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## Neural entrainment in coordination dynamics

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## Chapter 3

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# Activity in primary motor areas during motor learning

*A brain can improve till it fits in its environment.*

Ross Ashby

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## Abstract

*Motor tasks are well suited to induce readily identifiable brain states. Motor control is accompanied by activity in specialized areas with a continuous adjustment of the flow of information. In the present study we focused on interactions between hemispheres during the learning of a bimanual coordination pattern. To be able to associate neural activation with performances of the individual hands, we employed polyrhythmic movements during which the left and right fingers move at a rational frequency ratio. An increase in the stability of performance was observed in the form of a strengthened frequency locking, achieved primarily through an improved timing of the slow hand. The accompanying changes in brain states could be localized using synthetic aperture magnetometry of whole-head MEG that revealed significant changes in bilateral motor areas and cerebellum. As expected, the adapted motor output was reflected in changes in overall timing of motor areas. To further characterize the timing, we explored the role of  $\beta$ -oscillations, where a tighter modulation in motor areas contralateral to the adapted hand was found.*

Coordination of movements most likely involves ongoing interaction between left and right hemispheres. In fact, even for unimanual repetitive finger movements the spatiotemporal patterns of associated neural activity appear very rich. For instance, bilateral activation was found, implying an active cross-talk or coupling between hemispheres (Baraldi et al., 1999; Cheyne and Weinberg, 1989). In bimanual movements, this coupling is yet more evident as one finds frequency- and phase-locked patterns in the associated neural activities (Daffertshofer et al., 2000a). The aim of the current study was to gain more insight into the functional role of the oscillatory activities in the  $\beta$ -frequency band of the motor network and, in particular, in the timed coupling between oscillatory activities. To achieve changes in the network topology, we probed motor performance through slow adaptation and invited subjects to learn a polyrhythmic motor task requiring an integration of perceptual and motor components. Here, we present preliminary results, while an extensive analysis will be reported elsewhere.

### **3.1 Methods**

Subjects were asked to exert isometric flexion forces with their index finger in a 3:2 polyrhythm. To improve performance, we provided visual feedback by mapping the performance to the more accessible 1:1 coordination (Mechsner et al., 2001): left and right forces were shown as two disks that, in the case of proper performance, both rotated at the frequency of the fast finger. Target frequencies for the right and left hands were 1.2 Hz and 0.8 Hz, respectively. Pacing of the right hands frequency was provided at the right ear. Unimanual and bimanual isofrequency performances (eight repetitions of 25s each) served as control conditions before and after the learning trials (40 trials of 40s each). Brain activity was recorded using a 151-channel MEG system (CTF Systems Inc., Vancouver) using 3<sup>rd</sup>-order synthetic gradiometers. EMG was assessed from bilateral extensor and flexor digitorum and isometric forces were recorded using MEG-compatible sensors. Prior to digitization at 1250 Hz a low-pass filter at 400 Hz was applied. All signals were mean-centered and high-frequency noise was eliminated with a 2<sup>nd</sup>-order bi-directional Butterworth low-pass filter at 400 Hz. In addition, EMG signals were high-pass filtered at 10 Hz to remove movement artifacts and then

rectified using the Hilbert transform. To save computational costs, the signals were down sampled to 250 Hz and eventually normalized to unit variance to account for possible differences in signal strength.

In a previous study, we identified the topology of the neural network involved by comparing control conditions pre and post learning (Houweling et al., 2008b). Synthetic aperture magnetometry (SAM) provided optimal projections from sensor space to source space (Vrba and Robinson, 2001). Based on maximal differences in normalized source power between pre and post learning trials, the source locations of motor areas and cerebellar hemispheres were defined. Building on these findings we assessed the timing properties of the earlier pinpointed bilateral primary motor cortices (M1), see Fig. 2.4, left panels.

Stability of performance was indexed by the 3:2 phase locking at the movement frequencies between the right and left EMGs. Phase uniformity of the relative phases of the narrow-band filtered signals (2<sup>nd</sup>-order Butterworth filter, bandwidth 0.1 Hz) around the corresponding movement frequency was computed. Furthermore, the envelope of  $\beta$ -oscillations was extracted by applying the Hilbert transform after filtering the projected MEG signals in the  $\beta$ -band (20–30 Hz), referred to as  $\beta$ -M1<sub>Right/Left</sub>. We also computed power spectral densities via Welch's periodogram (window size: 4096 samples) for each signal and calculated the power around the movement frequency, to be applied as an indicator of quality of timing. Each curve was smoothed by applying a moving average filter (1<sup>st</sup>-order Savitzky-Golay with frame size 7). For statistical evaluation, we calculated Pearson's correlation coefficients between the individual learning curves and the spectral changes of both EMG and M1 for every subject and signal. We further looked at the progress of more global features and constructed, for each trial and each channel, a decomposition in eigenmodes of the normalized power spectral densities via principal component analysis (PCA) (Boonstra et al., 2007). The first five trials were disregarded to eliminate transients from the analysis; from then on the subjects were considered to be acquainted with the task at hand.

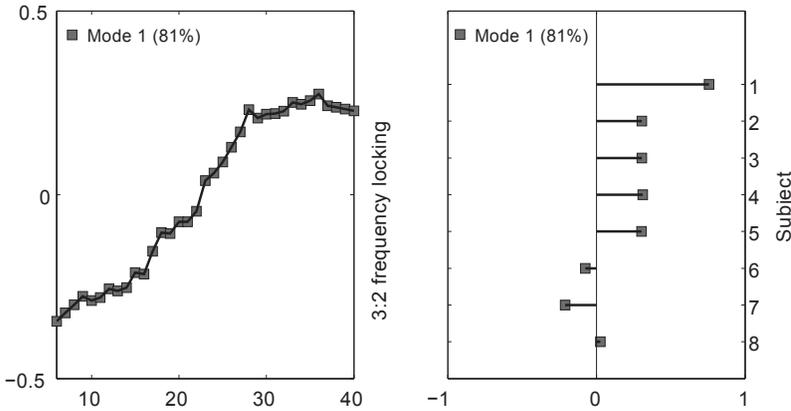
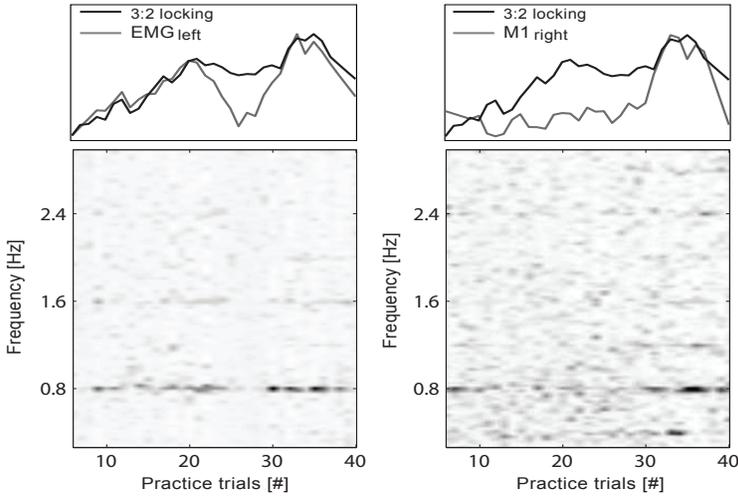


FIGURE 3.1: Left panel: learning is reflected in an increase in 3:2 phase locking between the EMG of the flexor digitorum in the right and left hand expressed by projection of the phase uniformity onto mode 1 (eigenvalue: 0.81). Right panel: corresponding eigenvector coefficients.

### 3.2 Results

Principal component analysis of the individual development of the 3:2 phase locking between right and left EMG showed that subjects learned the motor task (see Fig. 3.1). The projection onto the first mode, explaining 81% of the variance, reflects a monotonous increase in phase locking. Subjects 1–5 improved, as evidenced by the positive eigenvector coefficients in the right panel. Subjects 6 and 7 were able to perform the task from the very first trial onwards and Subject 8 failed to reach a proper performance and was therefore excluded from further analysis. The results for the M1s were not that homogenous, which was expected in view of the well-known degree of interindividual variability during motor learning.

The increase in phase locking was primarily caused by an adaptation of timing in the slow hand, as illustrated by the sample of Subject 3 in Fig. 3.2. Indeed, the correlations between the change in spectral power at the movement frequency and the individual learning curves were greater for the left EMG than the right EMG (cf. Table 3.1). This effect was mirrored in the M1s, as the correlation coefficients were larger for  $M1_{\text{right}}$  than  $M1_{\text{left}}$ , especially in the subjects whose performance improved. Note also the presence of higher harmonics in the spectrogram



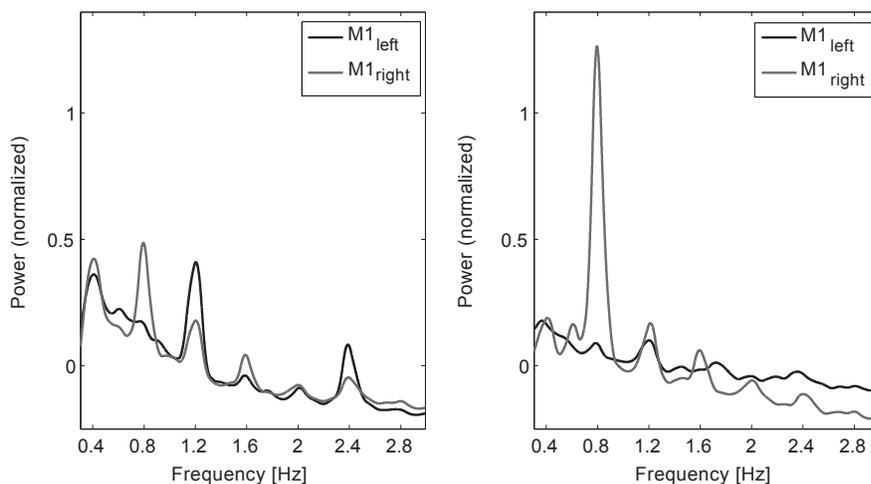
**FIGURE 3.2:** Distribution of spectral power over the frequency range 0.25 – 3 Hz during learning trials in left EMG (left panels) and M1<sub>right</sub> (right panels) in Subject 3. Depicted above is the progress of the average power (black lines) around the relevant movement frequency (0.8Hz) versus the learning curve (grey lines); the top graphs are scaled to unit interval.

of the left EMG. The fast frequency (1.2 Hz) and its higher harmonics can be discerned in M1<sub>right</sub>, as well as the first coinciding sub-harmonic of both movement frequencies.

The projections onto the first mode of the overall activity in M1s contained both the slow and fast frequency, where the power around the movement frequency of the contralateral end-effector was largest (see Fig. 3.3). Note that in the EMGs the ipsilateral frequency dominated. In contrast, the fast frequency was much less pronounced in the first mode of  $\beta$ -amplitude in M1<sub>right</sub>, and, surprisingly, also in M1<sub>left</sub>. This mode becomes increasingly more dominant as the eigenvalue grows from about 0.65 to a maximum of 0.78 in the last trial. Simultaneously the eigenvector coefficients, averaged over the subjects (3–5) that contributed most to this mode, increased progressively.

**TABLE 3.1:** Pearsons correlation coefficients between individual learning curves and spectral power at movement frequencies of left/right EMG and M1<sub>left/right</sub> (\*\* denotes  $p < .01$  and \* denotes  $p < .05$ )

	Subject #						
	1	2	3	4	5	6	7
left EMG	0.99**	0.89**	0.82**	0.39*	0.50**	0.62**	0.64**
right EMG	0.57**	0.76**	0.69**	0.76**	0.75**	-0.04	-0.17
M1 <sub>right</sub>	0.82**	0.06	0.68**	0.77**	-0.45*	-0.41*	-0.48**
M1 <sub>left</sub>	-0.47**	0.49**	0.16	-0.43*	-0.49**	-0.29	0.11
$\beta$ -M1 <sub>right</sub>	0.59**	0.42*	-0.12	0.71**	-0.34	0.28	0.09
$\beta$ -M1 <sub>left</sub>	0.06	-0.17	0.29	-0.65**	0.32	-0.73**	-0.06



**FIGURE 3.3:** Projection onto first mode of power spectral densities in M1s (M1<sub>left</sub>: black lines, M1<sub>right</sub>: grey lines) of overall activity (left panel) and  $\beta$ -amplitude (right panel) during steady state performance (averaged over trials 26–40) for Subjects 1–7.

### 3.3 Discussion

Motor learning was achieved primarily via an adaptation of timing in the slow hand, consistent with the findings of Summers and colleagues (Summers et al., 1993a) that during learning to tap a 2:3 polyrhythm the timing of the slow hand is integrated into that of the fast hand. Motor learning was accompanied by changes at multiple levels of neural activity. As expected, the changes in overall timing in both primary motor cortices matched the motor output. Improved timing of the slow hand correlated directly with an increase in power at the movement frequency in contralateral M1, in particular in subjects whose performance improved. Power spectral densities of bilateral M1s revealed that both fast and slow frequency components were observed, including sub- and higher harmonics. These findings suggest that an active neural cross-talk (Daffertshofer et al., 2005) was present, as evidenced further by a diminished power at the contralateral frequency in the EMGs. Furthermore, we found that  $\beta$ -activity was primarily modulated at the frequency of the slow hand. The presence of slow frequency modulation of the  $\beta$ -amplitude suggests that  $\beta$ -oscillations may be functionally related to motor learning, as encoding of movement-related information may be transferred and processed via slow amplitude modulation. Moreover, PCA revealed that the degree of  $\beta$ -modulation progressively increased during motor learning. Note that the correlation analysis, summarized in Table 3.1, does not allow for an equivalent conclusion, presumably because it was confounded by the presence of harmonics of the movement frequencies. To conclude, better timing is reflected both in the overall activity of the M1s, and in a tighter  $\beta$ -modulation in  $M1_{\text{right}}$ .