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# Principles of human locomotion: a review*

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*Abstract*— **In this article the principles of human locomotion are revisited and reviewed. This has been done in the framework of two European projects, where the elicitation of these mechanisms inform, on the one hand, the design of artificial bipedal walkers (H2R), and on the other hand the design of lower limb exoskeletons (BETTER) for rehabilitation of gait in post-stroke patients. Passive dynamics emerging from the morphology of the human musculoskeletal system, reflexes as stabilization mechanisms, modular control of movement as well as supra-spinal control of gait are reviewed to get insight on how these mechanisms can be used to explain human locomotion.**

## I. Introduction

The human musculoskeletal and neural-motor system is highly optimized for efficient locomotion. Efficiency, stability and voluntary modulation of human gait are a result of a combination of features spanning the human musculoskeletal, sensorimotor and neural systems. Salient aspects of these systems include (1) the functional morphology, (2) the synergistic coordination of motor activity, (3) the phase dependent modulation of muscle activity and (4) cognitive skills.

On the one hand, the functional morphology is highly optimized for efficient biped locomotion [1] as it allows exploiting the inherent dynamics to reduce energy consumption and control effort, and result in natural looking motions. Also a contribution of this functional morphology is the capability of self-stabilization, since the elastic properties of muscles and tendons increase stability without active control.

On the other hand, the synergistic feed-forward motor patterns, be it activated at kinetic or kinematic events or due to learned timing, create coordinated synergies of movement. Whilst feedback control occurs at various levels of complexity regarding the extension of perception and deployment of muscle action, phase-dependent modulation is a function of the current task or phase of motion, and as a result reflex action can be modulated, reinforced, or suppressed. Eventually, cognition plays a crucial role in learning and predicting the sensory consequences of actions, helping to deal with feedback time delays and allowing for planning the appropriate compensative actions (active and passive).

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This paper will address and review the various motor principles leading to efficient locomotion in humans. In so doing, we will analyze the functional morphology in section II, the contribution of reflex mechanisms to stabilize locomotion in section III, the orchestration and synergistic coordination of motor patterns in section II and eventually the supra-spinal control of gait in humans in section IV.

## II. Functional Morphology of the Human Musculoskeletal System

Research on the biomechanics of human locomotion provides valuable insights into basic principles for motor control. Human legged locomotion is so efficient partially because it does not power movements with independent motor actions at each joint. Muscles often span multiple joints, which results in energy-saving and power transfers when a movement simultaneously requires negative power at one joint and positive power at another joint [2]. This allows making effective use of passive elastic properties to generate part of the required force or power without metabolic cost, especially when muscle-tendon units span multiple joints [3]. Furthermore, multiple muscles spanning a joint allow efficient modulation of joint stiffness during dynamic movements, making fast adaptation to uneven surfaces and terrains possible.

Passive dynamic walking introduced, as a model, in under-actuated bipedal walkers and robots shows emerging, natural-looking walking gait with remarkable similarities to human walking. In this regards, passive dynamic walking, first introduced by McGeer [4], exploits the mechanical potential energy gained while walking down a slope, showing a stable gait without any or limited control or actuation. Limit Cycle (LC) walking machines represent a step forward in this direction. They combine the exploitation of passive dynamics with minimal feed-forward actuation in order to replenish energy losses and to increase stability. Examples of LC walking prototypes have been developed by TU Delft [5], Cornell University and MIT [6]. The Cornell and Delft bipeds demonstrate that basic walking can be accomplished with extremely simple control and very low energy consumption. However, due to absence of feedback control, passive dynamics bipeds cannot react to disturbances or external forces, even though human-like gait is achieved, walking is unstable as all other stabilization mechanisms found in humans are still lacking.

## III. Role of Reflex Function for Stabilization of Locomotion

Bipedal plantigrade walking in humans is unique compared to digitigrade locomotion in animals, in that the stance phase is made by ground contact first by the heel, then the foot sole and finally the toes. In addition support is afforded by maximal activation of the quadriceps muscle mediated via reflex mechanisms, focused to maintain balance during sudden perturbations. These reflex mechanisms are even more important to maintain balance during walking on uneven surfaces, and are mainly organized at the transcortical level in humans.

Activity within reflex pathways during normal walking is organized to mediate an opposite effect on the ankle and knee extensor motoneuron pools. As such under normal conditions reflex mechanisms are organized to permit maximal quadriceps muscle activation with knee joint stabilization during the early stance phase, in addition to inhibition of ankle extensor muscle hyperactivity. Specifically at the beginning of the stance phase, quadriceps contraction is maintained by a combination of control mechanisms including facilitation of GpI-II afferent input from Tibialis Anterior (in addition to Biceps muscle activation), excitatory cutaneous input from the foot, and reduced recurrent and presynaptic inhibition. In parallel prevention of Triceps Surae hyperactivity is mediated via an almost total absence of Ia heteronymous connections, a strong increase in presynaptic inhibition of Ia terminals, and a strong propriospinal mediated inhibition of plantarflexors evoked from intrinsic plantar muscle activation. Stabilisation of the ankle joint during the stance phase is mediated by low activity within recurrent and reciprocal Ia inhibitory mechanisms between ankle muscles. In addition stretch reflexes evoked within the Tibialis Anterior and Soleus muscles and mediated at the spinal and transcortical level, may contribute significantly to stabilization during the stance phase.

A separate set of control mechanisms are important for walking during unexpected perturbations, with an important role for afferent muscle and/or cutaneous feedback necessary to regain stabilization. Under such conditions, stretch-induced responses provide stability during the stance phase, important for example when the ground may give way or during foot slip, while cutaneous reflex activity is organized to permit foot clearance from an unexpected obstacle. Importantly reflex reactions under conditions of external perturbation are mediated mainly via transcortical pathways, which allows for an additional level of voluntary control during the perturbation to either stop movement or to shift weight onto the other leg. Significant stretch reflex responses mediated by Gp Ia or II afferents, or as transcortical responses, are mostly active during the stance but not swing phase. Additional ankle support is mediated via antagonistic ankle muscle stretch reflexes via heteronymous Ia input. In contrast, activation of low-threshold cutaneous reflex responses in ankle and knee flexors during the swing phase, are probably mediated via spinal, spino-bulbo-spinal and transcortical control mechanisms, which also depend on the stimulation of specific skin areas. In general cutaneous reflexes are tuned to withdraw the perturbed leg away from the perturbing stimulus, while maintaining voluntary muscle function during walking.

## IV. MODULAR CONTROL OF MOVEMENT

According to the hypothesis of modular control [7], muscle activations appear to be ruled by a low-dimensional set of descending inputs mediated by arrays of weighted connections, namely muscle synergies. Experimental evidences in animals and humans, over a wide range of motor functions [8], have mathematically confirmed this hypothesis, showing that multiple EMG can be reconstructed by the combination of a few activations and muscle synergy vectors. For instance, in locomotion, 4 to 5 motor modules (synergies) are sufficient to accurately describe the activity of all the main muscles involved [11].

Nevertheless, the physiological plausibility of this hypothesis is still controversial. Several questions have been coming out during the last years in the scientific community. Do muscle synergies and activations correspond to real neural mechanisms? Is the dependency between muscle activations just a result of biomechanical constraints? Can muscle synergies reflect specific neuromuscular pathologies? [12][13]. In order to answer these and more questions, different experimental approaches have been proposed. Here, we classify them into in-vivo and in-vitro approaches.

In-vivo approaches rely on the analysis of biomechanical and muscular behavior of biological structures. Kutch and Valero-Cuevas [14] presented an experiment on a cadaveric human hand to show that synergistic patterns come out with no need of any neural intervention. Increasing studies rely on the analysis of neurologically impaired people to show correlations between neural injury and muscle synergy organization [15][16]. More recently, experiments in force-field scenarios [17] have been proposed as a way to find correlation between muscle synergies and motor learning. None of the proposed studies have given a clear demonstration on the neural origin of the synergistic behavior, possibly because all these in-vivo approaches are characterized by an intrinsic difficulty of separating the biomechanical constraints from the neural factors. In addition, during in-vivo experiments, many unknown mechanisms intervene - such as sensory feedback processing, interlimb coordination, spasticity and other neurologically related mechanisms - which may mask the targeted principles.

In-vitro approaches are gaining relevance as a valuable tool to validate specific mechanisms while minimizing unknown factors. The two main actors of this kind of approach are neuro-musculoskeletal modeling and robotics. Neuro-musculoskeletal modeling is a very powerful method that permits to predict the effects of muscular activity on multi-limb dynamics, as well as to simulate the neural drive and its effect on muscle dynamics. This approach has been mainly used to demonstrate a clear correlation between synergies and motor functions [18]. Recently, an interesting comprehensive integration of human biomechanical principles within a synergistic control framework has been also proposed in simulated environment [19]. In comparison to neuro-musculoskeletal modeling, robotics permits on the one hand to create real-life representation of the human neuro-musculoskeletal system, which allow dealing with uncertainties and dynamics that are difficult to reproduce in simulated environments. On the other hand, the technical limitations of the robotic solutions prevent them to reproduce the high degree of freedom of human musculoskeletal system.

In our opinion, the complementary potentials of in-vitro and in-vivo approaches can be integrated to find out effective solutions for the validation of the modular control hypothesis. To this aim, the EU funded project H2R [20] "Integrative Approach for the Emergence of Human-like Robot Locomotion", proposes to combine physiological investigation and neuro-musculokeletal modeling within a robotic framework. The rationale behind this project is to formalize and integrate the modular mechanisms found in humans into hierarchically organized robotic platforms. This process is expected to result in human-like behavior as spontaneously emerging from such biologically motivated organization.

## V. Supraspinal Control of Human Walking

The abundant evidence of existence of spinal control of biped locomotion in animals is limited in humans possibly due to a greater cortical involvement and the differences between humans and other mammals (e.g. effects on gait of supra-spinal lesions). Regardless of the exact location of the CPGs (may be distributed throughout the spinal cord), its existence can be hypothesized considering that these circuits are influenced by peripheral and central inputs. It is common knowledge that brain lesions profoundly affect gait in humans. Thus, it is accepted that bipedal walking requires the interplay between the brain and spinal cord, with the final motor output shaped by sensory feedback from peripheral receptors. The basic motor pattern for stepping is generated in the spinal cord, while fine control of walking involves various brain regions including motor cortex, cerebellum and brain stem.

To some extent it has been possible to study the interrelationships between spinal and supra-spinal centres by different approaches that may provide direct (gait development in humans or observing the roles of cortical centres for walking applying trans-cranial stimulation or time-frequency domain analyses of EEG or EMG) and indirect (e.g. analysing neural contributions in brain and spinal lesions in animals and humans) evidences (reviews of gait neurophysiology in [1], [22]).

More recent studies with humans are providing a clearer frame of cortico-spinal interplay and engagement of cortical neurons. The current evidence suggests that the nervous system controls complex motor tasks by using a low-dimensional combination of motor modules (also known as synergies, see section III) and activation signals [23]. In a recent study, it was concluded that motor modules observed in sub-acute stroke patients during locomotion are different from those used by healthy controls, despite similar impulsive activation signals [23]. Since motor modules are modified in stroke with maintenance of the activation impulses, it can be speculated that supra-spinal centers can be shaped to promote recruitment of neural resources [24].

The BETTER Project combines brain-neural computer interface technology (BNCI) with robotic therapy to improve robot therapies by intelligently promoting the active participation of the patients during training and to understand direct neural correlates during walking. In stroke, cortico-motor activity changes can be observed to find possible correlates of improved motor performance. Excitability of the neural projections connecting relevant brain areas to a target leg muscle can be increased with a precise association between cortical potentials evoked by motor imagination and an afferent stimulation [25]. Based on this experience, ambulatory BCI for stroke rehabilitation using Movement Related Cortical Potentials, MRCPs, to drive robotic treatment has been proposed [26]. In other study, the EEG activity in the beta band observable during real and imaginary foot movements has been characterised as phenomena that reflects an active inhibition process [27].

Fewer studies have investigated direct neural correlates during actual gait, mainly due to restrictions that movement artifacts pose for neuroimaging techniques. Recent findings in [28] demonstrated that independent component analysis of EEG can reveal unique spatial and spectro-temporal electro-cortical properties for different lower limb motor tasks and showed feasibility of classification of human lower limb movements (ankle and knee tasks) from single-trial EEG. In [29] the synchrony between cortical signals recorded with EEG and EMG signals recorded from the tibialis anterior muscle during walking was investigated in steady-state treadmill walking. It was found that rhythmic cortical activity (24–40 Hz frequency band) is transmitted via the cortico-spinal tract to the investigated muscles during walking, showing that the motor cortex and cortico-spinal tract contribute directly to the muscle activity in the observed gait. During cycling, a recent study demonstrated that substantial sensorimotor processing occurs in the brain during pedaling in humans [30].

Other focus investigated in the BETTER Project is to drive the (robot) therapy to enhance the active participation of the user while attempting to walk. Thus, Wagner et al. investigated the spectral patterns in the EEG that are related to active and passive robot assisted gait [31]. The neurophysiological correlates of active participation during robot assisted gait training were investigated and demonstrated that cortical activity is related to lower limb movements in robot assisted gait that account for differences between active and passive walking in healthy humans.

In incomplete Spinal Cord Injury, SCI, increased activation of the motor cortex during foot movements has been observed and it has been hypothesised that these changes can be related to increase in evoked muscle responses [32]. Interestingly, spinal neuronal circuits undergo functional changes also after a stroke, with common but also divergent features compared to SCI subjects [33].

Monitoring and understanding cortical activation during walking is therefore helpful to relate changes in brain activity to functional improvements. Despite the exact role of the motor cortex in control of gait is unclear, available evidence may be applied to gait rehabilitation of patients with spinal and brain lesions.

## VI. Conclusion

Passivity in human walking accounts for efficient human locomotion. Net power transfer between human limb joints during gait complements this passive dynamics. However, the application of purely biomechanical or energy-flow principles lead to unstable walking. A number of stabilization mechanisms must then be orchestrated. While reflexes can be seen as mechanisms responsible for stabilization of human locomotion, modular control can be proposed as a mechanism to reduce the dimensionality of the control problem of human gait. In this scheme, supra-spinal centres would be responsible of modulation and activation of motor modules. Both in BETTER and H2R EC projects these principles are being used to develop technologies for rehabilitation of human gait in post-stroke patients and to model neuro-motor mechanisms responsible for efficient an human-like movement in gait respectively. In H2R, a bipedal walker will be used to validate models of all these mechanisms in achieving human-like walking in artificial robots, whilst in BETTER and HYPER, the analysis of supra-spinal involvement in gait in post-stroke patients is used to associate interventions at the periphery for a better rehabilitation.

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