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Corticomuscular coherence revealed during treadmill walking: further evidence of supraspinal control in human locomotion

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It is generally assumed that precision tasks, such as carving or painting, require a lot of attention and cortical control, whereas walking in the street may be considered as an automatic movement based on reflexes governed at the spinal level. A very recent study in *The Journal of Physiology* by Petersen *et al.* (2012) demonstrates that the motor cortex is particularly active during specific phases of the gait cycle, before the foot comes in contact with the ground. This is a new piece added to the gigantic puzzle of the neural control of human locomotion.

Accumulating evidence suggests that human locomotion is based on a very complex hierarchical system that includes several control networks located at both spinal and supraspinal levels. The spinal central pattern generator network consists of coupled antagonist oscillators specifically dedicated to extensor or flexor muscles acting at the different joints. Their mechanism allows the generation of simple and co-ordinated rhythmic movements, such as those involved in steady walking. Numerous experiments with spinal cats (i.e. cats with complete transection of the spinal cord) have demonstrated the presence of such central pattern generators in lower mammals, and a similar conclusion has been reached for primates. Regarding humans, the evidence is only indirect, as reported by Yang & Gorassini (2006).

Although the existence (and primary function) of a central pattern generator system in humans has become broadly accepted, many findings indicate that the cortex also plays an important role in human walking (Yang & Gorassini, 2006). Indeed, when lesions occur in the supraspinal region of the CNS, recovery of walking is extremely difficult and generally incomplete. This means that intact supraspinal centres are necessary for functional walking in humans.

Also, studies of direct transcranial magnetic stimulation of neurons in the motor cortex have shown that the motor cortex is likely to play a role in activating the dorsiflexors and plantarflexors during walking in humans (Petersen *et al.* 2001).

Additionally, as summarized by Presacco *et al.* (2011) and references therein, significant changes in motor and cognitive demands (i.e. spatial attention) have been observed in the context of bipedal walking in unknown or cluttered dynamic environments.

Functional neuroimaging studies have shown that the primary motor cortex is recruited during rhythmic foot or leg movements. Functional near-infrared spectroscopy has also allowed the detection of involvement of the frontal, premotor and supplementary motor areas during walking.

Finally, electrophysiological studies have provided arguments in favour of the possible cortical origin of the intramuscular and intermuscular EMG synchronization (coherence) observed in lower limbs during walking.

In this context, the work by Petersen *et al.* (2012) was aimed at investigating the coupling between EEG and EMG signals from leg muscles during treadmill walking. The authors report significant coherence between EEG signals recorded over the leg motor area (Cz electrode) and EMG from the tibialis anterior muscle in the 24–40 Hz frequency band before the heel strike, during the swing phase of the gait cycle. This result indicates that rhythmic cortical activity in this particular frequency band is transmitted to the lower limb muscles during walking. This work thus proves and confirms that the motor cortex contributes directly to the muscle activity involved in human locomotion.

The significant coherence values found for normal walking speeds (3.5–4 km h^{-1}) are located between −700 and −200 ms (with a peak between −450 and −350 ms) before the heel strike. Significant coupling from 8 to 12 Hz, with distinct peaks in early, mid- and late swing, was also observed. The same analysis was done with recordings made during slow walking (1 km h^{-1}), and analogous results were found, except that the 24–40 Hz coherence was more pronounced from −500 to −400 ms prior to heel strike.

According to the authors, these frequency characteristics are consistent on the one hand with those previously reported for corticomuscular coherence during finger or precision grip tasks in sitting subjects and, on the other hand, with those reported for intramuscular coherence of tibialis anterior during walking. Moreover, the presence of a significant imaginary part of the complex coherence indicates that the coupling in the study was not due to non-physiological artefacts. The negative sign of this imaginary part of the coherence suggests that the cortical activity was leading the muscle activity. Time lag estimates between EEG and EMG signals are consistent with the typical corticospinal conduction times. All these considerations reinforce the soundness of the findings made by Petersen *et al.* (2012), which provide new insight into two other recent analyses published in the literature.

First, in 2011, Gwin *et al.* investigated the cortical dynamics from EEG signals recorded during treadmill walking by using independent component analysis and inverse source modelling. They also confirmed that the human cortex is more active during locomotion than previously thought. In particular, they found successive event-related synchronizations (ERS) and desynchronizations (ERD) in phase with the gait cycle present in different regions of the brain and in numerous frequency bands comprised between 3 and more than 150 Hz. However, on the basis of this spectral analysis it is not possible to determine which cortical region is directly involved in the transmission of motor commands to the muscles. In contrast, coherence analysis reveals anatomical coupling between cortical activity and the motor output to the muscles by detecting common rhythmicities in EMG and EEG signals. According to the significant coherence values (24–40 Hz around Cz) found by Petersen *et al.* (2012), the multiple ERD-ERS detected by Gwin *et al.* (2011) in the 3–24 and 40–76 Hz bands are obviously not indicative of a direct corticospinal drive, at least, not to the tibialis anterior. Thus, one may think that these signals would rather reflect the control of sensory afferents (i.e. one of the hypotheses formulated by Gwin *et al.* 2011 themselves) unless residual artefacts may still partly

pollute the data. In line with this, it is interesting to note that in their very recent spectral study focused on the EEG rhythms elicited during robotic-assisted treadmill walking, Wagner *et al.* (2012) did not report multiple ERD-ERS in α, β and γ bands but found significant activities only in the 1–5 and 25–35 Hz intervals. Apart from the low frequencies, this result seems in agreement with those of Petersen *et al.* (2012), although the experimental protocols are slightly different.

Second, in another recent analysis, Presacco *et al.* (2011) showed that low δ band (0.1–2 Hz) contains information rich enough to allow a satisfactory decoding of EEG signals (i.e. conversion of these signals into the kinematics of the lower limbs via a linear filter) during treadmill walking. In fact, Raethjen *et al.* (2008) detected corticomuscular coherence at the stepping frequencies (0.5–3 Hz) between EEG and EMG signals of the tibialis anterior when subjects sitting on a chair performed self-paced voluntary rhythmic foot movements. This coherence was located in the central mid-line region extending further to the frontal mesial area. Nevertheless, no report of significant coherence at the stepping frequency was made by Petersen *et al.* (2012) for subjects walking on a treadmill (given that the presented results cover the 4–76 Hz interval). Further analysis is thus required to confirm (or refute) that the EEG decoding by Presacco *et al.* (2011) is well done on the basis of a direct corticospinal drive to the lower limb muscles.

The conclusion from these few observations is that an increasing number of studies agree that cortical activity does contribute to the muscle activity involved in human locomotion. However, the precise determination of temporal, frequency and spatial characteristics of the cortical control signals still requires further experimental investigation.

For instance, EEG–EMG coherence during treadmill walking could be studied with muscles other than TA. Also, such study could be carried out using a time-warping (or equivalent) technique (Gwin *et al.* 2011) in order to convert time information from milliseconds to percentage of the gait cycle. This would help to associate particular cortical activity to movement more easily. Indeed, at 1 km h^{-1}, the period of the gait cycle is about 1.9 s (as deduced from Fig. 1*C* of Petersen *et al.* 2012), which means that a heel strike occurs each 900 ms, while the period of the gait cycle at 4 km h^{-1} is about 1.1 s (following our own measurements on a treadmill), which means that a heel strike occurs each 550 ms. Hence, the peak values of coherence announced around −400 ms prior to the heel strike for both walking speeds happen at phases of the gait cycle that differ drastically. This should be taken into consideration in the future.

Finally, it should be emphasized that the analysis of Petersen *et al.* (2012) presents the strong advantage of determining the direction of information flux (downgoing in this case). As far as possible, future EEG analyses in ambulatory conditions should follow an equivalent approach, because the data in this context are strongly affected by an entanglement of downgoing, upgoing and artefactual contributions (Castermans *et al.* 2012).

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