Neural dynamics of human motor control

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Summary

The present thesis addresses the question how cognitive processes influence the neural control of action. Cognition was expected to modulate neural dynamics, in general, and oscillatory activity and its synchronization, in particular. To investigate this general expectation, several experiments were conducted in which task-related variables like force level, central and peripheral fatigue, movement tempo, and task difficulty, were varied to induce changes in the accompanying neural synchronization. Neural activity was recorded using electromyography (EMG) and magnetoencephalography (MEG), while participants performed either static isometric or dynamic rhythmic tasks.

In Chapter 1, basic concepts of synchronization in brain activity are introduced. It is argued that a focus on synchronization stands in the scientific tradition that considers processes as fundamental and is therefore complementary to more structure-oriented approaches that try to identify modular processes of specialized brain regions. Next, a concise sketch of the theory of complex systems is provided because this theory provides an adequate conceptual framework for studying the behavior and coupling of dynamical compounds like neural oscillators, as has been amply demonstrated in the field of neuroscience. This sketch is followed by a brief discussion of the pertinent literature on neural synchronization showing that synchronization can provide mechanisms of feature binding or motor integration. Finally, the thesis' main threads are outlined by introducing the investigated experimental tasks and applied data analysis methods.

In Chapter 2, two experiments are discussed that examined the effects of muscle fatigue on motor-unit (MU) synchronization between the quadriceps muscles of both legs. Muscle fatigue was expected to result in an increased common drive to different MUs of synergists within a leg and, hence, to increased MU synchronization. It was further expected that fatigue-related motor overflow may cause MU synchronization of homologous muscles of both legs, although to a lesser extent than for synergists within a leg. In the first experiment, different levels of fatigue were induced by varying posture (knee angle), while in the second experiment fatigue was induced by having participants produce different force levels in a fixed posture. Synchronization, quantified in terms of coherence between surface EMG, was found in two distinct frequency bands (6-11 and 13-18 Hz), more prominently so within a leg than between legs. The inter-limb synchronization in the 6-11 Hz frequency band increased with fatigue and resembled increased motor overflow during unimanual contractions. As such, the two phenomena may be related in that they both indicate a fatigue-induced increase in bilateral coupling. MU synchronization at 13-18 Hz was clearly different and depended on posture.

Chapter 3 reports a similar experiment that was designed to study the relation between bilateral MU synchronization and motor overflow. The bilateral coupling between homologous arm muscles was compared during fatiguing elbow flexion and extension contractions. Similar to the results of Chapter 2, MU synchronization was found in the 8-12 Hz frequency band, more strongly so when fatigued. This fatigue-related increase in bilateral MU synchronization was stronger between extensor than between flexor muscles, which appeared consistent with the literature on mirror movements and supported the alleged link between bilateral MU synchonization and fatigue-related motor overflow. In contrast to the study on leg muscles in Chapter 2, the arm muscles did not exhibit MU synchronization in the 13-18 Hz frequency band, which seemed consistent with the hypothesis that MU synchronization in the higher frequency band, as described in Chapter 2, was linked to balance maintenance. The results are discussed in terms of common bilateral input and substantiate the idea that common input is functionally organized.

The experiment reported in Chapter 4 deals with the effects of sleep deprivation (SD) on cortical brain activity during acoustically paced rhythmic force production. MEG was recorded during a rhythmic motor task that was conducted at two consecutive days between which SD was induced by keeping participants awake, i.e. participants did not sleep for at least 24 hours. Effects of SD on brain activity were examined via spatial distribution of spectral power over the scalp at different frequency bands and via auditory- and motor-evoked fields. For the latter, principal component analysis (PCA) revealed that auditory- and motor-evoked fields were attenuated after SD. Furthermore, an anterior shift of alpha power towards more frontal channels was found. At the behavioral level, SD resulted in a reduction of the lag (negative asynchrony) between produced forces and acoustic stimuli at higher movement tempos. Conjointly, these results are interpreted in terms of a change of central processing of afferent sensory input due to SD.

In Chapter 5, the event-related brain activity associated with the performance of an acoustically paced synchronization task is further examined. To gain insight into the neural dynamics causing the auditory- and motor-related activity, the amplitude and phase dynamics inherent in MEG signals were analyzed across frequency bands. By comparing amplitude and phase dynamics, a distinction was made between so-called evoked and induced responses. Again, PCA was used, this time, however, to compare amplitude and phase changes during mere listening, paced and unpaced tapping. Using PCA allowed for a separation of brain activity related to motor and auditory processes, respectively. Motor performance was accompanied by phasic amplitude changes and increased phase locking with the taps in the beta band. Auditory processing of acoustic stimuli resulted in a simultaneous increase of amplitude and phase locking with those stimuli in the theta and alpha band. The temporal overlap of auditory-related amplitude changes and phase locking indicated an evoked response, in accordance with previous studies on auditory perception. The temporal difference of movement-related amplitude and phase dynamics in the beta band, on the other hand, suggested a change in ongoing brain activity, i.e. an induced response supporting previous results on motor-related brain dynamics in the beta band.

Chapter 6 concerns a study on the changes in neural synchronization during motor learning. To this end, MEG and EMG activity was recorded while participants learned to perform a 5:3 polyrhythm. As this task involved bimanual rhythmic activity at distinct movement tempos, it was expected to elicit neural activity in bilateral motor cortices that could be readily disentangled. Building on the results of Chapter 5 regarding motor-related fields, synthetic aperture magnetometry (SAM) analysis was used in focusing on the beta band in order to separate bilateral activity in both motor cortices. On a behavioral level, performance converged onto the to-be-learned 5:3 polyrhythm in the course of the experiment. The SAM-based reconstruction of the activity of the motor cortices revealed phasic changes in beta activity related to force production of the contralateral finger. The degree of beta modulation increased during the experiment and was positively correlated with motor performance, in particular for the motor cortex contralateral to the slow hand. These findings support the view that activity in motor cortex co-varies closely with behavioral changes in the course of learning.

In Chapter 7, the epilogue, the theoretical framework presented in Chapter 1 is recalled in order to discuss the implications of the experimental results for the understanding of brain dynamics. It is concluded from those results that neural synchronization is ubiquitous during the execution of motor tasks. In particular, two distinct synchronization patterns stood out in the various experimental settings: the 10 Hz synchronization between bilateral EMGs and the beta modulation above the contralateral motor cortex during rhythmic motor tasks. Moreover, neural synchronization was consistently modulated by various task parameters, in line with the alleged functional role of neural synchronization. Neural synchronization therefore appears to be a significant characteristic of the neural dynamics of motor control and an essential vehicle for the understanding of the temporal aspects of neural motor control. The collective results are thus consistent with the theoretical framework capitalized upon in this thesis and contribute to current discussions as to how the brain processes information in general. Especially the absence of beta synchronization during rhythmic motor performance is deemed revealing in this regard, i.e. cortical beta activity was attenuated during periods of phasic motor control and corticospinal synchronization was largely absent during rhythmic motor control. These findings suggest that instances of rhythmic and static motor control differ fundamentally. Apparently, periodic synchronized behavior does not serve as a means for motor-related information transfer between cortical and spinal areas during rhythmic motor performance. In this context, recent literature is discussed on the mode of information processing employed by the central nervous system and possible other forms of synchronization that may be present during dynamic motor control. Based on this discussion, new directions for future research are suggested that can experimentally test these extensions of the initiated research program.