FUNCTIONAL ROLE OF PROPRIOCEPTIVE FEEDBACK IN BALANCE AND IN REACTIVE MOVEMENT

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Human movement is generated either by internal muscle forces, or by external forces that are attached to the body system. Most of our muscles act via lever arms on the bone system, thus generating rotational forces that produce consequently torques and joint moments. Therefore, studies dealing with control strategies of joint moments to achieve a desired movement or an intended task are addressing one of the most interesting topics.

In several papers the constraints and relative importance of sensory feedback are investigated. It seems that in a given task a complex interaction of feed-forward- and feed-back-mechanisms adjust the actual joint stiffness. By means of the H-reflex methodology, the spinal excitability for muscles can be determined. Under selective conditions, the inhibitory or facilitatory behavior of spinal reflex contribution can be investigated. Quite recently, the transcranial magnetic stimulation (TMS) has been developed to assess corticospinal excitability during human movement. Selective stimulation of the neurons in the motor cortex allows the determination of the relative contribution of corticospinal activation during movement. Application of both techniques, H-reflex and TMS, allows differentiation of spinally and centrally organized muscle activation.

The present paper highlights recent findings about neuromuscular control in balance and stretch-shortening cycle movements and reflects adaptations induced by balance training.

For both type of movements, the stiffness properties of the involved joint complexes are modulated by spinal and central modulation of the neuromuscular activation. Training adjusts/adapts this motor control specifically for balance tasks and for reactive movements.

Longitudinal training studies in which postural control (balance training) was exercised showed that the spinal and the cortical contributions were reduced after the training. Thus it was assumed that motor control was shifted towards supraspinal centers (Taube et al. 2007).

From stretch shortening cycle (SSC) it is known that high muscular stiffness is a prerequisite to enable proper performances and that feed-forward activation of the extensor muscles prior to ground contact is modulated by effective stretch reflex contributions (feed-back activation). This modulation, however, is largely dependent on the individual stretch load tolerance of the neuromuscular system.

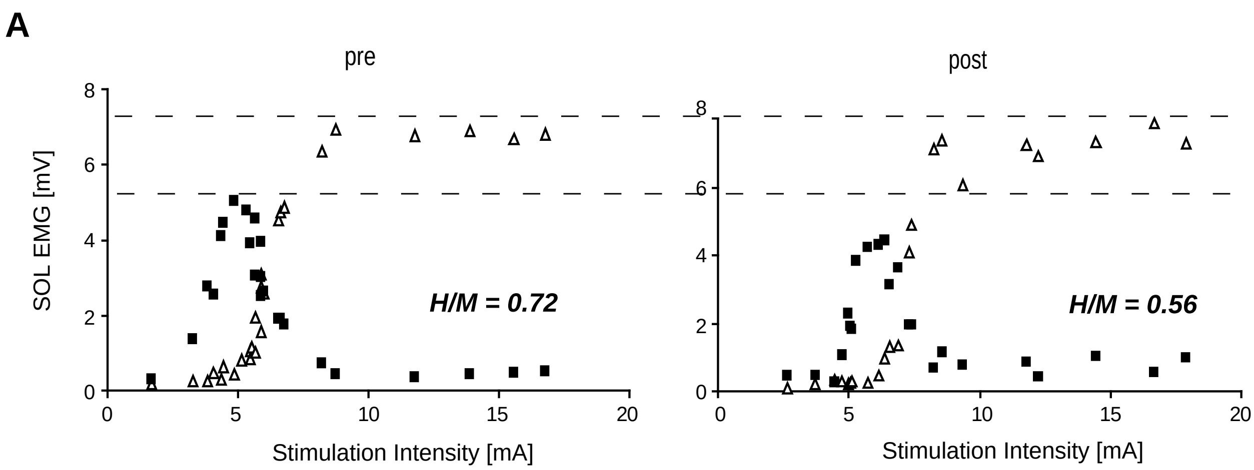
Recent results indicate that the “stereotyped” reflexes are much more modulated than expected previously. It has been shown that modulation of spinal circuitry is achieved by presynaptic inhibition.

BALANCE CONTROL: Human posture or balance control and motion are controlled by a complex interaction of centrally and peripherally organized neuronal networks. Task specific voluntary movement is permanently under the influence of information feedback from various sources of proprioceptive receptors. This control system is highly effective if the feedback is organized “in real-time” and even more effective if feed-forward mechanisms are anticipating the motor requirements. From mechanoreceptors in the fingertips it is known, that for a precision grip the actual forces are slightly higher than necessary to hold the object

(Johansson and Westling 1984, 1987). Further, it is well known (Eliasson et al 1995) that disturbances of load will result in compensatory forces occurring with a latency of 40 ms. From a biomechanical point of view, balance for example is characterized by changes of the centre of pressure (COP) with respect to the actual projection of the centre of mass (COM) to the supporting area during a distinct motor task (Winter 1996). The ability of the nervous system to detect joint positions, movement directions, and force applications is mainly processed by proprioceptive afferents. In addition, precise information is necessary to balance gravitational forces. From postural control and balance it is known, that reflexes largely contribute to keep the COP within the constraints of the supporting area. It has been shown that balancing on a narrow beam reduces the size of the spinal excitability compared to normal walking (Llewellyn et al. 1990). Similarly, spinal excitability is reduced during stance with eyes closed as compared to balancing with open eyes (Earles et al. 2000; Hoffmann and Koceja 1995).

On the basis of altered reflex excitabilities in different motor conditions the challenging question arises: To what extend is the proprioceptive input qualifying the balance capability and what other sources of the neurophysiological system are controlling them?

ADAPTABILITY OF SPINAL REFLEXES: In recent balance training studies, exercising on unstable ground (wobbling boards, discs, soft mats etc.) led to a suppression of the H-reflex (Fig. 1) (Gruber et al. 2007; Taube et al. 2007a, 2007b).



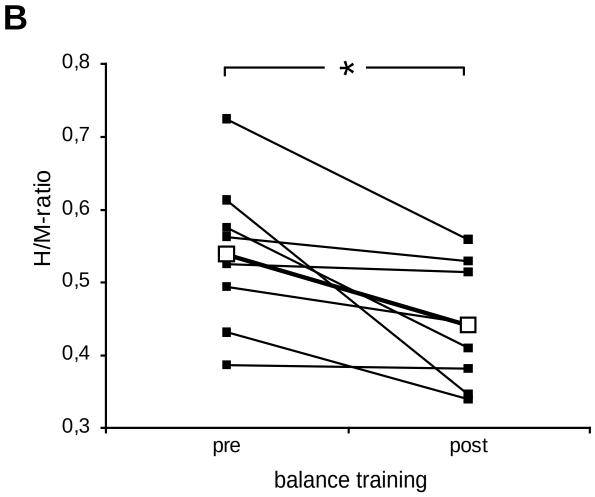


Figure 1: Adaptation of the H-reflex with balance training. H-reflex recruitment curves and resulting H_{max}/M_{max}-ratios recorded during perturbation on the treadmill. In A, H-reflex recruitment curves (■ H-reflexes, △ M-waves) from one subject before (pre) and after balance training (post) illustrate the reduction in H_{max}/M_{max}-ratio. B, H_{max}/M_{max}-ratios from each single subject (■) as well as the mean of all subjects (□) are displayed ($p < 0.05$ *). (Modified from Taube *et al.,* 2007b).

This may imply that balance training modifies spinal reflex circuits and may lead in general to reduced H-reflexes in subjects who face high postural demands over a long time. The reduced H-reflex excitability of ballet dancers might then be explained in this way (Nielsen and Kagamihara 1993). It has been speculated that these reductions are mediated by presynaptic inhibition of the alpha-motoneurons. From postural control studies (Katz et al. 1988; Koceja and Mynark 2000; Mynark et al. 1997) it has been consistently shown that presynaptic modulation of the Ia-afferents by centrally pathways is a major mechanism to modulate spinal excitability.

Recently the transcranial magnetic stimulation technique has been developed for application in human motor experiments. By means of rapid magnetic stimulation the neurons in the motor cortex can be artificially activated and, based on elaborated electrophysiological techniques, the relative contribution of the fastest corticospinal projections from the motor cortex down to the spinal motoneurons can be assessed (Taube et al. 2007a). These authors investigated these pathways before and after balance training, besides a reduced spinal excitability they also revealed reduced cortical influence after balance training.

In a functional interpretation they stated that reduced spinal excitability plus reduced corticospinal influence me be explained by a gradual shift from spinal and central control before balance training to an increased control by subcortical centres. Functionally such shifts would reduce reflex generated oscillations and, concomitantly, deliberate the motor cortex for other tasks.

STRETCH SHORTENING CYCLE (SSC): From studies investigating the reactive movement capacity it is known that proprioceptive reflexes are basically responsible to explain supramaximal muscular forces during stretch-shortening cycle (SSC) contractions. Especially the immediate transfer from the preactivated and eccentrically stretched muscle-tendon complex to the concentric push-off determines the efficacy of motor output in the SSC. Analysis of EMG-profiles of the leg extensor muscles during hopping, jumping or running revealed that the reflex contribution appears interindividually rather consistently with a latency of 30 – 40 ms after landing on force platforms (Figure 2).

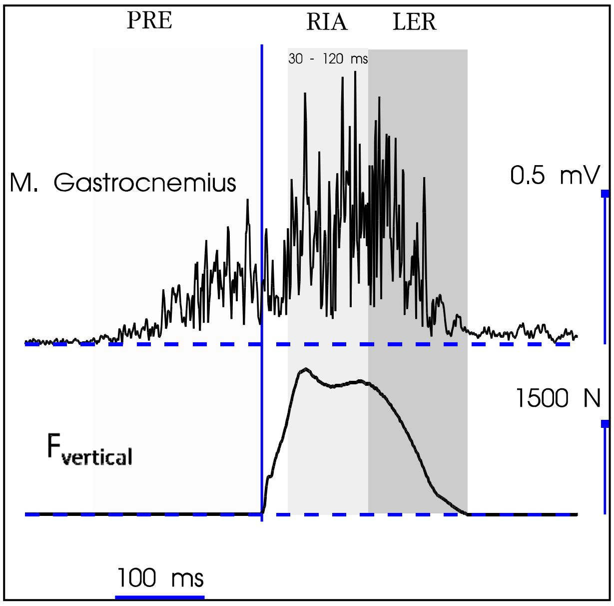


Figure 2: Schematic representation of an averaged (n=10) activation pattern of M. Gastrocnemius and vertical ground reaction force record. Drop Jumps were performed from 32 cm falling height. Preactivation, phases for reflex induced (RIA) as well as late emg responses (LER) are inserted.

On the basis of the concept that active stretch reflexes are essential for an effective reactive movement capability the challenging question arises: How is the interaction of feedforward organized activation of the muscles to stiffen the joints prior to landing related to the feedback organized reflex contributions and what other sources of the neurophysiological system are controlling them?

In order to sample closer details about the neuronal control during SSC we investigated spinal excitability by peripheral nerve stimulation and cortical excitability by application of TMS (Taube et al. 2008). In these experiments the H-reflexes were applied at distinct phases before and after the ground contact in order to assess the relative distribution of the spinal excitability for the reflex induced activation period. It could be demonstrated that spinal excitability is high at the early phases of ground contact coinciding with the latencies of the short latency, basically monosynaptic component of the stretch reflex contributions. However, as time of ground contact progresses, this excitability was systematically reduced. Conversely, the MEPs elicited by the TMS to study the central excitability was low at the early contact phases and increased towards later contact times (Figure 3).

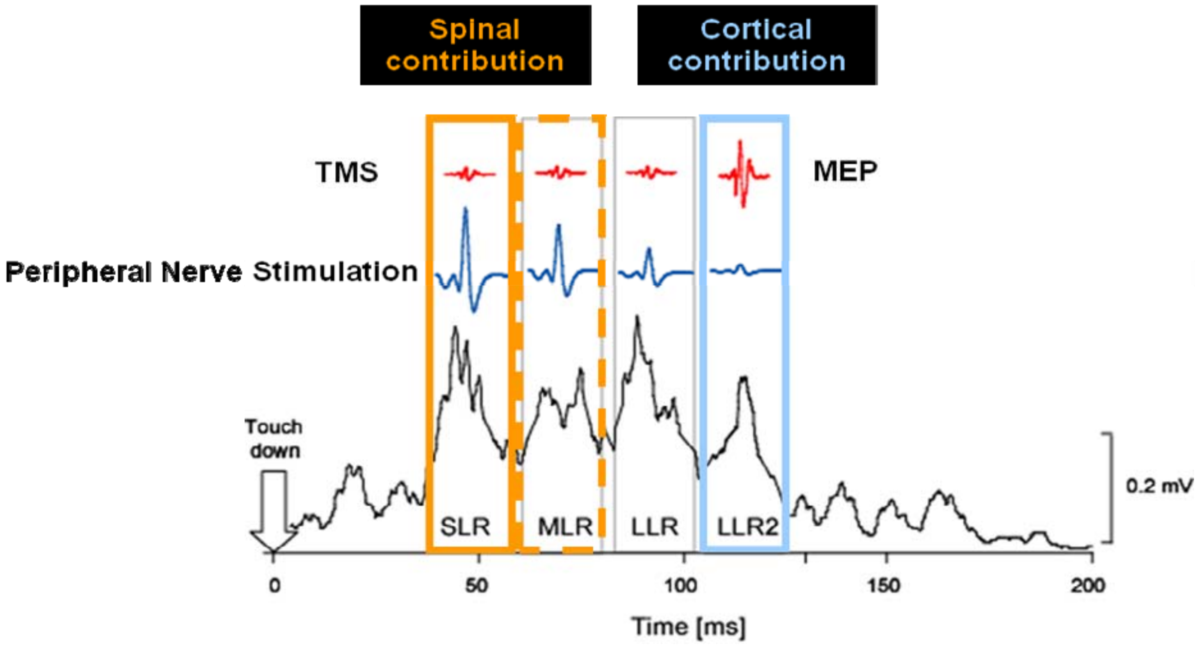


Figure 3: Reflex pattern of M. Soleus represents various components of reflex latencies following touchdown (Short- (SLR); Medium- (MLR) and Long-latency component (LLR; LLR2). Upon each component the relative size of H-Reflex, determined by peripheral nerve stiumaltion and of MEP, determined by transcranial stimulation (TMS) is inserted. Whereas the H-reflex size is decreasing with longer latencies, the amplitudes of the MEPs are increasing. Consequently, this has been interpreted as a reduced spinal excitability in favor of increased cortical control with longer latencies.

Functionally these observations led to the conclusion that the early phases after ground contact, characterized by the short latency reflex activity, are under spinal control. However, as ground contact time proceeds, the later components in the EMG of the leg extensors, characterized by the medium and long latency reflex activity, a more and more subcortical and finally cortical control must be assumed.

In summary, neuronal control of reactive movements in the SSC represent an activation profile that is controlled by different neuronal circuits. On the basis of recent electrophysiological methodological tools the classical distribution in preactivation, reflex and voluntary induced activation is preserved, but a fine-structured picture can be drawn: Especially during the period of reflex induced activity (30 – 120 ms after ground contact) the cortical control is progressively increased. This may be interpreted as an integration of feedback-mechanisms (stretch reflex activation) into the feed-forward-control by centrally organized the motor programs.

CONCLUSION: Proprioceptive feedback is essential not only for transmitting force, position and movement senses under human movement but also to assist neural activation. In balance, these contributions are suppressed as training proceeds. Concomitant to the reduced cortical control a gradual shift towards subcortical control during balance may be assumed. Moreover, in situations when strong activation is desired to achieve high muscle stiffness (SSC) the feed-forward control, already initiated by preactivated extensors, is substantially supported by segmental stretch reflexes. However, these reflex contributions are controlled for the short- and medium-latency component by spinal mechanisms. The later responses have been shown to be under subcortical or even cortical control.

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