# SYNERGISTIC CONTROL OF MUSCLE ACTIVITY DURING CHALLENGING LOCOMOTOR TASKS

**Alessandro Santuz[1]**
**[1] Max Delbrück Center for Molecular Medicine in the Helmholtz Association (MDC), 13125 Berlin, Germany**

This talk will explore the neuromotor control of challenging locomotor tasks using the concept of muscle synergies: modular sets of activation patterns that are common to functionally similar muscle groups and may exist to simplify movement control. I will argue that the structure of these synergies is largely conserved across different walking and running speeds, as well as in response to internal (e.g. aging) or external (e.g. uneven terrain) perturbations. The nervous system finely tunes the linear and nonlinear time characteristics of muscle synergies to cope with disturbances, rather than adjusting the relative muscle contributions, regardless of the nature of the perturbation. This suggests the existence of a common neural mechanism for managing various locomotor situations.

**KEYWORDS:** muscle synergies, locomotion, motor control, sensory feedback.

**INTRODUCTION:** In our daily lives, we constantly move through complex environments. The successful execution of challenging activities such as navigating uneven terrain, avoiding obstacles or coping with external disturbances is largely determined by locomotor actions that require the timely and coordinated activation of different muscles. However, given the tremendous number of muscles, joints and therefore degrees of freedom in our bodies, it is unlikely that muscles are activated individually to perform even the simplest motor task. Following ideas about central pattern generators that originated over a century ago (Brown, 1911) and were later developed (Bernstein, 1967), it has been suggested that the central nervous system may simplify the production of movement by orchestrating muscle activations into patterns that are directed to functionally related muscle groups. This strategy would allow to obtain the desired motor output with the minimum control effort (Tresch *et al.*, 1999). These patterns, called muscle synergies, would contain information about the extent to which each muscle should be involved (represented by spatial coefficients, also called muscle weights) and the timing of this involvement (represented by temporal coefficients, or activation patterns. In this talk, I will present experimental evidence that muscle synergies for locomotion remain largely invariant, regardless of the mode and speed of locomotion, as well as the presence of perturbations, whether internal (e.g. ageing or pathology) or external (e.g. uneven terrain or mechanical disturbances). Upon closer examination of the fine adjustments required to adapt to different conditions of locomotion, it becomes clear that most of the tuning is time-dependent, resulting in the modulation of activation patterns. Spatial tuning, which involves redistributing the relative muscle weights, is typically sparse and strictly task-specific.

**MUSCLE SYNERGIES FOR DIFFERENT LOCOMOTOR MODES AND SPEEDS:** Multiple studies from various research groups and cohorts have shown that walking and running, the two most common modes of locomotion during daily activities, share similar numbers and structures of muscle synergies (Ivanenko *et al.*, 2004; Cappellini *et al.*, 2006; Dominici *et al.*, 2011; Lacquaniti *et al.*, 2012; Hagio *et al.*, 2015; Santuz *et al.*, 2018, 2020*a*, 2020*b*; Mileti *et al.*, 2020). The modular organisation of locomotion typically reflects the main phases of the gait cycle: body weight acceptance, propulsion, and early and late swing. During body weight acceptance, the knee extensors play a major role, while propulsion is dictated by the characteristic activity of the foot plantarflexors. During the early phase of leg swing, the foot dorsiflexors and hip flexors are the primary contributors. In the late portion of the swing, the choral action of the knee flexors prepares the leg for the incoming touchdown.
The relative muscle contributions remain consistent between walking and running. However, the activation patterns undergo significant adjustments to adapt to the different duty cycle (i.e. the ration between the duration of the stance phase and the duration of the whole gait cycle) and velocity of execution. These adjustments result in a temporal widening of most of the

activation patterns required for running, relative to the duration of the gait cycle, compared to those needed for walking (Santuz *et al.*, 2020*a*, 2020*b*; Mileti *et al.*, 2020). In addition, the activation patterns result locally (i.e. within each gait cycle), but not globally (i.e. across all gait cycles), less complex in running than in walking, as indicated by the Higuchi's fractal dimension and Hurst exponent (Hurst, 1951; Higuchi, 1988; Santuz & Akay, 2020).
Similar tuning signatures of modular locomotion control are also visible within each gait mode when the speed changes (Cappellini *et al.*, 2006; Lacquaniti *et al.*, 2012; Kibushi *et al.*, 2018; Santuz *et al.*, 2020*b*). Although the relative muscle weights remain largely unaffected by speed, faster running (but not walking) requires relatively wider activation patterns (Santuz *et al.*, 2020*b*). Furthermore, in both walking and running, the local complexity of activation patterns decreases as the speed increases (Santuz *et al.*, 2020*b*). In elite athletes, when running speed reaches values that correspond to sprinting, sparse but defined redistribution of muscle weights also happen, such as the shift in contribution of the biarticular *rectus femoris* from knee extensor during weight acceptance to hip flexor during early swing (Santuz *et al.*, 2020*b*).

**TUNING OF MUSCLE SYNERGIES IN THE PRESENCE OF INTERNAL AND EXTERNAL PERTURBATIONS:** To maintain locomotor function in the face of disturbances or errors of execution, the neuromotor system constantly tunes muscle synergies. Similar to what happens for locomotor modes and speeds, the hallmarks of these coping mechanisms are mostly time-related and well conserved across perturbation types. Sources of internal perturbations that are known to affect the modulation of muscle synergies are ageing (Santuz *et al.*, 2020*a*; Dewolf *et al.*, 2021), young age (Dominici *et al.*, 2011; Sylos-labini *et al.*, 2020) and pathology (Martino *et al.*, 2015; Cappellini *et al.*, 2016; Janshen *et al.*, 2020; Santuz *et al.*, 2022; Rao *et al.*, 2023), while external perturbations are related to the characteristics of the environment and can include, among others, uneven or slippery terrain, obstacles and external forces (Chvatal & Ting, 2012; Martino *et al.*, 2015; Santuz *et al.*, 2018, 2020*a*, 2022).
Older adults cope with the physiological decline of the sensorimotor system by increasing the relative width of the activation patterns (Santuz *et al.*, 2020*a*). In a very similar way, the relative widening of activation patterns is a strategy used by patients with multiple sclerosis (Janshen *et al.*, 2020) or knee instability after total arthroplasty (Rao *et al.*, 2023) to cope with an internally perturbed state.
Widening of the activation patterns are also found in healthy adults walking or running on uneven (Santuz *et al.*, 2018) or unstable ground (Santuz *et al.*, 2020*a*). Moreover, in response to unpredictable mediolateral displacement or acceleration of the treadmill platform, healthy adults reduce the local complexity and dynamic instability (as measured by the short-term maximum Lyapunov exponents) of activation patterns (Santuz *et al.*, 2020*a*). Older, healthy adults partially lose the ability of their younger counterparts to down-regulate the local complexity and local dynamic instability of these activation patterns (Santuz *et al.*, 2020*a*). Recent advances in mouse genetics have revealed similar strategies in mice lacking certain forms of somatosensory feedback, further highlighting the parallel between internal and external perturbations. In a nutshell, animals acutely ablated of proprioceptors (sensory organs that detect and transmit information about changes in muscle length and tension) respond to the impairment by widening their activation patterns and reducing their global complexity, regardless of the presence or absence of external mechanical perturbations (Santuz *et al.*, 2022).

**CONCLUSION:** Although the sources of perturbations to locomotion can be very different in nature, the strategies adopted by the neuromotor system to cope with them are exceptionally conserved. Widening activation patterns relative to the duration of the gait cycle and reducing complexity/instability are all adaptive mechanisms that can be seen in response to both internal and external perturbations and in different cohorts ranging from elite athletes to neurological patients and healthy older adults. These similarities suggest that, despite the highly complex structure of the nervous system, the neural factors responsible for these coping strategies may share a common origin.

**REFERENCES**


Bernstein NA (1967). *The co-ordination and regulation of movements*. Pergamon Press Ltd., Oxford.

Brown TG (1911). The intrinsic factors in the act of progression in the mammal. *Proceedings of the Royal Society of London Series B, Containing Papers of a Biological Character* **84,** 308–319.

Cappellini G, Ivanenko YP, Martino G, MacLellan MJ, Sacco A, Morelli D & Lacquaniti F (2016). Immature Spinal Locomotor Output in Children with Cerebral Palsy. *Frontiers in Physiology* **7,** 1–21.

Cappellini G, Ivanenko YP, Poppele RE & Lacquaniti F (2006). Motor patterns in human walking and running. *Journal of Neurophysiology* **95,** 3426–3437.

Chvatal SA & Ting LH (2012). Voluntary and reactive recruitment of locomotor muscle synergies during perturbed walking. *The Journal of Neuroscience* **32,** 12237–12250.

Dewolf AH, Sylos-Labini F, Cappellini G, Ivanenko YP & Lacquaniti F (2021). Age-related changes in the neuromuscular control of forward and backward locomotion ed. Masani K. *PLOS ONE* **16,** e0246372.

Dominici N, Ivanenko YP, Cappellini G, D'Avella A, Mondi V, Cicchese M, Fabiano A, Silei T, Di Paolo A, Giannini C, Poppele RE & Lacquaniti F (2011). Locomotor Primitives in Newborn Babies and Their Development. *Science* **334,** 997–999.

Hagio S, Fukuda M & Kouzaki M (2015). Identification of muscle synergies associated with gait transition in humans. *Frontiers in Human Neuroscience* **9,** 48.

Higuchi T (1988). Approach to an irregular time series on the basis of the fractal theory. *Physica D: Nonlinear Phenomena* **31,** 277–283.

Hurst HE (1951). Long-term storage capacity of reservoirs. *Transactions of the American Society of Civil Engineers* **116,** 770–808.

Ivanenko YP, Poppele RE & Lacquaniti F (2004). Five basic muscle activation patterns account for muscle activity during human locomotion. *The Journal of Physiology* **556,** 267–282.

Janshen L, Santuz A, Ekizos A & Arampatzis A (2020). Fuzziness of muscle synergies in patients with multiple sclerosis indicates increased robustness of motor control during walking. *Scientific Reports* **10,** 7249.

Kibushi B, Hagio S, Moritani T & Kouzaki M (2018). Speed-Dependent Modulation of Muscle Activity Based on Muscle Synergies during Treadmill Walking. *Frontiers in Human Neuroscience* **12,** 1–13.

Lacquaniti F, Ivanenko YP & Zago M (2012). Patterned control of human locomotion. *The Journal of Physiology* **590,** 2189–2199.

Martino G, Ivanenko YP, D'Avella A, Serrao M, Ranavolo A, Draicchio F, Cappellini G, Casali C & Lacquaniti F (2015). Neuromuscular adjustments of gait associated with unstable conditions. *Journal of Neurophysiology* **114,** 2867–2882.

Mileti I, Serra A, Wolf N, Munoz-Martel V, Ekizos A, Palermo E, Arampatzis A & Santuz A (2020). Muscle Activation Patterns Are More Constrained and Regular in Treadmill Than in Overground Human Locomotion. *Frontiers in Bioengineering and Biotechnology*; DOI: 10.3389/fbioe.2020.581619.

Rao L, Horn N, Meister N, Preiss S, Taylor WR, Santuz A & Schütz P (2023). Comparable in vivo joint kinematics between self-reported stable and unstable knees after TKA can be explained by muscular adaptation strategies: A retrospective observational study. *eLife* **12,** e85136.

Santuz A & Akay T (2020). Fractal analysis of muscle activity patterns during locomotion: pitfalls and how to avoid them. *Journal of Neurophysiology* **124,** 1083–1091.

Santuz A, Brüll L, Ekizos A, Schroll A, Eckardt N, Kibele A, Schwenk M & Arampatzis A (2020*a*). Neuromotor Dynamics of Human Locomotion in Challenging Settings. *iScience* **23,** 100796.

Santuz A, Ekizos A, Eckardt N, Kibele A & Arampatzis A (2018). Challenging human locomotion: stability and modular organisation in unsteady conditions. *Scientific Reports* **8,** 2740.

Santuz A, Ekizos A, Kunimasa Y, Kijima K, Ishikawa M & Arampatzis A (2020*b*). Lower complexity of motor primitives ensures robust control of high-speed human locomotion. *Heliyon* **6,** e05377.

Santuz A, Laflamme OD & Akay T (2022). The brain integrates proprioceptive information to ensure robust locomotion. *The Journal of Physiology* **600,** 5267–5294.

Sylos-labini F, Scaleia VL, Cappellini G, Fabiano A, Picone S, Keshishian ES, Zhvansky DS, Paolillo P, Irina A, D'Avella A, Ivanenko YP & Lacquaniti F (2020). Distinct locomotor precursors in newborn babies. *Proceedings of the National Academy of Sciences* **In Press,** 1–9.

Tresch MC, Saltiel P & Bizzi E (1999). The construction of movement by the spinal cord. *Nature Neuroscience* **2,** 162–167.