

# **Synchronized sensorimotor beta oscillations in motor maintenance behavior**

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Substantial evidence supports the idea that the maintenance of tonic limb muscle contraction involves synchronized beta-frequency (15-30 Hz) oscillatory activity of neuronal assemblies throughout the motor system (Baker et al., 1999; Marsden et al., 2000; Brown and Marsden, 2001; Salenius and Hari, 2003). Beta local field potential (LFP) oscillations are synchronized between sites in primary motor cortex, and motor cortical pyramidal cell discharge tends to be synchronized with the LFP oscillations (Baker et al., 1997; Baker et al., 2003). Moreover, cortical LFP beta oscillations are synchronized with the electromyogram (EMG) of the engaged contralateral hand and forearm muscles during maintenance behavior, suggesting that beta oscillations contribute to the drive of spinal motoneuron discharge by the motor cortex (Salenius et al., 1997; Brown et al., 1998; Mima et al., 2001).

The involvement of postcentral cortical areas in the maintenance of sustained motor outflow, especially their effect on motor cortex, is not well understood. That the somatosensory cortex plays a role in motor maintenance behavior is to be expected since such behavior is known to heavily depend on somatosensory feedback (Rothwell et al., 1982). To investigate possible functional relations between somatosensory and motor cortices in maintenance behavior, we examined LFPs from both pre- and postcentral areas of two monkeys as they pressed a hand lever during the wait period of a visual discrimination task (Brovelli et al., 2004).

Spectral analysis based on multivariate autoregressive modeling was used to examine the characteristics of sensorimotor LFPs in the frequency domain. First, power spectral analysis showed that beta oscillations were prominent at many, but not all, recorded sites in both pre- and postcentral cortical areas contralateral to the hand used. Then, coherence spectral analysis allowed identification of specific pairs of sites that were synchronized in the beta range. Synchronization was observed between post- and precentral sites, as well as between postcentral sites. Overall, the strongest synchronization in both monkeys was between sites in three areas: the areas immediately anterior (primary motor cortex) and posterior (primary somatosensory cortex) to the central sulcus, and a third area inferior to the intraparietal sulcus. Finally, Granger causality spectral analysis was used to measure statistical directional influences among LFPs from pre- and postcentral sites. Granger causal influences were observed from primary somatosensory cortex to both motor cortex and inferior posterior parietal cortex, with the latter area also exerting Granger causal influences on motor cortex. Granger causal influences from motor cortex to postcentral sites, however, were much weaker in one monkey and not significant at all in the other.

Our study demonstrates that synchronized beta oscillations bind multiple areas into a large-scale sensorimotor network during motor maintenance behavior, and that they carry Granger causal influences from primary somatosensory and inferior posterior parietal cortices to motor cortex. Involvement of the inferior posterior parietal cortex is consistent with this area's known role in sensorimotor transformation (Rushworth et al., 1997). Overall, these results are consistent with the idea that beta oscillations are involved in a cortico-peripheral-cortical loop that provides continuous sensory information about peripheral conditions to the motor system during maintenance behavior (MacKay, 1997). They are also compatible with the concept of beta oscillations supporting a system-wide temporal entrainment mechanism (Marsden et al., 2000).

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