Neural entrainment in coordination dynamics

Houweling, S.

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Summary

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The present thesis focuses on the role of neural synchronization in the information exchange between distant components of the nervous system. Pinpointing this information transfer is a prerequisite for understanding the neural correlates of motor control, which comprise an intricate network including supplementary motor areas, premotor areas, primary motor areas, the corpus callosum and the cerebellar hemispheres. Motor performance entails a delicate orchestration of neural activity across this motor network. Various oscillatory processes are manifest during movement production and different frequencies are related to different task constraints and associated cognitive demands. Rhythmic activities in different brain areas map to motor units innervating the muscles involved. These interplays are central to this thesis. **Chapter 1** offers a succinct, general introduction to these issues as well as to the data acquisition and analysis methods used in this thesis.

The experimental task in the studies presented in this thesis consisted of rhythmic finger movements or rhythmic isometric force productions by the index fingers. Concurrent brain activity was recorded using magneto-encephalography (MEG) while the electric activity of the motoneurons innervating the muscles involved was recorded using electromyography (EMG). To identify brain sources that contributed to the brain activity as measured at the surface, a beamformer method was applied allowing estimation of active sites and, more importantly, local activity.

Two experiments were conducted building on earlier research on bimanual coordination involving the production of polyrhythms (*i.e.*, two frequencies that stand to each other as relatively prime integers other than 1, *e.g.*, 2:3 and 5:8). Polyrhythmic performance is an excellent task for disentangling (sub)cortical activity associated with left and right performances within the overall (sub)cortical activity, while requiring a functional coupling between left and right motor hemispheres. The left/right interactions were assessed with the aim to test several predictions of a heuristic model accounting for interhemispheric inhibition during uni- and bimanual coordination. One common view on movement coordination is that excitatory bilateral connections persistently lead to neural cross-talk in contralateral hemispheres. If so, the unintended, contralateral motor activity has to be inhibited in order to produce unilateral movements. If the stability of the motor performance is challenged, the inhibition may fail and the bilateral interaction may cause neural cross-talk and mirror movements.

Chapters 2, 3 and 4, concentrate on the neural changes that occur during the learning of a complex bimanual task. Learning is considered to be a neural process that supports the adaptation to task requirements. The adaptation is evident as improvement at the behavioral level and accompanied by comparably slow neural plasticity. Chapter 5, in contrast, focuses on neural changes during polyrhythmic tapping while rapidly increasing the target tempo, which imposed the required tapping frequency via acoustic pacing. At a critical tempo, the stability of production of the bimanual coordination pattern is lost resulting in a transition from steady to unstable performance, permitting detailed study of the so-induced movement instabilities.

For the learning study, a group of musically untrained subjects were invited to produce a 2:3 polyrhythm during a session of about 80 minutes (20 minutes pre-test-protocol, 40 minutes training/learning, and 20 minutes post-test-protocol; during the test-protocol unimanual [left and right] and bimanual isofrequency movements were performed). Analysis of the behavorial data showed that the improvement of bimanual coordination was achieved primarily via amended timing of the slow hand. Next, this improvement at the behavioral level was linked to neural activities, as recorded with MEG and EMG, in the frequency ranges 7–11 Hz (α-band), 20–30 Hz (β-band) and 40–70 Hz (γ-band).

Chapter 2 describes the effects of training of the 3:2 polyrhythm on neural activity during unimanual and bimanual isofrequency movements, as performed during the pre- and post-tests. The largest changes in power were found in the motor cortices and cerebellar hemispheres. These changes were broadband since they covered the complete frequency domain under investigation. The after-effects were larger for the right motor cortex than for the left motor cortex. Such left/right differences were not found in the cerebellar hemispheres. An event-related analysis based on the movement cycle revealed an amplitude modulation of β-activity in the motor cortices, and an amplitude modulation of α-activity in the cerebellar hemispheres. This modulation of α-amplitude was reinforced after training. Likewise, the coupling between bilateral motor areas increased around the movement frequency, which reflected improved motor timing. Furthermore, the inter-hemispheric γ-synchronization between primary motor areas decreased, which may reflect reduced attentional demand after training. These changes in synchrony between distant areas were an effect of sustained practice, and they were only weakly correlated with performance improvement.

The decrease and increase of local synchrony of β-activity in the motor cortex during the movement cycle, however, became more pronounced as performance improved. This was particularly evident in the motor cortex contralateral to the slow hand. We concluded in **Chapter 3** that increased β-modulation in general displays an improvement of the neural mechanism controlling movement timing. Accompanying the increase in cortical β-amplitude, a brief episode of increased cortico-spinal synchronization between EMG and contralateral motor cortex was found. **Chapter 4** further shows that improvement of task performance correlates strongly with increased synchronization between the ensemble of cortical motoneurons and alpha motoneurons of the muscles involved. This finding suggests that precise timing in muscle control benefits from a mechanism that employs cortico-spinal synchronization.

When learning a bimanual coordination task the timing of left and right muscle activity is of crucial importance. The two hands, however, are not controlled independently, which may lead to interference of limb movements. In terms of the aforementioned heuristic model one can hypothesize that with increasing stability, or improved coordination, the bilateral coupling decreases. The learning studies in Chapters 2, 3, and 4 did not succeed in bringing such differential stability in bilateral coupling clearly to the fore. It may well have been that the slower time scale of adaptation during learning prohibits observing subtle changes in the overall the well-tuned neural cross-talk. Therefore, a transition study was conducted, in which abrupt changes were induced in cross-talk to test the interhemispheric inhibition model in detail.

In the experiment in question, a group of percussionists tapped a 5:8 polyrhythm while the target tempo was continuously increased. The 5:8 pattern lost stability when the tempo of the fast finger reached about 5.1 Hz, as evidenced by a sudden drop in 5:8 frequency locking between the left/right tapping signals. **Chapter 5** describes how the accompanying pattern of desynchronization and synchronization of β-activity (corresponding to the movement 'on/off' cycles) in motor cortex during the movement cycle changed while the tempo increased. The β-modulation decreased, while the temporal distance between the episodes of desynchronization and synchronization diminished. Here it could be argued that coordination is limited by certain constraints of the underlying neurophysiologic mechanism. That is, the time required to build up local changes in synchronization within a neuronal ensemble could limit the central control of the muscles involved. The time scale of this mechanism presumably has repercussions for the interactions between the cerebral hemispheres: the movement instability was accompanied by an increased cross-talk, indexed as the ratio between the amounts of spectral power at both movement frequencies, between the motor cortices. That cross-talk occurred at the movement frequency, suggesting that the bilateral phase locking over movement cycles is mediated by high-frequency (β-)oscillations and constrained by its phase dynamics.

In the epilogue, **Chapter 6**, the findings presented in the preceding chapters are embedded in and contrasted against current ideas about motor control. The integration of different structures in the nervous system required for motor control seems to be established by means of synchronization of their neural activity. The functional role of oscillatory neural activity and synchronization across the motor network therefore renders studying motor control in the framework of phase oscillators a productive approach. And *vice versa*, paradigms in motor control are particularly apt to investigate the underlying mechanisms of synchronization. After a general discussion of neuronal mechanisms and their attributed functions, future lines of research are proposed that build on the knowledge gained throughout the work reported in this thesis. With the insights that progressed from these studies, this thesis contributes to a better understanding of the form and function of the oscillatory processes that have been observed at multiple levels in the central and peripheral nervous system.