Keynotes

THE ADAPTIVE SSC: FROM FATIGUE RUNS ON EARTH TO THE REBOUNDS ON MARS

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In natural forms of ground locomotion such as running and jumping, the functional phases include the stretching of the preactivated muscles followed by their shortening. This is called stretch-shortening cycle (SSC). SSC is a natural but complex activity that combines the available structuro-functional resources: the contractile and elastic structures with the central and reflex activation patterns. SSC may thus be used as a model to reveal the neural adjustments and the associated muscle-tendon responses to internal and external constraints. This presentation will focus on the neuro-mechanical adjustments to the acute and delayed SSC fatigue effects and to partial unweighting on lower body positive pressure treadmill. Both testing conditions emphasize the adaptive quality of the SSC, and demonstrate Time-, Task- and SSC phase-dependent neuro-mechanical adjustments.

KEY WORDS: stretch-shortening cycle; muscle activation; fatigue; unweighting

THE NATURE OF STRETCH-SHORTENING CYCLE: In natural forms of ground locomotion, the SSC of muscle function comes from the observation that body segments are periodically subjected to impacts. SSC consists in a series of consecutive preactivation, braking and push-off phases. Clear evidence exist that the muscle activations are specifically adjusted to the SSC task and phase (Nicol and Komi, 2010; Taube et al. 2012). This reveals the complexity as much as the adaptability of the neural control of SSC through the involvement of both feedforward (predictive motor control) and feedback (reactive reflex control) mechanisms.

The preactivation is well known as pre-programmed, and optimally adjusted prior to ground impact (Komi et al. 1987, Arampatzis et al. 2001). The impact loads and the nature of stretches involved in the subsequent active braking phase of SSC are usually very fast, of short duration and controlled simultaneously by reflex and central neural pathways. The use of the ‘braking’ instead of the original ‘eccentric’ phase comes from the ultrasonography studies showing that most but not all lower limb extensor muscles experience eccentric action when the muscle-tendon unit lengthens. For instance, the medial gastrocnemius may either work in a concentric, isometric or eccentric manner depending on the stretching load in jumping, whereas its fascicles present a short-lived stretch while shortening at the very early stance phase of running (Ishikawa and Komi 2008). It was originally assumed that the short-latency stretch reflex (SLR) would enhance leg stiffness and thus increase the SSC performance (Komi and Gollhofer 1997). Although quantified in passive stretch conditions, this is supported by in-vivo tendon force measurements (Komi and Nicol 2010). However, both adjustment of stiffness and changes of the SLR are now considered as following an optimum function with a u-shape rather than being linear in running (Cronin et al. 2011; Taube et al. 2012). The active braking phase is followed, without delay, by the push-off phase performed through concentric muscle action. This final SSC phase can be illustrated as a recoil action resulting in low EMG and metabolic

activity, but high mechanical efficiency. This potentiation appears clearly in the instantaneous force-velocity curve obtained by in-vivo Achilles tendon force recordings (Ishikawa and Komi 2008). At submaximal running speed, the EMG activity may even get close to zero during the push-off phase.
Consequently, SSC is considered as important for locomotion since it takes up the unnecessary delays in the force-time relationship by bringing the pre-activated force up to the level necessary to meet the expected impact loading. It also helps the concentric action (push-off) to generate larger peak power (maximal efforts) or more economically (submaximal efforts). SSC is a natural but complex and adaptive activity, which in itself gives opportunities to examine the neuro-mechanical adjustments to internal and/or external constraints.

NEURO-MECHANICAL ADJUSTMENTS TO INTERNAL CONSTRAINTS (SCC-TYPE-FATIGUE): In fatiguing SSC exercises, the impact loads are repeated over time, stressing metabolic, mechanical and neural components. Since the active braking phase of SSC is simultaneously controlled by reflex and central neural pathways, they provide an excellent basis for studying neuromuscular adaptations to exhaustive exercise. Submaximal SSC tasks are of major interest to reveal the richness of the neuro-mechanical adjustments to fatigue, but the pre-fatigue measurements should be performed once the SSC pattern is optimized (Regueme et al. 2005).
The fatigue responses during exercise are expectedly very individual, although certain general patterns can be described (Nicol et al. 2010). The cyclicity of the repeated SSC muscle actions favours the interaction of feedforward and feedforward controls. Compensatory EMG and/or joint kinematics changes may thus occur during the preactivation phase and influence the regulation of the post-landing stiffness. In this line, exhaustive SSC exercises are usually characterized by an initial increase in preactivation. This results in more extended limbs and increased muscle-tendon stiffness prior to impact, leading to increased ground impact peak and longer contact time (Gollhofer et al. 1987). The subsequent drop in force after impact is considered as an important indicator of reduced tolerance to repeated stretch loads as fatigue progresses (Nicol et al. 2006). This deterioration of the SSC efficacy during the braking phase may be temporarily compensated by an increased muscle activity during the push-off phase leading to even faster fatigue progression. Depending upon exercise intensity, this represents a vicious circle leading to a progressive reduction of the capacity to maintain the task.The concept of "time-dependent" adjustments relies on the findings of several SSC fatigue studies on the time course of the SSC exercise and its recovery period. The experiments of Horita's et al. (2000) can be used as concrete examples of how the kinematics, EMG, and kinetic parameters change during the time course of a fatiguing rebound exercise on the sledge apparatus. Observation of a clear turning point in the adjustments to fatigue after the middle stage of the exercise, with opposite neural strategies (compensatory *vs.* protective) for the thigh and shank muscles, demonstrates the variety of time-, muscle- and SSC phase-dependent neural adjustments. In running, extreme fatigue may lead to a re-organized SSC pattern through the adoption of a 'smoother' running style with a lower aerial time and a higher duty factor, therefore leading to a higher step frequency (Nicol et al. 1991, Millet et al. 2009). These results emphasize the variety and the efficacy of the neuro-mechanical adjustments to the increasing fatigue during submaximal SSC exercises.
The basic pattern of SSC fatigue response is "bimodal", showing an acute reduction in performance, an intermediate recovery within 1–2 hours, followed by a secondary reduction (up to 7 days) (Nicol et al. 2006; Nicol and Komi, 2010). After exhaustive forms of SSC, this bimodality is first characterised by both large (20-40%) acute and 1-2 days delayed drops in maximal voluntary force, maximal activation and stretch-reflex response. These changes may significantly influence the regulation of joint and muscle stiffness, leading to reduced maximal SSC performances. The intermediate recovery may either be partial or complete. The delayed recovery phase is typically associated with delayed-onset muscle soreness (DOMS): a sensation of dull pain and discomfort, increasing in intensity during the first 2 days, remaining symptomatic for 1-2 days, before disappearing 5-7 days after exercise. Sore muscles are often stiff and tender, and their ability to produce force is reduced for several days. Particularly important in terms of injury prevention is the precocity of the complete DOMS disappearance, as it occurs prior to the complete structuro-functional recovery. Consequently, DOMS cannot be used to follow the exact recovering process. Submaximal SSC testing tasks are of particularly interest as they reveal "SSC-phase dependent" neural adjustments that differ from the global muscle inhibition observed in maximal test conditions and vary along the recovery period. This can be illustrated by the results of Regueme et al. (2007) that reveal compensatory central and reflex adjustments at post that differed from the attempt at day 2 to protect the recovering muscle-tendon complex from the stressful stretching phase. Activation of

small (III and IV) afferents within the damaged muscles is proposed as an attractive factor to cause both acute and delayed presynaptic inhibition with subsequent reduction in the stretch reflex response, but also to result in inhibition and/or facilitation at the supraspinal level.

NEURO-MECHANICAL ADJUSTMENTS TO EXTERNAL CONSTRAINTS (PARTIAL UNWEIGHTING): Since the first rebounding steps of Eugene Cernan on the Moon in 1972, locomotion in microgravity has been investigated in space flight and parabolic flight conditions. Earth-based reduced gravity simulators have also been developed to study man's self-locomotion in different unweighting conditions. More recently, reduced gravity simulators have been used for rehabilitation. As compared to the classical harness devices, the lower body positive pressure (LBPP) technology uses small increases in air pressure to produce a lifting force via an airtight chamber applied distally to the subject's pelvis. This leads to a reduction of the bodyweight while the lower limbs still experience normogravity (Donelan and Kram 2000). In rehabilitation, LBPP treadmill is considered as allowing locomotion with reduced lower limb muscle activation (Liebenberg et al. 2011) and vertical ground reaction forces (Grabowski and Kram 2008). On LBPP treadmill, partial unweighting is reported as resulting in increased flight and stride durations but stable contact time, with larger reductions in vertical ground reaction forces than in the impact peak force and loading rate (Grabowski and Kram 2008). Unexpectedly, the unweighting effects on muscle activity have not been much investigated. Liebenberg et al. (2011) reported clear reductions in the global activation of lower limb muscles and suggested that any unweighting condition (from 60 to 90 % BW) could be used to maintain a specific activation pattern. More recently, however, muscle-dependent neural adjustments to the unweighting have been demonstrated (Hunter et al. 2014, Jensen et al. 2016), but none of these studies examined the exact SSC phase in which the EMG changes occurred. Our recent studies (Sainton et al. 2015, 2017) detailed the time course of the neuro-mechanical adjustments during two runs on LBPP treadmill that included 3 successive running conditions of 3 min (at 100% body weight (BW), 60 or 80% BW, and 100% BW). Vertical ground reaction forces and EMG activity of 7 leg muscles were analysed for the first and last 30 s of each running condition, and along the progressive 10-15 s transitions. The neural adjustments to both unweighting and reloading were expected to be muscle- and SSC phase-dependent.Unloading led to increased flight time, unchanged contact time and reduced vertical ground reaction forces whereas reloading resulted in the opposite changes. The transition analyses highlight the linear relationships between the unweighting- and reloading-induced changes with most mechanical stride parameters, and the rapidity of the neural adjustments. Confirming our expectations, the neural changes were SSC-phase dependent. The unchanged preactivation of most muscles supports the major intervention of a passive leg retraction before impact (Müller and Blickhan 2010). The braking phase presented selectively reduced activation of the vastii and soleus muscles whereas only the triceps surae activity was reduced during the push-off. Considering the use of LBPP treadmill in rehabilitation, additional detailed studies are needed on the neural adjustments over longer and repeated periods of running.

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