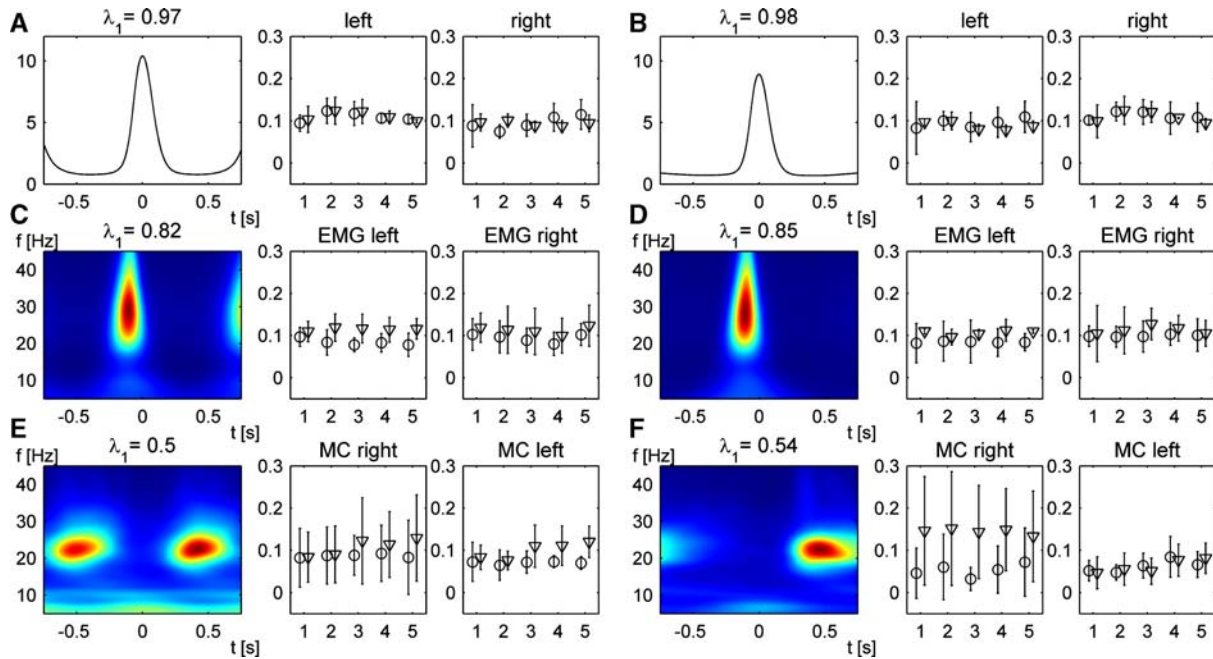


Fig. 4. Projections and eigenvectors of PLS analyses: (A) First mode of PLS of the force trajectories of the fast hand averaged with respect to the force maxima explaining 97% of the variance. Left panel shows the projection and the right panels show the eigenvector coefficients of the corresponding conditions. Circles refer to participants that started with the fast frequency on the right hand and triangles to participants that started with the fast frequency on the left side (error bars indicate the between-subject standard deviation; x-axis, time in second; y-axis, force output). (B) First PLS mode of the force trajectories of the slow hand explaining 98% of the variance. (C) First PLS mode of the event-related wavelet power of the EMG of the fast hand explaining 82% of the variance. Left panel shows the time–frequency plot corresponding with the projection (red: increase in power, blue: decrease in power; x-axis, time in seconds; y-axis, frequency in Hz) and the right panels show the corresponding eigenvector coefficients. (D) First PLS mode of the event-related wavelet power of the EMG of the slow hand explaining 85% of the variance. (E) First PLS mode of the event-related wavelet power of the reconstructed source data of the contralateral motor cortex of the fast hand explaining 50% of the variance. (F) First PLS mode of the event-related wavelet power of the reconstructed source data of the contralateral motor cortex of the slow hand explaining 54% of the variance.

increase between 20 and 25 Hz (Figs. 4E and F). The beta power was inversely related to the produced force in that it was minimal during maximum force production and increased when the force decreased again. In the motor cortex contralateral to the fast finger the increase in beta power peaked around 400 ms after the force maximum (Fig. 4E), while in the motor cortex contralateral to the slow finger the increase occurred slightly later, at about 500 ms (Fig. 4F). The modulation of beta power was noticeably related to the force production of the contralateral hand as the event-related power revealed no evident pattern when averaged with respect to the force maxima of the ipsilateral hand (results not shown here).

#### Analysis of brain–behavior covariates during motor learning

The eigenvector coefficients revealed a significant increase of the modulation of event-related beta power over trials both for the motor cortex contralateral to the fast ( $F(4,28)=5.17$ ,  $P=0.003$ ) and the slow finger ( $F(4,28)=4.17$ ,  $P=0.009$ ), suggesting a relationship with motor performance (Figs. 4E and F, right panels). The ANOVA revealed no other significant effects. The direct comparison with the bimanual performance score, i.e., the Pearson correlation between brain scores of frequency locking in individual data segments and brain scores of event-related power in the motor cortices, showed that beta modulation was indeed positively correlated with motor performance. For the motor cortex contralateral to the fast finger the correlation was significant for two of the nine participants (mean correlation:  $0.13 \pm 0.23$ ), but

grouped over all participants the correlation coefficients did not differ significantly from null ( $T(8)=1.70$ ,  $P=0.127$ ). For the motor cortex contralateral to the slow finger the correlation was significant for four of the nine participants (mean correlation:  $0.29 \pm 0.30$ ) and grouped over all participants the correlations differed significantly from null ( $T(8)=2.91$ ,  $P=0.019$ ).

#### Discussion

We studied learning-related changes in cortical activity during isometric, bimanual force production, coordinated as a 3:5 polyrhythm. Motor learning was evidenced as improved performance of the polyrhythm with practice quantified as the strength of frequency locking between the fingers' force trajectories that increased at the 3:5 target ratio. The degree of beta modulation was directly correlated with the behavioral outcome, especially for the motor cortex contralateral to the finger performing the slow component of the polyrhythm. Put differently, our results clearly indicated that when participants learned to perform the bimanual polyrhythm, the accompanying event-related beta modulation was enhanced, in particular in the contra-lateral motor cortex of the more-difficult-to-adjust end-effector, here, the slow finger. Hence, these data suggest that motor learning was associated with a change in neural activity in cortical motor areas that differed across hemispheres. This suggestion is consistent with the insight gleaned from behavioral data that learning a polyrhythm is achieved by interleaving the timing of the slow hand into that of the fast hand (Summers et al., 1993a).

When moving voluntarily, neurons in the motor area have been proposed to shift from an activated state (~ERD) to a resting state (~ERS) following movement termination, or from a processing to an idling mode (Pfurtscheller et al., 1996). We have shown that this idea finds principal support during rhythmic motor production, as was already reported in, for instance, Toma et al. (2002) and Boonstra et al. (2006). That is, beta amplitude was relatively lower during individual motor events and increased in between such movements (Fig. 4). Importantly, however, rhythmic movement lacks movement termination as participants are in a continuously active motor state. Hence, we here submit that event-related beta synchronization is probably unrelated to movement termination. To strengthen that argument we note that post-movement beta rebound often exceeds the level of beta activity during rest and decreases back to base level 1 s after movement termination (Jurkiewicz et al., 2006). This suggests that event-related beta synchronization does not just reflect a passive shift back to a resting state, but is likely to have a more active role, such as active immobilization or inhibition of cortical networks (Salmelin et al., 1995; Cassim et al., 2001; Pfurtscheller et al., 2005).

We analyzed the interdependence of brain and behavior via PLS, i.e., using the statistical co-variation between signals. Using this measure the causality in the relation between brain and behavior cannot be determined. To do so, we examined phase synchronization between MEG and EMG but failed to pinpoint a statistically significant coupling. Indeed, the absence of cortico-muscular synchronization is in line with other studies reporting vanishing synchronization during dynamical movements (Kilner et al., 2000). Likewise, the presence of enhanced beta modulation during motor learning that we report is compatible with other studies on altered cortical activity during motor skill acquisition (Recanzone et al., 1992; Pascual-Leone et al., 1994; Sanes and Donoghue, 2000). Our results also complement reports on enhanced event-related alpha desynchronization during (implicit) motor learning (Zhuang et al., 1997), increased cortico-spinal beta synchronization following visuo-motor skill learning (Perez et al., 2006) and increased interhemispheric synchronization during the early stage of bilateral learning (Andres et al., 1999). Taken together, these findings suggest that the change in beta modulation reflects a reorganization of neural activity in the motor cortex during skill acquisition. Interestingly, one finds a general consensus that event-related beta synchronization is, at least primarily, generated in the contralateral motor area located anterior to the central sulcus (Salmelin et al., 1995; Jurkiewicz et al., 2006) or near the postcentral sulcus (Parkes et al., 2006). Notice that our focus on activity in the primary motor cortex was not meant to imply that activity in other brain areas was not altered in the course of motor learning. Several studies showed various changes in, for instance, supplementary motor areas, premotor cortex, and singulate motor cortex (Sadato et al., 1997; Debaere et al., 2001; Schaefer et al., 2005). Here we simply have to conclude that these areas did not display significant changes in the frequency regimes under study. That is, concentrating on the beta band primarily extracts activity in primary motor areas.

The functional role of these changes in the beta band remains to be clarified, in particular in light of the high variability in ERD and ERS across events and participants.<sup>3</sup> Here, it seems important to

note that the strength of beta modulation can also be affected by other motor parameters, for instance, it is diminished at higher movement frequencies (Toma et al., 2002) and higher force levels (Daffertshofer et al., in press). The common denominator of these diverse studies is a reduction of beta modulation with increased motor demands. For the present study, this appears consistent with the view that during the initial stage of motor learning additional attention is required as the motor skill is not yet automated (e.g., Halsband and Lange, 2006). This interpretation finds more support by the stronger increase in beta modulation of the motor cortex contralateral to the slow finger which is known to be the bottleneck for proper performance of a challenging polyrhythm (Daffertshofer et al., 2005). In agreement, we observed that beta modulation of the contralateral motor cortex of the slow finger was directly correlated with the motor performance itself.

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