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Angaben zur Veröffentlichung / Publication details:

Raethjen, Jan, and Muthuraman Muthuraman. 2012. "Corticomuscular coupling in human locomotion: muscle drive or gait control?" *The Journal of Physiology* 590 (16): 3631–32.
<https://doi.org/10.1113/jphysiol.2012.232645>.

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Corticomuscular coupling in human locomotion: muscle drive or gait control?

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An intact gait is one of the most important and commonly used human motor functions. It is an automated repetitive motor pattern that does not require constant conscious control. Therefore its generation has been attributed mainly to spinal and subcortical regions of the central nervous system. An involvement of the motor cortex in gait control has only recently emerged mainly from animal studies (see Petersen *et al.* 2012). However, the bipedal upright gait of the human is unique.

The electroencephalogram (EEG) allows non-invasive measurement of synchronous rhythmic activity in populations of cortical neurons in man. By simultaneously recording the peripheral muscle activity (electromyogram (EMG)) during movements, it is possible to look for cortical rhythmic activity that is correlated (coherent) with the peripheral muscle activity and thus plays a role in cortical control of movements. Such corticomuscular coherence analysis is widely applied in studies of the human cortical motor system (e.g. Witham *et al.* 2011), but has not been applied during gait, largely due to movement and muscle artefacts in EEG recordings during walking.

In a recent issue of *The Journal of Physiology*, Petersen *et al.* (2012) show that such EEG–EMG coupling studies are possible in subjects walking on a treadmill if advanced processing techniques are used for artefact removal. They demonstrate beta-band (13–40 Hz) coherence between artefact-cleansed EEG and EMG during late swing and early stance phase and show a predominantly corticomuscular flow of information in this frequency band. This is the first direct evidence of a cortical involvement in muscle activation during human gait. Their findings suggest that the complex cyclic leg motor behaviour during gait is under cortical control at least intermittently.

However, as mentioned by the authors, it is not possible to assess the importance of this cortical drive for gait control. EEG–EMG coherence in the beta-band is only shown in the phase of the gait cycle when the anterior tibial muscle is activated isometrically before heel strike. This coherence was even stronger during isometric contractions performed independently of gait, as has been shown for many upper and lower limb muscles previously (e.g. Witham *et al.* 2011). Its function is still under debate. The coherence disappears in dynamic isotonic movements and there is not only cortico-muscular interaction but also feedback from muscle to cortex in this frequency band. Thus it has been argued that the beta-band coherence may fulfil other functions, such as calibrating and stabilizing the corticospinal system after dynamic movements (Witham *et al.* 2011). This may also be the role of the EEG-coherent EMG-activity in the late swing phase and its direct relation to gait itself may be questioned.

How could the EEG and EMG data be used to search for cortical activity related to the repetitive sequence of movements during gait? As illustrated in Fig. 1C of the paper by Petersen *et al.*, the repetitive activation of the anterior tibial muscle can be viewed as rhythmic bursts, reflecting the individual cadence (rhythm) of gait and so if the cortex is directly involved in controlling gait, this rhythm should be represented cortically. Thus there should be EEG activity that is coherent with the lower frequency of these muscle bursts. For other rhythmic motor behaviours of the hand and also the feet, this approach revealed similar cortical representations in the primary motor cortex of the studied limb (Raethjen *et al.* 2008) and advanced methods for coherent source analysis have even shown that the subcortical parts of the central motor network are involved (Pollok *et al.* 2004). EMG-coherence of subcortical parts of the motor network has not been unambiguously shown for the higher frequency (e.g. 15–30 Hz) band for which the representation is mainly cortical (Schoffelen *et al.* 2008; Muthuraman *et al.* 2012).

Taking the novel results of Petersen *et al.* and these considerations together, one may speculate that there is a dual

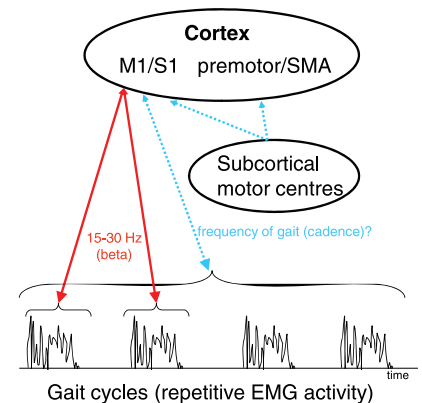


Figure 1. Hypothesized dual corticomuscular interaction during gait
Red lines indicate intermittent muscle drive in the 15–30 Hz (beta) band described by Petersen *et al.* (2012). It is only present during each muscle activation in the gait cycle as indicated by the repetitive EMG activity shown schematically at the bottom. It predominantly involves the primary sensorimotor cortex (M1/S1). The blue broken lines indicate the hypothesized second corticomuscular interaction at the low frequency of the gait cycle itself as indicated by the rate of the repetitive EMG activation drawn schematically at the bottom. The low frequency of repetitive movements may be represented not only in the primary sensorimotor but also in secondary cortical motor areas, e.g. premotor and supplementary motor cortex (SMA), and subcortical motor centres, e.g. basal ganglia, thalamus and cerebellum.

involvement of the cortex in the oscillatory control of repetitive automated movements such as gait: an intermittent localized drive at 15–30 Hz during each short isometric muscle contraction (burst), and an additional ongoing activity controlling the movement rhythm and involving large parts of the central motor network (see Fig. 1). Whereas the former is shown by Petersen *et al.* (2012), further work is needed to observe the latter and a possible connection between the two. Comparisons between different upper and lower limb repetitive motor patterns may also reveal further gait-specific cortical network components, e.g. cortical locomotor regions of man.

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Acknowledgements

Support by the Deutsche Forschungsgemeinschaft (DFG, SFB 855) is gratefully acknowledged.