Adaptive control of dynamic balance in human walking

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GENERAL DISCUSSION

MAIN FINDINGS

Adaptive control of dynamic balance is necessary to stay upright in human walking [1], and while it takes human infants over a year to learn how to walk [2], we walk autonomously for the majority of our life. It is at the point that mobility deteriorates, due to aging or pathology [3-5], that we may come to realize how being ambulant enriches our lives [6]. Although prevention programs for mobility decline and gait rehabilitation are aimed at increasing safe walking performance, we are yet unable to restore adaptive walking performance to a normal level after it deteriorates [7]. Currently, we do not fully understand the underlying mechanisms of adaptive control of dynamic balance in able-bodied and pathological populations. Therefore, the aim of this thesis was to increase our understanding of adaptive control of dynamic balance in human walking.

Through a series of five experiments, this thesis brought insight into adaptive control of dynamic balance in both able-bodied and post-stroke individuals. A synergistic structure that controls the speed dependent modulation of muscle activity was proposed as a means for adaptive neuromuscular control in human walking (chapter 2). Furthermore, mediolateral dynamic balance control was shown to adapt to walking with asymmetric belt speeds, i.e. a sustained perturbation of gait, through a complementary mechanism of relative foot placement and mediolateral foot roll-off (chapter 3). To better understand the control of relative foot placement, we proposed bilateral temporal control as a mechanism that regulates dynamic balance during symmetric, asymmetric and adaptive human walking. This mechanism may potentially explain pathological walking strategies to increase balance on an injured leg (chapter 4). When the balance control problem during split-belt adaptation was eliminated through external balance support, it was found that locomotor adaptation and learning decreased, emphasising the key role that adaptive control of dynamic balance plays in human walking and locomotor learning (chapter 5). In chapter 6, knowledge from chapters 3 and 4 was applied to understand reactive stepping in people post-stroke. There it was shown that anteroposterior and mediolateral paretic stepping strategies co-vary during the paretic recovery steps following a slip-like perturbation. This means that an improvement in frontal plane balance may come at the cost of reduced sagittal plane balance during paretic reactive stepping. The results from chapters 4 and 6 suggest that spatiotemporal stepping asymmetries in people post-stroke may not be a threat for dynamic balance, but rather a strategy to enhance dynamic balance control through unloading of the paretic leg. This thesis has shown that adaptive control of dynamic balance is an interaction between passive movement, e.g. resultant forces acting within and upon the body, and active control by the central nervous systems. In sum, learning to walk is learning to adaptively control dynamic balance and exploit the body's passive dynamic properties in an efficient manner for safe bipedal locomotion.

ADAPTIVE NEUROMUSCULAR CONTROL OF HUMAN WALKING

To generate movement, we must produce moments of force over our skeletal joints [8]. These moments can be generated by either external forces, e.g. gravity, or internal forces, e.g. muscle contractions [8]. To actively control body movement, and not be dependent on the mere gravitational forces working on our body mass, control of muscle contractions is necessary. We can record the activity of muscles through wire or surface electromyography [9,10], by which we gain insight into coordination of muscles to control joint and segmental rotations.

In chapter 2, based on surface electromyography, we found that a synergistic structure might control the speed dependent modulation of muscle activity in human walking. The adaptation of walking speed is one of the most fundamental and frequently exhibited adaptations in human movement. Therefore, if a synergistic structure of functional muscle groups regulates neuromuscular control of human walking, such a structure should reflect this adaptability. In this chapter we described a single synergistic structure that scales with gait speed [11,12] and thereby can control muscle activity during human walking at multiple gait speeds. While this structure can account for walking at a large range of velocities, the question remains whether this synergistic structure can also account for other walking tasks, such as turning or stepping over obstacles.

Although synergistic approaches to understand adaptive neuromuscular control of human walking bring a lot of knowledge to the field of locomotor control, I would like to consider three personal points of critique. First, the functional muscle groups that are found through principal component analysis or other factorization analyses could reflect neuromuscular control, but also the biomechanical constraints of human walking. Considering that human walking has an invariant task structure, muscle groups will always contribute to (sub-)tasks of gait in a consistent and predictable way. One of these sub-tasks in walking is propulsion, as without propulsion we will not progress forwards. To propel ourselves forward we generate push-off power, for which we need ankle plantarflexion. The muscles that contribute to ankle plantarflexion, the m. triceps surae [13], will then be active at the same time, resulting in a functional muscle group. One can then question whether the found muscle synergy that includes the m. triceps surae is a reflection of synergistic neuromuscular control, or rather the logical biomechanical requirement of that (sub-)task. Second, in the literature, motor synergies are often recalculated for every task, or phase of a task, after which these synergies are compared for further assessment [14,15]. However, according to the definition of muscle synergies as introduced in chapter 1 of this thesis, a true synergistic organization of muscle activity consists of a single library of patterns that controls all movements [16]. Muscle synergies are then an invariant set of control signals, reweighted for each task or condition. The problem that arises with this approach is that an extra control layer is necessary to weigh these control signals for each task. However, this additional control is often neglected in literature and reweighing synergies for every task may lead to a virtually infinite number of control possibilities rather than reduce its complexity. Indeed, in recent work on simplification of neural control through muscle synergies, Zelik, La Scaleia, Ivanenko and Lacquaniti (2014) stated that: *'The results obtained here based on simple neural architectures highlight the need for more sophisticated formulations of modular control or alternative motor control hypotheses and motivate future research to identify specific, testable neural mechanisms that can accommodate muscle coordination for disparate locomotor tasks'* [17]. Third, a cut-off criterion based on the percentage of variance accounted for by a factorization analysis is often chosen to select the number of synergies, e.g. 80 or 90 % variance accounted for [18,19] (chapter 2). This means that 10 to 20 % of variance in muscle activation is not accounted for. While muscle synergies can then describe the average behavior of individuals during a task, it can very well be that actual adaptive behavior lays in the 10 to 20 % of unaccounted variance.

To (dis)prove the theory of muscle synergies we yet need to come up with a refutable or falsifiable experimental paradigm. This experimental paradigm would have to alter the biomechanical constraints of walking, for instance through crouch gait. A single synergistic structure should then be able to describe both upright and crouch gait without recalculation or post-hoc comparison of synergies for each task. Finally, this synergistic organization of muscle activity should be able to explain adaptive behavior. The remainder of this thesis employed a more complex adaptation paradigm than the adaptation to different walking velocities, namely the adaptation to asymmetric walking velocities, i.e. split-belt walking.

ADAPTIVE CONTROL OF DYNAMIC BALANCE

In chapter 3 we showed that parameters of dynamic balance control adapt to a sustained perturbation of gait, which suggests an important role of dynamic balance in locomotor adaptations. In addition, when the balance control problem was reduced through external support during that same sustained perturbation, healthy young adults showed reduced locomotor learning (chapter 5). The findings in chapter 5 indicate an important role of dynamic balance control in locomotor adaptation. When participants were allowed to hold on to handrails during split-belt walking, balance control itself was no longer a problem because participants could stabilize themselves. Participants holding on to handrails were perturbed less during early split-belt walking, and therefore had less need to adapt their stepping pattern to the asymmetric belt speeds. Subsequently, switching back to tied-belt walking was not a problem as no adaptation took place during split-belt walking. Consequently, these participants did not learn the novel locomotor task, as was reflected by the reduced after-effects. Based on these findings, one can argue that maintaining dynamic balance is an important task goal, which shapes adaptive locomotor control and learning. As without learning to adaptively control dynamic balance, we would be able to progress forwards through space for a short period, but fall over eventually. Furthermore, while balance assistance is often used in clinical practice to relearn people to walk, clinicians should take into account that balance assistance may reduce learning effects.

A SPATIOTEMPORAL STEPPING MODEL FOR ADAPTIVE CONTROL OF DYNAMIC BALANCE

In this thesis, control of dynamic balance was described and quantified by the margin of stability [20]. The margin of stability contains valuable information about stepping strategies and center of mass control [21,22]. However, to adequately use the margin of stability, it is important to thoroughly grasp its potentials and limitations and to understand how the mediolateral and the anteroposterior margins of stability can be controlled during human walking. Therefore, a spatiotemporal stepping model for adaptive control of dynamic balance is proposed and visualized here (Figure 1).

The mediolateral margin of stability is defined as the distance between the extrapolated center of mass position and lateral edge of the base of support. Therefore, the mediolateral margin of stability can be controlled by changing the lateral base of support or by moving the extrapolated center of mass position. First, by increasing the lateral base of support, i.e. making a wider step, the margin of stability becomes larger, and logically, by making a narrower step, the margin of stability becomes smaller [21]. Second, the lateral excursion of the extrapolated center of mass can be increased, by bilaterally increasing stance time, i.e. decreasing cadence, which leads to a smaller margin of stability (chapter 4). Vice versa, bilaterally decreasing stance time, i.e. increasing cadence, decreases the lateral excursion of the extrapolated center of mass, and increases the mediolateral margin of stability [23] (chapter 4). Third, increasing the stance time on one leg, but not the other (walking with asymmetric stance times), leads to a shift in the mediolateral extrapolated center of mass position to the side with the longer stance time, and the mediolateral margin of stability becomes smaller on the side with the longer stance time. Hereby, asymmetric mediolateral margins of stability are created, with a smaller mediolateral margin of stability on the leg with longer stance time, and a larger mediolateral margin of stability on the side with the shorter stance time (chapter 4). This mechanism can be exploited, for instance to improve dynamic balance when walking on an injured leg, by standing on the non-injured leg longer and increasing the mediolateral margin of stability on the injured leg, possibly making it more robust against perturbations.

While the margin of stability is often defined at heel-strike, the margin of stability can be 'fine-tuned' through an ankle (chapter 3) [21,24] or hip strategy [25,26] during the stance phase. By using a mediolateral ankle strategy during the stance phase of gait, the location of the center of pressure under the foot can be altered after foot placement, thereby increasing the base of support when the margin of stability at heel-strike was small, or decreasing the base of support when the margin of stability at heel-strike was large. Similarly, a hip strategy can be used to move the trunk, head and arms, which generates a moment around the hip in the frontal plane [25]. By using a hip strategy, the location of the extrapolated center of mass can be moved medial or lateral, to in- or decrease the mediolateral margin of stability. For example, in narrow-ridge walking, large upper body movements are exhibited to generate a hip moment, regulate the body's center of mass and remain stable [25]. While the relation between foot placement

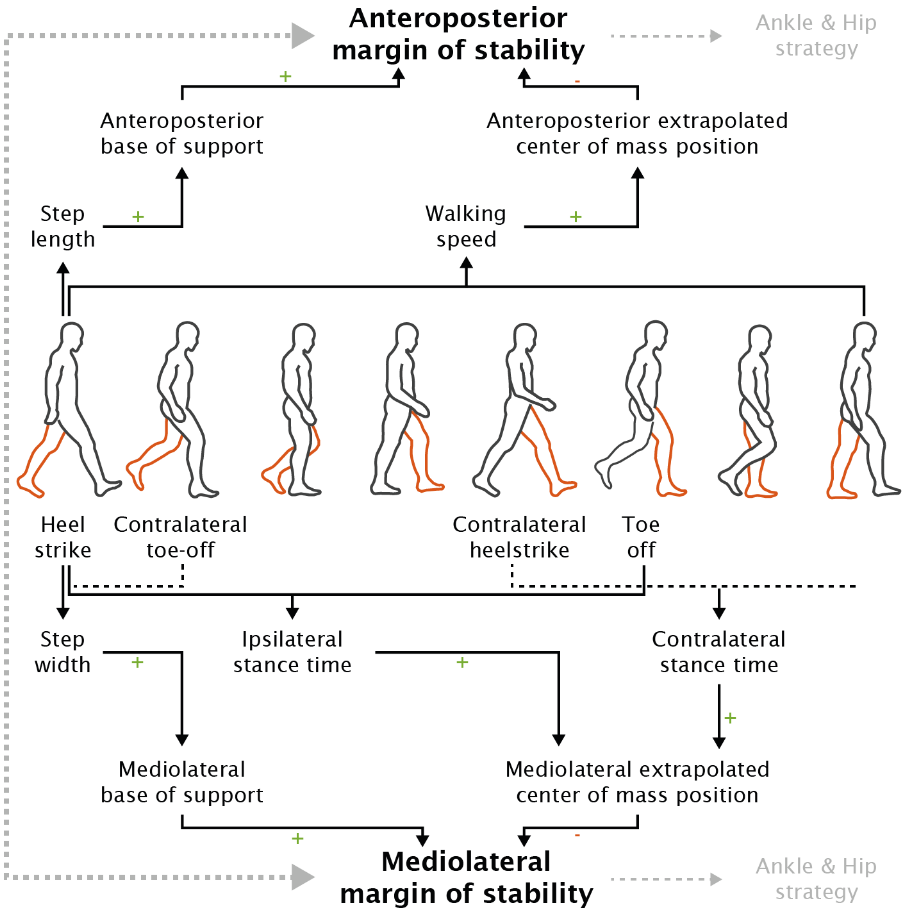

Figure 1 – A spatiotemporal stepping model for adaptive control of dynamic balance in the frontal and sagittal plane. A '+' indicates a positive effect, a '–' indicates a negative effect. The anteroposterior margin of stability is positively affected by step length and negatively affected by walking speed, and might be fine-tuned during stance by an ankle and / or hip strategy. The mediolateral margin of stability is positively affected by step width and negatively affected by bilateral stance times, and is fine-tuned during stance by an ankle and hip strategy. Note that a unilateral increase in contralateral stance time will lead to an increase in the contralateral mediolateral margin of stability (chapter 4). The large grey arrows on the left side of this figure depict the possible covariation between frontal and sagittal plane margins of stability (chapter 6).

and stance time follows logically from the linear inverted pendulum model, the model neglects the effect of an ankle or hip strategy. Previous research and this thesis (chapter 3) show that foot roll-off can be seen as an addition to this model to gain more insight in balance control strategies. For instance, Hof et al. (2017) [21] found that people with an upper leg prosthesis showed a larger margin of stability on the prosthetic than non-prosthetic side to compensate for the lack of mediolateral degrees of freedom in the prosthesis' ankle joint, and therefore the lack of mediolateral foot roll-off during stance. Interestingly, in chapter 3 we found a strong covariation between the mediolateral margin of stability and mediolateral foot roll-off. There are two hypotheses for this covariation that have yet to be investigated: (i) There is an optimal mediolateral margin of stability that can only be reached through active control of mediolateral foot roll-off after foot placement. (ii) The mediolateral foot roll-off is a product of passive dynamics in gait, which hypothetically works as follows; When we have a small margin of stability, our extrapolated center of mass position is more lateral to the edge of the base of support, resulting in an outward momentum of the body during foot roll-off, resulting in a passive outward mediolateral foot roll-off, and vice versa for a large margin of stability.

The anteroposterior margin of stability was not described in Hof's original work [20], but gained considerable interest and attention in more recent research [22,23,27,28]. Similar to the mediolateral margin of stability, the anteroposterior margin of stability can be controlled in multiple ways. First, the anteroposterior margin of stability can be increased by increasing the anteroposterior base of support, i.e. step length [23]. Second, the anteroposterior margin of stability can be increased by placing the anteroposterior extrapolated center of mass position more posterior, which can be achieved by reducing the walking speed [23]. Effects of ankle and hip strategies seem less evident, but may still be present in the anteroposterior direction. For instance, large upper body movements are made in response to a slipping or tripping perturbation (e.g. in chapter 6), generating a moment around the hip in the sagittal plane to regulate the anteroposterior position of the extrapolated center of mass. However, further research is needed to define whether the ankle and hip strategies are actively controlled or exploited to regulate the anteroposterior margin of stability during human walking.

Caution is advised when interpreting the anteroposterior margin of stability. While a negative mediolateral margin of stability would require a sidestep to prevent a fall [29], the anteroposterior margin of stability can be either positive or negative, while still resulting in stable gait [22,28] (chapter 6). When the anteroposterior extrapolated center of mass is in front of the leading leg's base of support, one can make the next step and maintain dynamic balance [30,31]. In addition, when the anteroposterior extrapolated center of mass is behind the leading leg's base of support gait can still be stable, while a person progresses forwards. Only when the extrapolated center of mass is behind the trailing leg's base of support, a backward step is necessary to remain stable [32]. Furthermore, different definitions of the anteroposterior base of support limit interpretation between studies. For example, in work by Hak et al. [22,23] the anterior base of support was defined as the posterior (heel marker) border of the leading foot. By this definition, the anteroposterior margin of stability will most often be positive during healthy unperturbed walking [22]. However, when the anterior border (toe marker) of the leading foot is chosen instead (chapter 6), the anteroposterior margin of stability can have both negative and positive values for the same behavior, and thus stable gait. Furthermore, when center of pressure positions are used to define the base of support (chapters 3 and 4), it is difficult to define a posterior or anterior border of the foot, and the center of pressure position of the leading foot will be used instead. Considering these differences between interpretations and methodologies, caution is necessary when reporting and interpreting margins of stability in human walking.

ADAPTIVE CONTROL OF DYNAMIC BALANCE IN PATHOLOGICAL WALKING

Regulation of the margin of stability contains both passive and active components (chapter 4), and exploitation of the passive properties of the margin of stability may allow for simple, yet effective adaptive control of dynamic balance in pathological populations. For example, people post-stroke show a shorter stance time on the paretic leg than the non-paretic leg [33], by which they increase the paretic mediolateral margin of stability (chapters 4 and 6). Interestingly, when we consider asymmetric margins of stabilities while walking in a straight line, the mediolateral margin of stability can only be increased asymmetrically by walking with asymmetric stance times, as increasing the mediolateral base of support on one leg and not the other, would lead to a walking in a curved path. However, unilaterally increasing the anteroposterior base of support, i.e. walking with asymmetric step lengths, would still result in walking a straight line. This implies that an asymmetric anteroposterior margin of stability can be acquired by walking with asymmetric step lengths, as is indeed commonly seen in people post-stroke [33].

In chapter 6, we examined balance strategies in reactive balance control in people post-stroke during a slipping experiment on a split-belt treadmill. There, we found asymmetric anteroposterior and mediolateral margins of stability during unperturbed walking and in the recovery steps following the perturbation. Furthermore, we found a covariation between the anteroposterior and mediolateral margins of stability in the paretic recovery step following the perturbation. This covariation implies that improving sagittal plane dynamic balance compromises frontal plane balance during reactive stepping with the paretic leg. Therefore, gait rehabilitation could be focused on decoupling the mediolateral and anteroposterior margins of stability during reactive stepping with the paretic leg, e.g. through perturbation-based training. In addition, to gain further insight in balance strategies post-stroke, it would be interesting to assess whether people post-stroke prioritize balance in one plane over the other.

THE SPLIT-BELT WALKING PARADIGM

The split-belt walking paradigm has led to advances in knowledge of locomotor adaptation [34], learning [35], retention [36], savings [37], optimization [38] and coordination [14,39]. More recently, advances in knowledge on adaptive control of dynamic balance during split-belt walking are seen (chapters 3, 4, 5 and 6) [27,40,41]. Furthermore, split-belt walking has been utilized in clinical practice to reduce pathological gait asymmetries [42]. The goal of such clinical approaches is to reduce pathological gait asymmetry and for example, results in a temporary reduction of step-length symmetry in people post-stroke [42]. However, one can question whether reduction of step length asymmetry is the right approach in post-stroke rehabilitation, as this thesis (chapters 4 and 6) indicates that the stepping asymmetry seen in people post-stroke may be a strategy that enhances adaptive control of dynamic balance in this population.

It should be kept in mind that split-belt walking is an artificial, laboratory-based task. The ecological validity of treadmill walking [43,44], let alone split-belt treadmill walking [45], compared to overground walking can be questioned. While it allows for long continuous data recording and training sessions, humans show different kinetic and kinematic parameters when walking on a regular treadmill [43,44] and walk with a wider base of support on a split-belt treadmill [45] compared to overground walking. The major benefit of studying locomotor adaptations on a split-belt treadmill is that it allows us to study how humans perform a completely novel walking task, in a controlled environment. Therefore, especially the implications from split-belt literature are deemed to find their way to rehabilitation practice. For instance, in chapter 5 the split-belt paradigm was utilized to study the effects of external balance support on locomotor learning, which lead to direct implications for gait rehabilitation.

ENERGETIC OPTIMIZATION OF HUMAN LOCOMOTION

Human walking can be described as a series of falling motions, each terminated by the next step to prevent an actual fall. Therefore, one can argue that the goal of locomotion is to progress forwards through space without falling. However, when we succeed to stay upright during walking, we still show adaptation in our walking pattern when task demands change, e.g. in split-belt walking (chapter 3). The question then comes to mind, why we change our walking pattern when we are already successful in progressing forwards while maintaining our balance. An answer to this question may lie in the energy or metabolic cost of human walking [46].

When gait is stable, humans may explore their movement possibilities to find a walking pattern that is most efficient, i.e. they optimize their walking pattern. Multiple options are available for optimization in human walking, e.g. shortest trajectory of limb motion, minimal fluctuation in center of mass height, or reduction of joint friction and impact forces. However, energetic optimization of human walking is very likely from both an evolutionary and empirical perspective. From an evolutionary perspective, all mammals, and therefore humans, may want to reduce the energy cost of movement. Since nutrition is scarce, energetic optimization of movement reduces the need for food, and thereby increases chances of survival. From an empirical perspective, there are studies showing that humans naturally walk with a step width [47], cadence [48] and velocity [49] that is at their energetic optimum. In addition, during split-belt adaptation, humans slowly reduce the energy cost of walking (chapter 3) [38,50]. Furthermore, during split-belt walking humans learn to take advantage of the treadmill's moving belts to reduce energy cost, up to the point where they cross the level of perfect step length symmetry, and go to a 'positive' step length asymmetry [51]. Ergo, an efficient stepping pattern is preferred over a spatiotemporally symmetric pattern. The knowledge that humans optimize their energy cost of walking when balance is safeguarded may help us to better understand and appreciate pathological walking.

HEAD, ARM AND TRUNK MOVEMENTS IN HUMAN WALKING

This thesis focuses on human walking; therefore, it seems logical to focus on lower-limb movements. However, human walking is not merely a movement of the legs, but rather of the whole body [52]. These movements can be captured using full-body marker sets, which contains information about the role of head, arm and trunk movements in human walking. For example, it was suggested that arm swing reduces energy cost of walking and increases stability [53]. In contrast, other studies described arm swing as a passive result of the movement of the human body, which reduces energy cost, but does not affect stability [54,55]. While many studies have described the effects of arm swing in unperturbed walking [52-55], it may also help us to better understand recovery steps in response to perturbations. In chapter 6 of this thesis, we found that regulation of the extrapolated center of mass position partially underlies changes in the anteroposterior margin of stability in reaction to slipping perturbations in walking post-stroke. This regulation may have been the result of upper-body movement, resulting in backward momentum of the body to stay upright, reducing the need for a stepping strategy to maintain dynamic balance. This illustrates that potentially valuable information lies in (the analysis of) head, arm and trunk movements in experiments on human walking, leaving room to explore in the future.

CONCLUDING REMARKS

The aim of this thesis was to increase our understanding of adaptive control of dynamic balance in human walking. The studies in this thesis have provided us with knowledge on adaptive neuromuscular control, adaptive control of dynamic balance, exploitation of passive properties of the human body, the effects of external support on locomotor learning and reactive stepping in people post-stroke. By assessment of the margin of stability, we gained insight in healthy and pathological adaptive control of dynamic balance, illustrating that this complex parameter can be regulated by simple changes in movement. The role of adaptive control of dynamic balance in locomotor learning was stressed by showing that handrail holding dramatically reduces learning outcomes. And finally, our current understanding of asymmetric strategies to control the margins of stability suggests that gait asymmetries in patient populations may enhance adaptive control of dynamic balance. In future research, a unified framework of both active and passive regulation of adaptive control of dynamic balance in human walking is necessary to further understand able-bodied and pathological human walking. This thesis brings us one step closer to understanding human walking, but many more of these small steps are necessary. In conclusion, this thesis describes adaptive control of dynamic balance in human walking as both an active and passive mechanism, utilizing temporal and spatial strategies to remain stable, while finding an efficient locomotor pattern.

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