

## **Supraspinal mechanisms of fatigue**

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In whole animals, fatigue can be defined as an exercise-induced decrease in ability to produce force from muscle. Much of the loss of force occurs through changes in muscle fibres but some occurs because of failure of neural drive to the muscle. In humans, transcranial magnetic stimulation (TMS) of motor cortex can evoke small increments in force from the elbow flexor muscles even during maximal voluntary contractions (MVCs)<sup>1</sup>. Such increments imply that motor cortical output was not fully recruited by voluntary effort. Thus, TMS could evoke extra descending volleys which could increase firing of motoneurons, and this additional firing could evoke force from muscle fibres. That is, no site below the point of stimulation was working maximally. During fatiguing exercise, the increments in force evoked by TMS during maximal efforts grow larger. This suggests that a component of the force loss of fatigue is due to inadequate drive from the motor cortex. Such supraspinal fatigue occurs during sustained and intermittent isometric MVCs<sup>2</sup>, during repeated concentric and eccentric MVCs<sup>3</sup>, and when fatigue is produced by sustained or repeated submaximal contractions. The mechanisms underlying supraspinal fatigue are unclear. Excitatory and inhibitory EMG responses to TMS both change during fatiguing contractions but these changes can be dissociated from the failure of voluntary activation. An increase in the increments of force evoked by TMS represents an effective decrease in voluntary descending drive. This could occur through decreased activity in the motor cortex. However, it could also occur despite unchanged or increased motor cortical activity if subcortical changes, such as altered muscle contractile properties or altered responsiveness of motoneurons to synaptic input, need increased descending drive to counter them. In either case there is a supraspinal component to fatigue. If TMS can evoke larger force increments, then output from the motor cortex is both insufficient and submaximal so that performance could improve if the untapped cortical output could be harnessed voluntarily.

1. Todd et al. *J. Physiol.* 551:661-671, 2003
2. Taylor et al. *J. Appl. Physiol.* 89:305-313, 1999
3. Löscher & Nordlund. *Muscle Nerve* 25:864-872, 2002