ADAPTIVE RESPONSES OF NEUROMUSCULAR SYSTEM TO TRAINING

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INTRODUCTION: Contractile strength training has been investigated in a large variety of training designs. The purpose was to better understand the adaptive mechanisms of the human movement system to physical activity. In principle, for classical strength training two modalities of functional adaptations can be substantiated from those studies: Strength training can either lead to enhancements in the contractile muscular properties of the protein structures themselves or can lead to improvements in the neural supply of the contracting muscle or muscle group. Each type of adaptation can be addressed specifically by the design of the training programme, basically substantiated by the height of the training load, volume of training session and duration.

Evidence has been produced, that training with relatively high number of repetitions within one set (i.e. 6 – 15 maximum repetition (RM) load), associated with an extensive exhaustion of the trained muscle group is preferentially followed by an enhancement in strength and power. Athletes working with this methods show adaptations in the muscular tissue, enhanced cross-sectional areas, altered pinnation angles and high endocrine involvement (Rutherford and Jones, 1992; Walker et al., 1998). However, many studies report also improvements in strength and in power capabilities after strength training without a substantial adaptation of the muscular profile. Thus, an alternative functional response modality must be considered. In recent publications evidence has been produced that spinal and supraspinal mechanisms can be drastically enhanced by a specific type of training. In contract to the muscular adaptations after training with high number of RMs, neuronal adaptation is associated with training using low number of repetitions (1 – 8 RM load), high loads, intensive or explosive type of contraction and sufficient long periods between sets (Aagaard et al., 2001).

The present paper is focused on the neuromuscular adaptive mechanisms that may come along with intensive strength training and with sensorimotor training.

The motoneuron in the spinal cord is in latest consequence directly linked to the muscle fibres. Due to the fact that the functional properties of the motor units (MU) are directly dependent on the discharge characteristics of the activating spinal motoneuron, it appears logical to separate the various adaptive responses of the neuromuscular system to training in accordance to the different modalities of training.

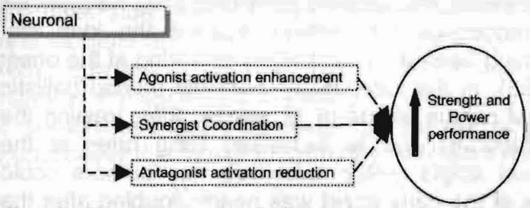

Fig. 1 Neuronal adaptations to strength training can be achieved either by enhanced activation of the agonistic muscles, by appropriate coordination of the synergists or by functional decreased activation of the antagonistic muscles. (mod. from Sale, 2002)

INCREASED MUSCLE ACTIVATION: Increased muscle activation can be achieved by either alteration in recruitment properties of activated motoneurons, in firing frequency or in motor synchronisation or in a combination of those three modalities.

From electromyography (EMG) studies it is clearly demonstrated, that vigorous intensive strength training is quite often associated with an enhanced EMG input to the trained muscle. Despite the methodological limitation of this methodological approach, a tremendous number of studies have consistently shown that neural adaptation can account for the observed gains in strength (Narici et al., 1989; Moritani and deVries, 1979; Hakkinen et al., 1985a; Hakkinen et al., 1985b; Hakkinen et al., 1987).

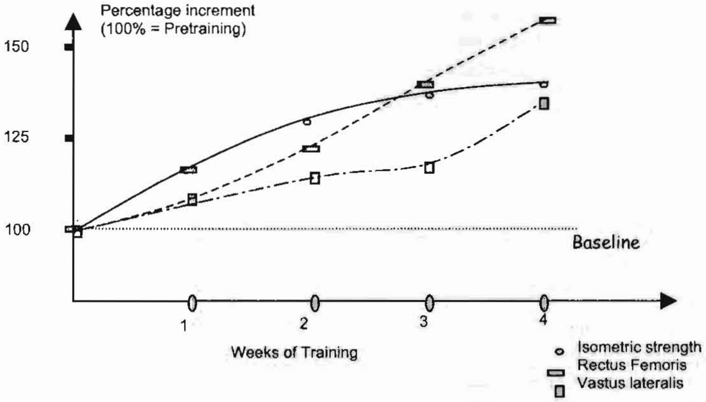

Fig. 2 Isometric strength training over four weeks of training was associated by a substantial enhancement of strength and a muscle specific neural adaptation, obtained from surface EMG recordings. (mod. from Rabita et al., 2000)

From a functional point of view, adaptation in rate of force development (RFD) is much more often required after strength training than enhanced maximum forces (MVC). Especially from dynamic, explosive type of strength training it is known, that an increase in rate of force development (RFD) is closely related to improvements in neural drive of the trained muscles (Jansson et al., 1990; Gruber and Gollhofer, 2004). It has been shown that neural adaptations caused by an explosive type of training are primarily responsible for an increase in the speed of voluntary muscle contraction. By analyzing single motor unit recordings the authors were able to demonstrate the preservation of the orderly motor unit recruitment pattern. However, motor units were activated earlier and showed increased firing frequencies after training. From intramuscular EMG recordings the authors support the idea that explosive type of training is associated with high frequency discharges occurring at the onset of muscular action (Van Cutsem et al., 1998). In the latter study, subjects trained ballistic dorsiflexion actions with 30 to 40 % of 1 RM over a period of 12 weeks. After training the RFD was drastically (+80%) enhanced, basically due to increased firing rates at the beginning of the isometric test action. From single motor recordings the authors could demonstrate that the frequency of discharge at the early onset was nearly doubled after the training. Functionally, the MU´s have "learned" to activate with higher starting frequencies leading to enhanced rates of force development on the motor unit level.

Principally, the observations of a changed discharge frequency are obtained from studies investigating only a small number of single motor units. Therefore, it is not clear, if this type of training also alters the recruitment level, or even the recruitment order of the motoneurons involved. Studies from Patten et al. (2000) have demonstrated that ballistic training caused a slight shift in recruitment threshold to the left, leading to an earlier recruitment of the motor units. However, the authors also clearly stated that the order of recruitment was preserved, which is in accordance to findings from Garland et al. (1996).

It is important to notice that normal healthy subject should generally be able to recruit all the MU of a muscle during maximal isometric actions. Therefore the only explanation of neural adaptation can be seen in the improved firing rates after training. It is well known, that predominantly in large muscles recruitment of MUs occurs up to 80% of MVC (Enoka and Fuglevand, 2001), whereas in small muscles the recruitment is finished at 50% MVC. Thus a large variety of force output can be addressed by alterations in the firing pattern of the MU.

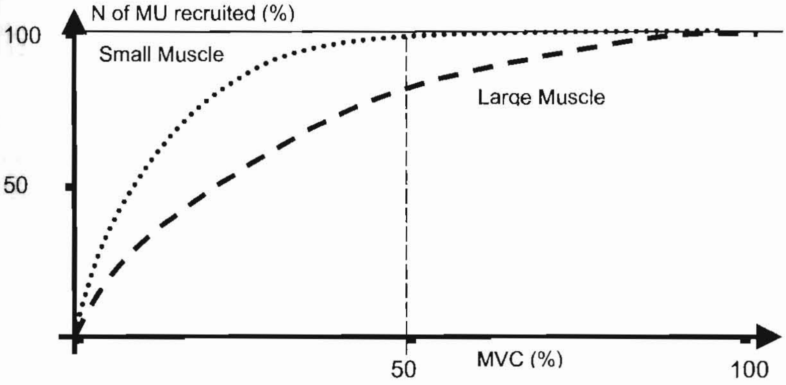

Fig. 3 Isometric strength (%MVC) and recruitment of individual MUs in small and in large muscles. It is important to notice that both types of muscle are nearly fully activated at a level of 50% MVC. (mod. from Enoka and Fuglevand, 2001)

SPINAL MECHANISMS ACTIVATING THE MOTONEURONS: In Fig. 4 the various inputs of the central nervous system to the motoneuron of a distinct muscle group are illustrated. Motoneurons receive signals not only from the central pathways from brain structures; they are also largely influenced by selective inputs from peripheral feedback afferents. Afferent input from sensors in the skin, capsules, ligaments, tendons and muscle are mediated either directly to the motoneuron, or they are connected via interneuronal structures. It is noteworthy that most of the peripheral afferents are looped back either facilitating or inhibiting the spinal motoneuron.

One of the most important feedback-loops is the Ia-afferent from the muscle spindles. This reflex pathway directly facilitates the homonymous MUs (i.e. extensors) and inhibits the antagonist muscle (i.e. flexors) of the ipsilateral side. On the contralateral side the afferents are connected in the opposite manner, facilitating the flexors and inhibiting the extensors. On the other side afferents from Ib-Golgi-Tendon-Units (GTO) generally inhibit homonymeous and facilitate antagonistic MUs. Influences from skin- and joint-receptors converge together with the Ia and Ib afferents onto the Ib-interneuron pool. However, is has also been shown in humans that especially in stance and locomotion the Ib-inhibition is reversed into facilitation. This reflex pathway is dependent on the load acting on the lower limb (Gollhofer et al. 1989). Functionally this Ib-mechanism has been addressed as the load-receptor modulation.

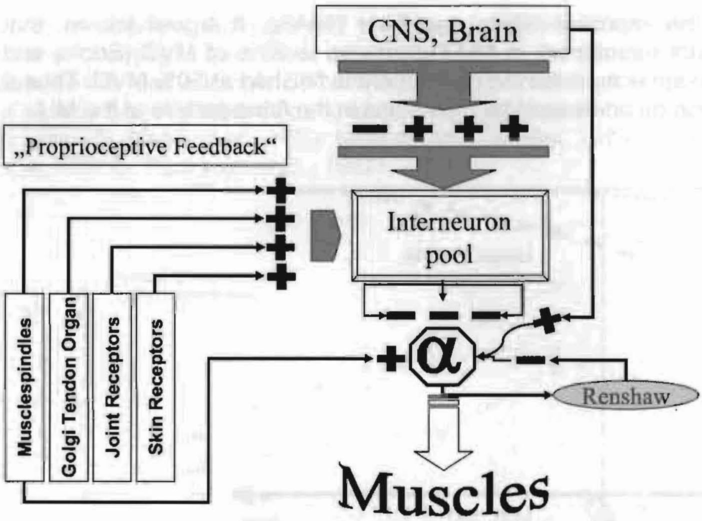

Fig. 4 Various sources of afferent influence of the spinal MU. Please notice that most of the feedback are inhibitory; reducing the activation level of the motoneuron.

From a functional point of view the spinal network of feedback represents the backbone of the neural adaptations due to learning and training. By modulations originating from changed inputs from the brain as well as from the sensors of the proprioceptive system the input from interneuron pool onto the α-motoneurons, i.e. the activation of the last common path to the muscle can drastically adjusted to either the mechanical needs of a distinct movement or to the level of experience and training of the individual.

SENSORIMOTOR TRAINING: For rehabilitation of injuries to the locomotor system, sensorimotor training is widely accepted to restore neuromuscular functions. The various receptors in the joint complexes, in the tendons and ligaments, in the muscular and skin structures are assumed to be trained in order to enhance proprioceptive contributions in functional situations. Thus, proprioceptive training aims to improve the efficacy of the afferent feedback, in order to attain functional limb control and to achieve appropriate neuromuscular access to the muscles encompassing joint complexes. Konradsen et al. (1993) and Tropp (1986) compared postural stability of healthy subjects and with individuals with chronic ankle instability. Other approaches have investigated the sensory angular reproduction of different joint dynamics under active or passive conditions (Freeman et al., 1965; Glick et al., 1976; Lofvenberg et al., 1995; Tropp, 1986). These studies demonstrated a proprioceptive deficit during reproduction of distinct angular dynamics in case of chronic ankle instability.

Enhancement of proprioceptive generated muscle activation has been assumed from experiments of the knee (Perlau et al., 1995) and ankle joint (Jerosch and Bischof, 1994). However, only few controlled studies are available demonstrating an improved afferent supply to the muscles after training.

In a series of experiments, Gollhofer and coworkers investigated the neuromuscular adaptations following sensorimotor training interventions. Based on longitudinal studies, the author presents experimental data that demonstrate the adaptability of the afferent and efferent contributions. In those studies the hypothesis was verified if a specifically designed sensorimotor training will have a positive impact on the neural activation and strength during a maximal isometric leg extension. The authors (Gruber and Gollhofer, 2004) investigated 12 female subjects before and after a 4 week training program with a total of eight training sessions. Each training (60 min in duration) comprised various exercises for balance and body stabilization. No classical strength training exercises were allowed during the entire training period. EMG of the shank muscles as well as force parameters of the isometric maximum strength measurements revealed significantly increased neuromuscular activation and isometric power after the training period. The sensorimotor training revealed best neuromuscular adaptations at the initiation of the force production. Explosive strength and neuromuscular activation at the onset of voluntary actions seemed to be efficiently enhanced.

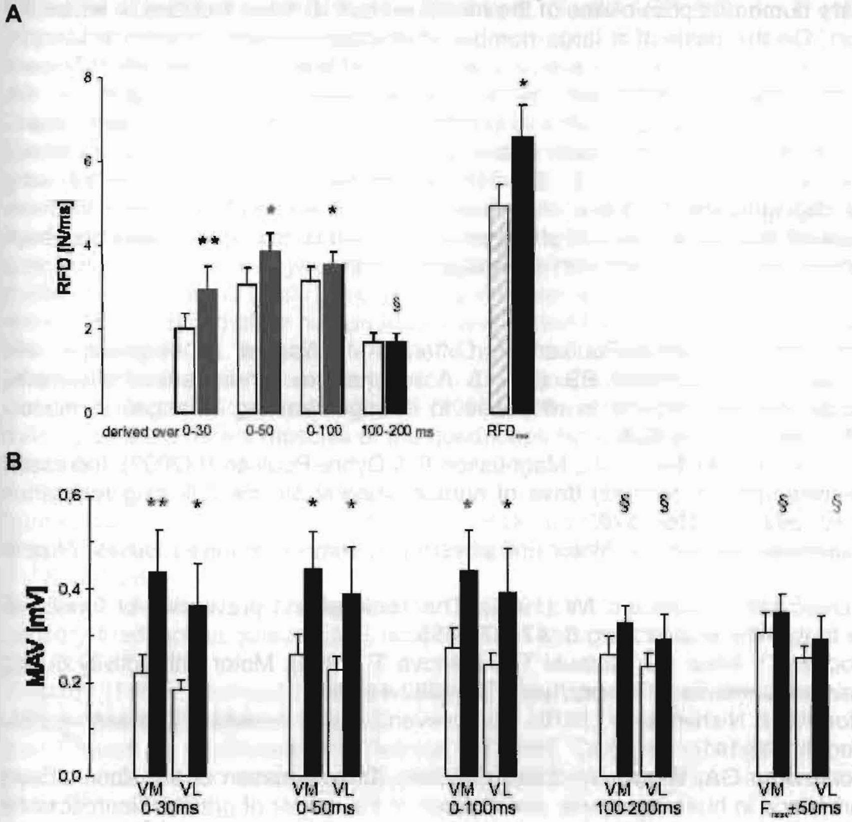

Fig. 5 (A) Rate of force development (RFD) (means (±SE)) in the time intervals of early force production before (open bars) and after (filled bars) the four week sensorimotor training. (B) Mean activation amplitudes (MAV) (means (SE)) of the muscles vastus medialis (VM) and vastus lateralis (VL) before (open bars) and after (filled bars) the sensorimotor training. * $p < .05$; ** $p < .01$

Increments in strength and in neural activation reflect adaptive processes on the motoneuron level. From walking (Sinkjaer et al., 2000) and from voluntary ramp contractions (Macefield et al., 1993) it has been shown that afferent feedback is provided especially at the onset of muscular action. Meunier and Pierrot-Deseilligny (1989) indicated that both homonymous and heteronymous contributions of Ia afferents facilitate muscular actions. From a functional point of view it must be pointed out that enhanced gain in neuromuscular control is of vital importance for stiffening of muscles encompassing joint systems. Thus it may be suggested that sensorimotor training has a great impact on the proprioceptive supply of the trained muscle. The enhancement has been interpreted as a modulation of the presynaptic inhibition of the α-motoneuron. In contrast to classical strength training (Hakkinen et al., 1998; Aagaard et al., 2002) the increased RFD values were not associated with increased maximum strength. Thus it may be assumed, that sensorimotor training is beneficial for an enhanced access of the neuromuscular system to the motoneuronpool, but not for an enhanced contractile force under maximum conditions.

The gain in neuromuscular activation may arise from enhanced reflex contributions acting on a spinal level, induced by the training.

CONCLUSION: Neuromuscular adaptation is neither unique in occurrence nor easy to identify. There are numerous possibilities of the neural system to either facilitate or inhibit the final motoneuron. On the basis of a large number of electromyographic studies evidences have been produced indicating a high specifity of the neural adaptation seen after different training regimen. Recently, additional techniques revealed detailed insights in the mechanisms on the spinal level. By means of H-reflex techniques the degree of presynaptic influences on the motoneuron excitability can be addressed, by means of additional transcranial magnetic stimulation (TMS) the central and peripheral adaptations following training can be distinguished. In future, the various tools of electrophysiological methods need to be combined in order to examine changes in the motor cortex, spinal reflex pathways and to explain changes in the motoneuron discharge properties.

REFERENCES:

Aagaard P, Andersen JL, Dyhre-Poulsen P, Leffers AM, Wagner A, Magnusson SP, Halkjaer-Kristensen J & Simonsen EB (2001). A mechanism for increased contractile strength of human pennate muscle in response to strength training: changes in muscle architecture. *J Physiol* 534, 613-623.

Aagaard P, Simonsen EB, Andersen JL, Magnusson P & Dyhre-Poulsen P (2002). Increased rate of force development and neural drive of human skeletal muscle following resistance training. *J Appl Physiol* 93, 1318-1326.

Enoka RM & Fuglevand AJ (2001). Motor unit physiology: some unresolved issues. *Muscle Nerve* 24, 4-17.

Freeman MA, Dean MR & Hanham IW (1965). The etiology and prevention of functional instability of the foot. *J Bone Joint Surg Br* 47, 678-685.

Garland SJ, Cooke JD, Miller KJ, Ohtsuki T & Ivanova T (1996). Motor unit activity during human single joint movements. *J Neurophysiol* 76, 1982-1990.

Glick JM, Gordon RB & Nishimoto D (1976). The prevention and treatment of ankle injuries. *Am J Sports Med* 4, 136-141.

Gollhofer A, Horstmann GA, Berger W, Dietz V (1989). Compensation of translational and rotational perturbations in human posture: stabilization of the center of gravity. Neuroscience letters105, 73-78.

Gruber M & Gollhofer A (2004). Impact of sensorimotor training on the rate of force development and neural activation. *Eur J Appl Physiol* 92, 98-105.

Hakkinen K, Alen M & Komi PV (1985a). Changes in isometric force- and relaxation-time, electromyographic and muscle fibre characteristics of human skeletal muscle during strength training and detraining. *Acta Physiol Scand* 125, 573-585.

Hakkinen K, Komi PV & Alen M (1985b). Effect of explosive type strength training on isometric force- and relaxation-time, electromyographic and muscle fibre characteristics of leg extensor muscles. *Acta Physiol Scand* 125, 587-600.

Hakkinen K, Komi PV, Alen M & Kauhanen H (1987). EMG, muscle fibre and force production characteristics during a 1 year training period in elite weight-lifters. *Eur J Appl Physiol Occup Physiol* 56, 419-427.

Hakkinen K, Newton RU, Gordon SE, McCormick M, Volek JS, Nindl BC, Gotshalk LA, Campbell WW, Evans WJ, Hakkinen A, Humphries BJ & Kraemer WJ (1998). Changes in muscle morphology, electromyographic activity, and force production characteristics during progressive strength training in young and older men. *J Gerontol A Biol Sci Med Sci* 53, B415-B423.

Jansson E, Esbjornsson M, Holm I & Jacobs I (1990). Increase in the proportion of fast-twitch muscle fibres by sprint training in males. *Acta Physiol Scand* 140, 359-363.

Jerosch J & Bischof M (1994). [The effect of proprioception on functional stability of the upper ankle joint with special reference to stabilizing aids]. *Sportverletz Sportschaden* 8, 111-121.

Konradsen L, Ravn JB & Sorensen AI (1993). Proprioception at the ankle: the effect of anaesthetic blockade of ligament receptors. *J Bone Joint Surg Br* 75, 433-436.

Lofvenberg R, Karrholm J, Sundelin G & Ahlgren O (1995). Prolonged reaction time in patients with chronic lateral instability of the ankle. *Am J Sports Med* 23, 414-417.

Macefield VG, Gandevia SC, Bigland-Ritchie B, Gorman RB & Burke D (1993). The firing rates of human motoneurones voluntarily activated in the absence of muscle afferent feedback. *J Physiol* 471, 429-443.

Meunier S & Pierrot-Deseilligny E (1989). Gating of the afferent volley of the monosynaptic stretch reflex during movement in man. *J Physiol* 419, 753-763.

Moritani T & deVries HA (1979). Neural factors versus hypertrophy in the time course of muscle strength gain. *Am J Phys Med* 58, 115-130.

Narici MV, Roi GS, Landoni L, Minetti AE & Cerretelli P (1989). Changes in force, cross-sectional area and neural activation during strength training and detraining of the human quadriceps. *Eur J Appl Physiol Occup Physiol* 59, 310-319.

Patten C & Kamen G (2000). Adaptations in motor unit discharge activity with force control training in young and older human adults. *Eur J Appl Physiol* 83, 128-143.

Perlau R, Frank C & Fick G (1995). The effect of elastic bandages on human knee proprioception in the uninjured population. *Am J Sports Med* 23, 251-255.

Rabita G, Perot C & Lensel-Corbeil G (2000). Differential effect of knee extension isometric training on the different muscles of the quadriceps femoris in humans. *Eur J Appl Physiol* 83, 531-538.

Rutherford OM & Jones DA (1992). Measurement of fibre pennation using ultrasound in the human quadriceps in vivo. *Eur J Appl Physiol Occup Physiol* 65, 433-437.

Sale, DG (2003). Neural Adaptation to Strength Training. In: *Strength and power in sport (ed: PV Komi)*, 281 – 314.

Sinkjaer T, Andersen JB, Ladouceur M, Christensen LO & Nielsen JB (2000). Major role for sensory feedback in soleus EMG activity in the stance phase of walking in man. *J Physiol* 523 Pt 3, 817-827.

Tropp H (1986). Pronator muscle weakness in functional instability of the ankle joint. *Int J Sports Med* 7, 291-294.

Van Cutsem M, Duchateau J & Hainaut K (1998). Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. *J Physiol* 513 (Pt 1), 295-305.

Walker PM, Brunotte F, Rouhier-Marcer I, Cottin Y, Casillas JM, Gras P & Didier JP (1998). Nuclear magnetic resonance evidence of different muscular adaptations after resistance training. *Arch Phys Med Rehabil* 79, 1391-1398.