Human Locomotion and the Motor Cortex

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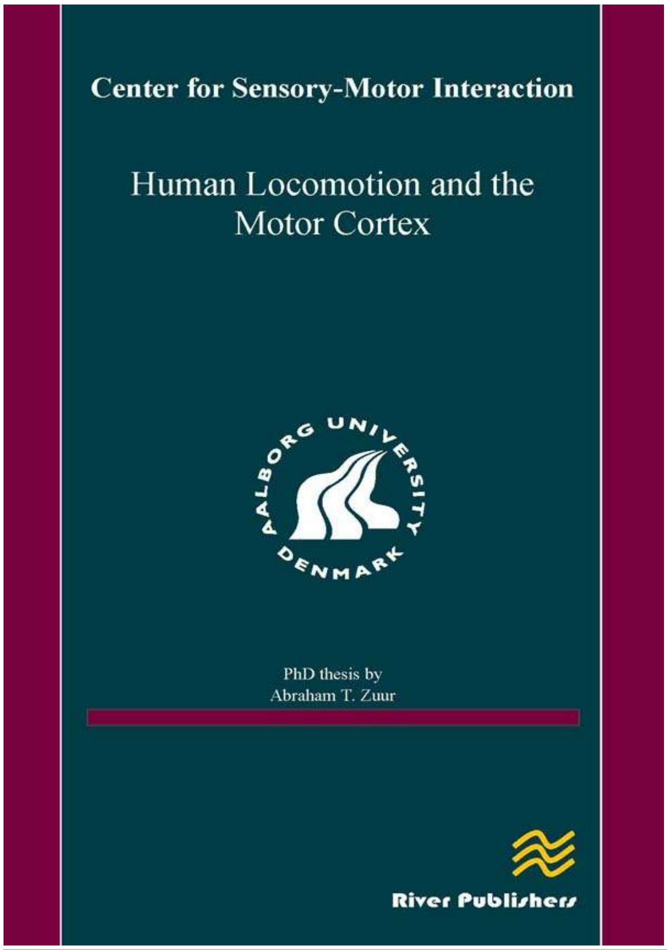
Human walking displays an impressive precision and the ability to adapt to different terrains. It is suggested that both spinal as well as supra-spinal structures play an important role in this rhythmic task. The current thesis focuses on the role the motor cortex plays in this task. Although there are experimental findings and clinical observations suggesting that one of the supraspinal structures involved in walking is the motor cortex, it is not generally accepted that the motor cortex is of major importance in human locomotion. The motor cortex is generally considered to be important in voluntary movement and the choice to term walking as non-voluntary movement may be more than just semantically important and this matter is discussed in the thesis.

The thesis includes five original research papers which show that output from the motor cortex is integrated with contributions from spinal structures in rhythmic tasks such as walking and hopping. In study I it is shown how the motor cortex contributes to motoneuronal drive in conjunction with sensory feedback mediated by spinal reflex loops. The integration between afferent feedback and motor cortex is further displayed in study II, in which we show that afferent input may relay to corticospinal neurons from where it is fed back to the muscle and may produce a large functional directed response during walking. Study II thereby displays a role for the motor cortex in error correction during walking. Study III shows not only that afferent feedback from agonist muscles is relayed to corticospinal neurons during walking but also that feedback from the antagonist is relayed to the motor cortex where signals from both muscles increase the excitability of the motor cortex. This organisation is somewhat reversed from the organisation of antagonist afferent input to the spinal cord, but it may be hypothesised that both spinal and supra-spinal structures contribute to a balanced response to a perturbation. The motor cortex also plays a role during normal, unperturbed walking. In study IV we show that output from the motor cortex may be suppressed during walking and standing by exciting intracortical inhibitory interneurons using subthreshold transcranial magnetic stimulation. The results may be explained by the suggestion that there is less corticospinal output during walking. Alternatively, it may be suggested that it is more difficult to stop the corticospinal neurons or motoneurons from firing during walking. The final study showed that muscle activity can still be suppressed during a dynamic contraction during sitting and it also suggests that the observed effects cannot be unambiguously related to changes in corticospinal output.

In conclusion, the studies in the thesis further confirm a role for the primary motor cortex in driving the muscle during rhythmic tasks like walking and hopping. It shows a role for the motor cortex in mediating afferent feedback to both agonists as well as antagonists, underlining the integrative nature of the neural system. Indirect measurements of the ability of intracortical inhibitory neurons to suppress corticospinal neurons suggest that the motor cortex is involved in both walking and standing, but that the control is very different.



e-ISBN: 9788792982643
Available From: July 2013
Price:

KEYWORDS:
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