Friedrich-Schiller-*University Jena*
Faculty of Social and Behavioural Sciences
Institute of *Sport Science*

seit 1558

Adjustment of posture as a measure to accommodate uneven ground

Dissertation

for the award of the academic degree

doctor philosophiae (PhD)

submitted to the Council of the Faculty of Social and Behavioural Sciences
of the Friedrich-Schiller-University Jena
by Soran Aminiaghdam (M.Sc.)
born on 16.09.1982 in Mahabad

Assessors

1. Prof. Dr. Reinhard Blichan

2. Prof. Dr. Astrid Zech

3. Assoc. Prof. Mansour Eslami (Babolsar)

Oral examination date: **09.01.2018**

Acknowledgements

Without the generous contribution and support from several people and organizations the completion of this dissertation would undoubtedly not have been possible. I would like to acknowledge the financial support of my research and PhD training provided by the Institute of Sport Science and Graduate Academy within Friedrich Schiller University Jena, Berufsgenossenschaft Nahrungsmittel und Gastgewerbe (BGN), the European Society of Biomechanics and the International Society of Biomechanics.

Foremost, I would like to express my sincere gratitude and appreciation to my academic advisor, Prof. Dr. Reinhard Blickhan, senior-professor and former chair Science of Motion within the Institute of Sport Science, for his invaluable guidance and constructive contribution throughout my PhD study. His pursuit of excellence has set a role model of a devoted scientist and researcher and encouraged my development as an independent researcher.

I am grateful of Dr. Christian Rode for his insights and collaboration throughout my PhD. I have honestly learned a tremendous amount from you regarding theoretical principals in biomechanics and appreciate your critical thoughts and constructive feedbacks to my articles before and during publication process.

I would also like to express my gratitude to Dr. Roy Müller, who supported me with his expertise in the operation, maintenance, and troubleshooting of biomechanics laboratory equipment and in the development of Matlab codes and algorithms.

Special thanks also to Dr. Michael Günther for providing a scientific and thoughtful guidance.

It is a pleasure to also thank the individuals who participated in my studies and to Martin Götze, Johanna Vielemeyer and Sacha Balcerowski for assisting me in data collection and processing.

I am indebted to all reviewers of my articles and to all referees of my dissertation for providing their constructive and critical comments helped to improve the quality of the work presented in the thesis.

I would like to show my gratitude to my all teachers in my life who have paved the way for being who I am today. To my friends, specially Jamal Esmaelpoor for his substantial assistance

in improving my programming skills, who have always been the wonderful source of support and encouragement. All I can do is to thank them as graciously as possible.

Lastly, I would like to express my deepest appreciation and love to my wife, Mina, for her continuous support, patience and input during and beyond my PhD research. To my family and particularly my mom, for being always there. You are wonderful. I am thankful to have you, your unconditional love and patience.

Zusammenfassung

Die Rolle der Rumpforientierung bei der menschlichen Fortbewegung beim Überqueren von gleichmäßigem und unebenem Boden ist sowohl aus theoretischer als auch aus experimenteller Sicht trotz ihrer Relevanz für klinische Anwendungen und die Robotik schlecht verstanden. Die Ganguntersuchung hat bisher oftmals die Fortbewegung auf ebenem Untergrund bei gestörter oder nicht gestörter Haltung oder auf unebenem Untergrund untersucht. Die Erforschung der reaktiven und proaktiven Antworten auf interne und externen Destabilisierungen, nämlich Haltungs- und Bodenstörungen, hilft uns, die Grenzen unseres Bewegungsapparates zu charakterisieren. Das Verständnis der zentralen Gangdynamik, die mit der Fortbewegung über unebenen Boden mit Fokus auf die funktionale Rolle des Rumpfes verbunden ist, könnte zu einer klareren Identifizierung von Mechanismen führen, die der Kontrolle beim Menschen zugrunde liegen. Dies kann Implikationen für die klinische Praxis und die Entwicklung von Robotern mit Beinen haben.

In dieser Arbeit haben wir durch die Erforschung des biomechanischen Verhaltens des menschlichen Gehens in Gegenwart einer erwarteten zweifachen Störung, nämlich einer Veränderung der Rumpfhaltung und der Bodenhöhe, einen Einblick in die funktionelle Rolle des Rumpfes bei der Fortbewegung erhalten. Zuerst präsentiert diese Arbeit den Einfluss der Rumpforientierung auf die Beinfunktion mit Betonung auf der Analogie zwischen Fortbewegung bei Vögeln und Menschen (Kapitel 2). Durch die Untersuchung der menschlichen Beinfunktion beim Gehen unter Veränderung der Rumpfkinematik - bis zur maximalen sagittalen Beugung – und durch ihren Vergleich mit jener von kleinen Vögeln, haben wir festgestellt, dass das Nachahmen der Haltung der Vögel ein vergleichbares effektives Verhalten der Beine trotz unterschiedlicher Körpergröße und Morphologie der segmentierten Beine erzeugt. Darüber hinaus zeigte der erstmalige Vergleich zweier einfacher Beinmodelle, nämlich Feder und Dämpfer in Serie versus parallele Feder und Dämpfer, dass das erstere Modell dem letzteren in der Vorhersage der axialen Beinkräfte während der Standphase des Gehens mit verschiedenen Graden der Rumpforientierung überlegen ist.

In Kapitel 3 zeigen wir, wie relevante Parameter, die zur Bodenreaktionskraft (GRF) in Beziehung stehen (erster und zweiter Peak der vertikalen GRF; Belastungs- und Entlastungsgeschwindigkeit; Brems-, Vortriebs- und vertikaler Impuls sowie die Kontaktzeit und die Geschwindigkeit) durch Interaktionseffekte zwischen Haltung und Schritt beeinflusst werden. Interessanterweise führte die zunehmende Rumpfflexion nicht zu einer großen Variation der kinetischen Parameter des Ganges bei der Überquerung von unebenem Untergrund. Mit anderen Worten, bei einer erhöhten Rumpfflexion tendierten die Änderungen der kinetischen Parameter zwischen den Schritten zu einer Abnahme im Vergleich zum aufrechten Gehen auf ebenem Boden. Die Voranpassungen wurden nur beim Gehen mit aufrechtem Rumpf im vorbereitenden Schritt vor Bodensenkung beobachtet. Wir behaupten, dass der Rumpf genutzt werden könnte, um die Absenkung im Bodenniveau auszugleichen, indem er während des Schritts rückwärts gedreht wird. Im Vergleich zu Schritten auf ebenem Untergrund wurde beim Schritt auf abgesenkten Boden eine zwei- bis dreifach größere Rückwärtsrotation beobachtet. Dieses Resultat war unabhängig von der Oberkörperhaltung und könnte möglicherweise ein Resultat des Versuchs sein, die kinetische Energie zu kontrollieren, die während des Schrittes gewonnen wurde. Obwohl das Gehen mit einer gebeugten Haltung energetisch belastend sein könnte, wurden keine signifikanten Änderungen in den schrittbezogenen GRF-Parametern während des unebenen Gehens festgestellt. Demzufolge stellte die gebeugte Haltung für die gesunden Probanden keine große Herausforderung in Bezug auf die Kontrolle der Fortbewegung dar.

Schließlich präsentiert Kapitel 4 das adaptive kinematische Verhalten des Gehens gesunder Menschen beim Ausgleichen von unebenem Boden mit veränderter Rumpforientierung. Zu diesem Zweck wurden die Wechselwirkung zwischen Rumpfhaltung und Schritt auf zahlreiche kinematische Parameter analysiert. Diese Parameter bestehen aus Hüft-, Knie- und Sprunggelenkwinkeln; effektive Beinlänge und -winkel; vertikale Position des Schwerpunkts (CoM), zu den Zeiten des Aufsetzens und Abhebens. Die schrittspezifischen Effekte der Haltung auf das kinematische Verhalten des Gangs beim Aufsetzen unterschieden sich von denen beim Abheben. Wir argumentieren, dass der Rumpf eine kompensatorische Rolle mit einer ausgeprägteren Bewegungsstrategie im vorwärtsgebeugten Gang spielt. Die Rückwärtsdrehung des Rumpfes hilft höchstwahrscheinlich beim Ausgleichen der Bodenunebenheit. Diese Strategie ist nützlich für die Aufrechterhaltung der vertikalen Position des CoM nützlich. Das Beugen des Rumpfes schien die Stabilität der periodischen Bewegung nicht zu beeinträchtigen da fast alle kinematischen Parameter nach dem Schritt auf das Ausgangsniveau des Bodens wiederhergestellt, das heißt gleich zur ebenen Fortbewegung, waren. Dieser Mechanismus ähnelt der Fähigkeit kleiner Vögel beim Ausgleichen großer Störungen in rauem Gelände ihre stark gebeugten Beine zu nutzen.

Eine kurze Synopsis der wichtigsten Ergebnisse früherer Kapitel (Artikel) wurde in Kapitel 5 zusammengefasst. Die Ergebnisse dieser Arbeit deuten darauf hin: Erstens, menschliche Fortbewegung mit gebeugtem Rumpf teilt einige biomechanische Prinzipien, z.B. die effektive Beinfunktion, mit der der Vögel; Zweitens führen Feder und Dämpfer in Serie im Vergleich zu parallelen Feder und Dämpfer zu einer besseren Vorhersage der axialen Beinkräfte; Schließlich kann die weitere Betonung der freiwilligen Bewegungen des Rumpfes beim Ausgleich von Bodenunebenheiten Klinikern und Therapeuten bei der Entwicklung eines effektiveren Interventionsprogramms für die Fallprävention helfen, was möglicherweise zu einer erhöhten Gangstabilität bei Patienten und älteren Erwachsenen mit schlechten Gangmustern und schlechtem Gleichgewicht führt. Allerdings erfordern unsere Erkenntnisse weitere Studien an gesunden und pathologischen Populationen, um die Rolle der Haltung mit einem Schwerpunkt auf der Rumpfdynamik in der menschlichen Fortbewegung zu evaluieren.

Abstract

The role of trunk orientation in human locomotion while crossing even and uneven ground is poorly understood from a theoretical and experimental perspective, despite significant relevance to clinical and robotic applications. Gait research has often individually investigated locomotion on level or uneven surfaces or when posture is disturbed or not. An exploration of the reactive and proactive responses to a complex of internal and external destabilizing agents, namely postural and ground perturbations, helps us to characterize the boundary constraints of our locomotor apparatus. Understanding the key gait dynamics that associated with locomotion across uneven ground with an emphasis on the functional role of trunk could lead to a clearer identification of mechanisms underlying control in humans with implications for clinical practice and the development of the legged robots.

In this work, we gained more insight into the functional role of trunk in human locomotion through the exploration of the biomechanical behavior of human walking in the presence of an expected twofold perturbation. First, this work presents the influence of the trunk orientation on leg function with stress on the analogy between locomotion in birds and humans (*Chapter 2*). By examining the human leg function during walking under changes in the trunk kinematics — up to the maximal sagittal flexion — and comparing it to that of small-bodied birds, we found that mimicking the birds' posture induces a comparable behavior in leg function despite a different body size and morphology of the segmented legs. Furthermore, comparison of two simplified models for the first time, namely spring and damper in series and parallel spring and damper, revealed that the former model predicts the axial leg forces superior than the latter model during stance phase of walking with various degrees of trunk orientation.

In *Chapter 3*, we show how the relevant parameters related to the ground reaction force (GRF) involving the first and the second peaks of the vertical GRF; loading and unloading rate; braking, propulsive and vertical impulses as well as the contact time and the velocity are influenced by the interaction effects between posture and step. Interestingly, increasing trunk flexion did not lead to a great deal of variation in kinetic parameters of the gait while traversing uneven ground. In other words, with increased trunk flexion, the between-step changes in the

GRF kinetic parameters tended to decrease relative to upright walking on level ground. The pre-adaptations were observed in the approaching step to the drop merely during walking with an upright trunk. We assert that the trunk could be utilized to negotiate the changes in ground level by exhibiting a backward rotation during step down. Such backward rotation was observed 2- to 3-fold greater than those of level steps, regardless of trunk posture, in an attempt possibly to control the kinetic energy gained during stepping down. Although walking with a bent posture might be energetically strenuous; however, transforming into a zig-zag-like, crouched posture from upright was found not to require significant changes in the between-step GRF parameters while uneven walking, and neither pose dramatic control challenges to the locomotion of able-bodied individuals.

Finally, *Chapter 4* presents the adaptive kinematic behavior of able-bodied walking while negotiating uneven ground with altered trunk orientations. To this end, the interaction effects between posture and step on numerous kinematic parameters were analyzed. These parameters comprised of hip, knee and ankle joint angles; effective leg length and angle; vertical position of the center of mass (CoM) at the instants of touchdown and toe-off. The step-specific effects of posture on the kinematic behavior of gait at touchdown were found to differ from that of toe-off. We argue that the trunk plays a compensatory role with a more pronounced movement strategy in trunk-flexed walking during stepping down. Showing a backward rotation, the trunk most likely facilitates the negotiation of changes in ground level. This strategy is useful for the maintenance of the vertical position of the CoM. Bending the trunk did not seem to impede the stability of the periodic movement as almost all kinematic parameters restored to the undisturbed path within a range observed during upright walking at the end of the step-up following a step-down. This mechanism may resemble the ability of small birds in adjusting their crouched legs during locomotion to cope with large perturbations in rough terrain.

A brief synopsis of main findings of previous chapters (articles) has been summarized in *Chapter 5*. The results of this work suggest: First, human locomotion with an increased trunk flexion shares some biomechanical principles, e.g. the effective leg function, with that of birds. Secondly, the spring and damper in series performs better than parallel spring and damper in predicting the axial leg forces. Finally, further emphasis on the voluntary movements of the trunk for negotiating uneven ground may guide clinicians and therapists in developing more effective fall-prevention intervention programs, leading possibly to enhanced gait stability in patients and older adults with poor gait patterns and balance. However, our findings warrant further studies in both healthy and pathologic populations to evaluate the role of posture with an emphasis on trunk dynamics in human locomotion.

Table of Contents

List of figures

Chapter 1

1 General introduction

1.1 Evolution of bipedalism

It is astonishing that there is still room to learn about something as apparently straightforward as the way we walk. Yet how and why humans evolved to walk bipedally remains of research interest. Bipedalism has traditionally been associated to the beginning of humanity's expedition from prey to predator, and from Africa's Rift Valley to world sovereignty (Radford 2013). Bipedality of the earliest-known hominids has been demonstrated (Haile-Selassie 2001; Galik et al. 2004), and ample fossil evidence shows that australopithecines habitually walked by at least 4.4 million years ago. (Dean 1990; Ward 2002). Bipedal gait is commonly performed by humans, birds, and sometimes by apes and monkeys (Alexander 2004; Hirasaki et al. 2004). Bipedal posture and locomotion are key distinctive attributes of the earliest known hominins (Galik et al. 2004; Zollikofer et al. 2005). Thanks to efficiencies derived from evolution, growth and learning, humans are highly adapted for locomotion (Alexander 2003). They are adept walkers. Our muscular (Alexander 2003), skeletal (Lovejoy 2005) and neural (Dietz 2003) systems have evolved and well-suited to locomotion through successive generations. We acquire and implement walking coordination strategies across our lifespan (Forssberg 1985) and able to cope with new locomotor environments swiftly (Davidson and Wolpert 2005).

The human musculoskeletal system and human gait have been widely investigated (Rose and Gamble 1994). While extensive focus has been placed on the mechanics of discreet human walking for its clinical implications (e.g., implant design and surgical intervention), little is known about the circumstances under which natural selection formed our frame over the last several million years. Laboratory examination of the modern human bipedal posture are often not relevant adequately in interpreting such anatomical transformation processes.

Comfortable human wandering is believed not to be the primary target of natural selection, our frame has presumably been evolved in much more challenging situations, such as traversing uneven terrain, escaping predators, or in response to exhaustion-induced circumstances (Lovejoy 2005). In other word, the apparent proficiency observed in modern human gait is the consequence of the refinement of locomotor skills mastered under more demanding circumstances. Attempts to recreate locomotion in early hominins or in other animals help to expand our understanding of how anatomical features in humans and earlier bipeds operate in different locomotor patterns and therefore to characterize the adaptive capacities and limitations of specific morphologies. This warrants studies on human locomotor behavior in experiments using e.g. altered postures or movements through complex environments which often requires unsteady behavior to maintain stability against perturbations (Lee et al. 2014; Qiao and Jindrich 2014).

1.2 Bipedality in animals, and their differences from humans

Comparisons of a broader range of bipeds, environments, and terrestrial locomotor techniques provide opportunities for the recognition of new research questions. Our understanding of evolution of locomotor system in terrestrial taxa has been improved thanks to the abundant relevant scientific endeavours (Lauder 1991, 2003). However, literature suggests lack of adequate basic data from a diversity of species which in turn restricts further detailed analysis of terrestrial locomotion (Kawano and Blob 2013; Birn-Jeffrey and Higham 2014; Blob et al. 2014; Lee et al. 2014; Qiao and Jindrich 2014). Therefore, data collection comprising of cross-species biomechanical comparisons and perturbation experiments addressing the performance of the locomotor apparatus under the range of behaviours are of research importance.

In addition to bipedal walking and running in human, some other birds and mammals use two legs during locomotion. Birds walk, run on the ground or sometimes use grounded running (Rubenson et al. 2004; Hancock et al. 2007). Apes and Japanese macacques sporadically walk bipedally (Napier and Napier 1967), kangaroos and a few rodents hop bipedally (Bartholomew and Caswell 1951), and some lizards run bipedally (Snyder 1952).

In the apes’ bent-hip-bent-knee walking, the sagittal trunk flexion is about 20° from vertical and the knee is strongly bent at mid-stance, to ~100° in bonobos (D'Août et al. 2002) compared with ~170° in human walking. D’Août et al. (2002) also reported a different phase relationship between knee and ankle movements from human walking during bipedal or quadrupedal locomotion. In addition, compared with ordinary Japanese macaques, the trained macaques are known to walk with more upright trunk and more stable trunk (Hirasaki et al. 2004).

In chimpanzee, the CoM of the body locates in front of the hip owing to inclined trunk geometry (Alexander 2004). Interestingly, the trajectory of the CoM in chimpanzees resembles that of humans, i.e. higher during the single-stance phase and lower during the double-stance phase (Kimura 1996). Given in the steady state bipedal walking ground reaction force (GRF) vector must be vertical and in line with center of mass (CoM) (i.e., relative position of the center of pressure (CoP) to the CoM), chimpanzees achieve this by keeping the knee anterior to the hip throughout the stance phase. However, both humans and apes are using the whole length of the foot, from heel to toe, during ground contact (Alexander 2004). In human walking, the ground contact initiates with heel while in chimpanzees it is the lateral midfoot that strikes the ground (Vereecke et al. 2003).

Another taxon that walk with an upright trunk is penguin, but other birds use pronograde posture (almost horizontal trunk orientation). Like apes but in a greater extent, trunk geometry in most of birds leads to a forward displacement of the CoM relative to hip (Andrada et al. 2014). Similarly, the knee remains anterior to the hip throughout the stance phase (Alexander 2004). However, such bipedal locomotion with pronograde posture in small birds is associated with some restrictions over the effective leg (connecting hip to CoP) (Andrada et al. 2014) as balancing the trunk against gravity, when the CoM is shifted anteriorly, requires increased hip extension torques throughout stance (Andrada et al. 2013).

Lizard sometimes run bipedally, with tilting trunks upward at mean angles of 1–6° during fast quadrupedal running and 8–15° during fast bipedal running (Irschick and Jayne 1999). Due to long tails, most lizards keep the CoM much closer to the hip. In contrast to apes and birds, the hips do not fall behind knees (Alexander 2004). One prominent feature that differentiates bipedal locomotion of lizards from that of mammals is that lizards use wider step width. The study by Irschick & Jayne (1999b) found the step width of 2.0–2.8 times tibia length in lizards. The corresponding value in normal adult human walking is about 0.25 (Donelan and Kram 2001).

In general, bipedalism in majority of nonhuman primates is characterized by an inclined trunk, crouched hindlimb joints throughout stance phase, and an initial midfoot contact with the ground (Wunderlich and Schaum 2007).

1.3 Walking in human

Since a full appreciation of bipedalism requires considering multiple traits, the description of human bipedalism is more complicated than its simple definition of "movement performed only on two legs," in dictionary. Indeed, our specific frame or posture is determined by an important role of the neuromechanical mechanisms. Furthermore, some typical morphological features including: size and shape of the bones of the foot, structure of musculature, and the orientation of the human body and head differentiate modern human bipedal posture from our ancestors and present-day mammals (Ivanenko et al. 2013). It is only human to use habitually an erect bipedal gait with a heel-strike well in front of the body. A linear relationship between the time course from initiation of independent locomotion and the adult brain mass, which has been documented among 24 different mammalians (Garwicz et al. 2009), suggests: the bigger the brain size, the longer the time to initiate walking. Attempts to develop diverse functions such as stance, balance and orientation matching locomotor control therefore require maturation of large parts of the central nervous system (CNS) (Lacquaniti et al. 2012).

1.3.1 Bipedal posture

The interdependency of regulation of posture and locomotion takes place across different levels of the CNS, spaning from the motor cortex to the basal ganglia, the brain stem and the spinal cord to begin motion by means of arranging required spatial frameworks (Grasso et al. 2000). These spatial organizations permit postural adjustments during locomotion (Garcia-Rill 1986; Grasso et al. 1999). Furthermore, the activation of mechanisms involved in adjustment of postural muscle tone and the spinal stepping generator known as central pattern generators (CPGs) are interdependent (Mori 1987).

Postural tone of the skeletal muscles is believed to be a foundation of habitual human posture (Ivanenko et al. 2013). Postural tone is an unconscious, low-amplitude, long-lasting muscle tension distributed in a specific pattern along the entire body axis. Experimentally disturbing this muscle tension lead to changes in postural orientation (Kluzik et al. 2005; Wright 2011) as well as gait parameters (Ivanenko et al. 2006; Selionov et al. 2009). A quotation from Sherrington (1906) "posture follows movement like a shadow," underlines the interaction between posture and movement because without an appropriate postural tone execution of fine movements are not possible. He believed that the global locomotion might be altered as a result of disturbances of tonic activity (Sherrington 1906).

Uprightness of the body as a hallmark characteristic of human has two aspects to it: erectness of the trunk and bipedality during stance and gait (Ivanenko et al. 2013). The development of uprightness cannot be made possible without the sense of balance (Tobias 1992). In addition to these two most striking traits of human uprightness, other characteristics of the upright posture of man are proposed to be: an arched form of the feet, the relative length of the lower limb bones, the size and shape of hip and knee joints, the inside oblique position of the thigh bones, the position and structure of the pelvis and chest, shape and orientation of the vertebral column, and the structure and orientation of the skull (Wright et al. 2012; Ivanenko et al. 2013).

1.3.2 Bipedal gait

Walking and running are two ubiquitous forms of human locomotion (Fig. 1-1). Human walking is characterized by a forward and backward oscillation of the upper limbs as well as pendulum and inverted pendulum motion of the legs during the swing phase and the stance phase, respectively (Fig. 1-2). One gait cycle (two consecutive steps) of walking constitutes stance and swing phases. The stance phase is composed of single- and double-support phases and the body is raised during the single-support around midstance (Fig. 1-2).

One feature that further differentiates human walking from other gaits is the profile of the GRF, where two vertical peaks (in early and late stance) are distinguished by a trough in midstance, owing to a partial unloading from the opposite limb (Winter 1991; Borghese et al. 1996). Meanwhile, the trunk is systematically used for both stability and locomotion. Therefore, locomotion — through harmonized interactions between upper limbs, trunk, and lower limbs — must satisfy a quiet movements while being tolerant to internal (e.g., body posture) and external perturbations (e.g., uneven terrain) (Dietz et al. 1987; Hirschfeld and Forssberg 1991).

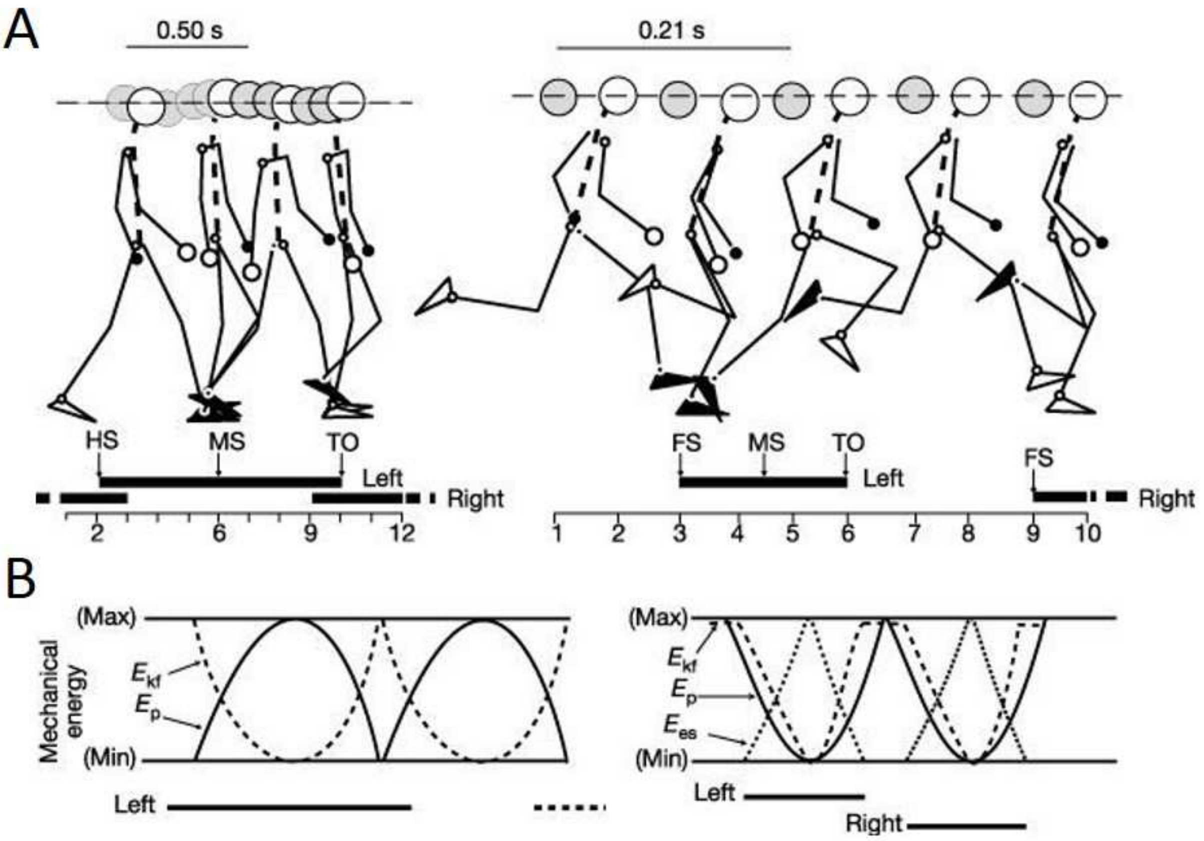

Fig. 1-1. Biomechanics of human gait. (A) walking (left) and running (right) kinematics. The CoM during walking is located highest at mid-stance (MS) and lowest near toe-off (TO) while during running, the CoM reaches the highest elevation during the aerial phase and the lowest at MS, when the hip, knee and ankle are flexed. Furthermore, the trunk is also more inclined and the elbow more flexed. (B) represents biomechanical contrasts between human gaits. By means of inverted pendulum mechanism during walking forward kinetic energy (E_{kf}) is exchanged for gravitational potential energy (E_p) between heel-strike (HS) and MS; the exchange is reversed between MS and TO. However, during running, a mass-spring mechanism generates E_p and E_{kf} to be in phase, so that both minimize between foot-strike (FS) and MS. Modified from Bramble and Lieberman (Bramble and Lieberman 2004).

In human walking, potential energy (E_p) and kinetic energy (E_{kf}) of body CoM are in continuous exchange (Fig. 1-1B). This process of mechanical energy reconversion or energy recovery — represented as inverted pendulum mechanism — is known to minimize the muscular energy expenditure (Cavagna et al. 1976). Such reduction in energy expenditure is considered as one of the key attributes of human walking (Saibene and Minetti 2003). During a preferred walking velocity, the efficiency of energy exchange between kinetic and potential energy can be nearly 70% (Cavagna et al. 1977).

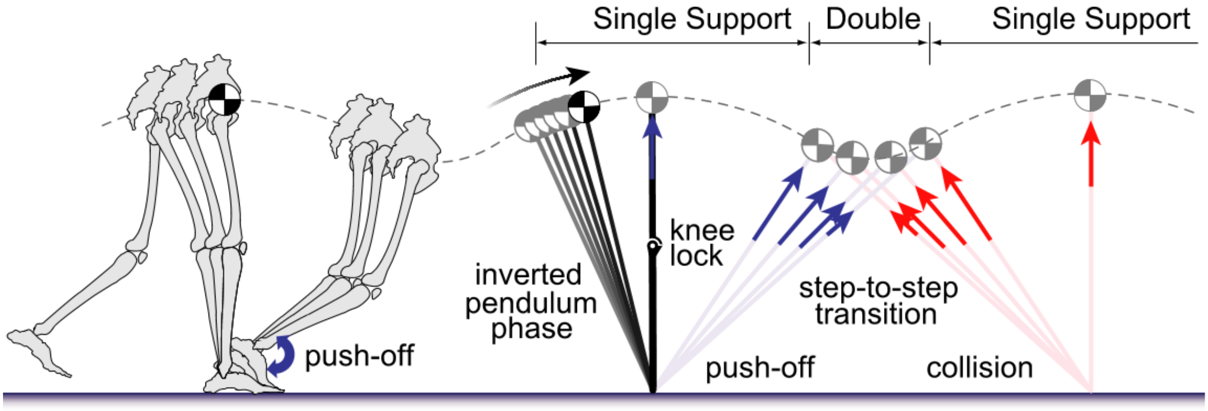

Fig. 1-2. The CoM and the inverted pendulum. The CoM during single support phase is supported, without requiring work or force, by the inverted pendulum. The CoM velocity during double support is redirected by each leg's force acting along the leg. Zero net work (positive work by trailing leg and the negative work by leading leg on the CoM) during double support is performed to ensure redirection for the next step. Adapted from Arthur D. Kuo (Kuo 2007).

The unique human bipedal gait — as one of the most highly automated motor behavior — and heel-to-toe rolling pattern (Bramble and Lieberman 2004) requires a multi-dimensional neuromotor organization integrated at various levels of CNS. This involves a specific intersegmental coordination, motor patterns, equilibrium, and walking experience when learning plantigrade gait at the beginning of independent walking (Forssberg 1985; Ivanenko et al. 2007; Dominici et al. 2011; Lacquaniti et al. 2012). Nevertheless, we are able to execute compulsory gait techniques such as "stoop-walking," in some occupational settings, e.g., in a low-seam coal mine (Gallagher et al. 2011) or trunk-flexed posture during sport mauvers like those adopted in speed skating or ice hockey.

1.4 The role of trunk in human walking

Balance during locomotion may be interpreted as a dynamic relationship between the CoM trajectory and the base of support which permits the forward progress of the body while remaining upright (Winter 1995). An alteration of the trunk posture may cause instability when this relationship is subject to some changes (Saha et al. 2008; Leteneur et al. 2009). The trunk orientation is realized to influence the kinematics, kinetics and energetics of lower limbs during weight bearing activities (Teng and Powers 2015). The trunk segment accounts for 36% of the body mass (Winter 2009). Therefore, a small deviation in the trunk posture can affect the locations of the CoM and the CoP, and accordingly, the orientation of the GRF vector (Oberländer et al. 2012). Depending on walking pattern and velocity, the trunk angle has been reported to vary within a range of ±8° about vertical axis in the ordinary gaits (Thorstensson et al. 1984; Goh et al. 1998). It has been shown that a forward inclination of the trunk leads to lower knee extensor moments during walking, stair ascent and hop-landing (Asay et al. 2009; Oberländer et al. 2012; Leteneur et al. 2013). In general, we can investigate the influence of the trunk posture on lower limb dynamics using two approaches: between-subject and within-subject comparisons.

A study by Leteneur et al. (2013) found that the difference in the sagittal plane trunk posture between natural forward and backward leaners is ~4°. While ankle kinetics exhibited no significant group differences, individuals with a forward trunk inclination demonstrated significantly greater peak hip extensor moments and lower peak knee extensor moments compared with the backward leaners (Leteneur et al. 2013). Similar findings were reported in a study by Shimokochi et al (2009), suggesting a relationship between the location of the CoP and the kinetics of the lower limbs in a single-leg landing: a more anteriorly located CoP, a reduced knee extensor moment and a higher ankle plantar flexor moment. This is because a forward displacement of the CoP can be a result of a more forward inclination of the trunk in the sagittal plane (Shimokochi et al. 2009).

The altered kinematics, kinetics and muscle activation patterns during weight-bearing tasks by means of experimentally induced changes in the sagittal plane trunk orientation have been documented (Grasso et al. 2000; Blackburn and Padua 2008; Saha et al. 2008; Blackburn and Padua 2009; Kluger et al. 2014). Grasso et al. (2000), Saha et al. (2008) and kluger at al. (2014) investigated adjustments in lower limbs biomechanics during walking with altered trunk orientations (i.e., 25° and 50°). These forms of gait were found to be associated with more crouched legs, changed GRF patterns and energy absorption/generation at the ankle and hip, respectively (Grasso et al. 2000; Saha et al. 2008; Kluger et al. 2014). In addition, the trunk-flexed gaits lead to significant increases in the activation of gluteus maximus, rectus femoris, vastus lateralis, biceps femoris and gastrocnemius (Grasso et al. 2000).

The influence of the natural trunk orientation on lower limb energetics in runners has also been examined (Teng and Powers 2015). The finding of this study showed that an increased energy absorption and generation of the knee extensors and decreased energy generation in the hip extensors in individuals with a relatively upright trunk posture. On contrary, runners with a more anteriorly flexed trunk demonstrate a greater energy generation in the hip extensors and reduced energy absorption and generation in the knee extensors.

In summary, an increase in the trunk flexion during walking, running and landing can influence the lower extremity biomechanics. However, the dynamics of lower limb while adopting maximal trunk flexion during walking and crossing uneven ground were not addressed in these previous studies. Examining how modifying the trunk orientation in the sagittal plane during walking affects the lower limb biomechanics can provide insights into the development of control strategies in the bio-inspired bipedal robots, and into fall-preventive measures in patients and older adults with diminished postural capacities, as well as into boundary constraints associated with human locomotion with implications for the evolution of bipedal locomotion.

1.5 Models: mechanical description of basic dynamics of human gait

Human walking is determined by a greatly multiplex synergy of the force-bearing structures of the musculoskeletal system (Wang et al. 2015). Although, human and artificial legs are very complex in structure and neural control, their basic mechanical behavior during walking can be described using a simplified phenomenological gait model, namely bipedal spring- mass model. These models can provide insight into the principles of legged locomotion, and eventually give a pivotal guidance for the design and development of legged robots. A spring-like behavior in human and animal legs during stance, characterized as compliant legs, is produced by means of a properly adjusted muscle activation and the synergies across leg muscles with passive elastic structures (e.g., tendons) (Geyer et al. 2003). Hence, such behavior cannot be described as a simple linear spring. With the motion of the body mass during the stance phase of walking, the leg spring is compressed and uncompressed alternately to store and return the elastic energy, respectively (Wang et al. 2015). Observed the same compliant stance-leg function in walking and running, a bipedal spring–mass model is capable of reproducing the stance dynamics of walking (Fig. 1-3). Therefore, walking is known to be a bouncing gait like running rather than a stiff-legged inverted pendulum (Geyer et al. 2006). This is in contrast with a preceding interpretation of the leg behaviour, suggesting that the leg behaves as an inverted pendulum.

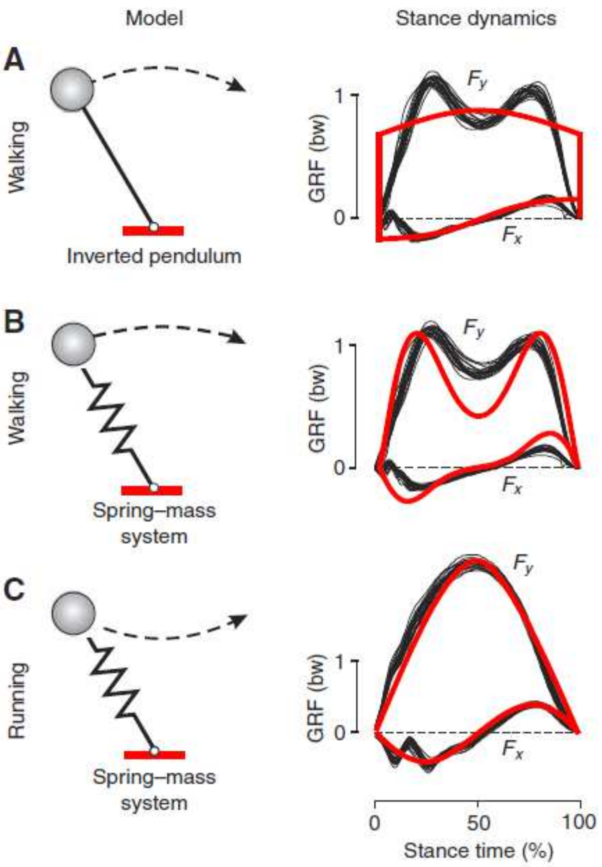

Fig. 1-3. Reproduction of stance phase GRF patterns by simple inverted pendulum and spring–mass models. (A) A simple inverted pendulum generates a poor prediction of the GRF (red) of that observed during human walking (black). (B) A more precise reproduction of GRFs by an inverted pendulum model, if the model includes a leg spring. (C) The reproduction of pattern of vertical GRF (Fy) and horizontal forces (Fx) in running by means of a simple spring–mass model. Using appropriate values for leg spring stiffness and angle of attack, absolute values of forces can be matched. Figure modified from Geyer et al. (Geyer et al. 2006) and Roberts et al. (Roberts and Azizi 2011).

The global dynamics of human (Shen and Seipel 2012) and avian (Andrada et al. 2013) bipedalism can also be represented using the spring-loaded inverted pendulum (SLIP) model which is consisted of a massless springy leg and a point mass. In simulations of bouncing gaits by SLIP model the GRF is reproduced in a symmetric pattern. However, in other locomotion conditions when, for example in birds with a pronograde trunk posture, the vertical GRF is right-skewed and more vertically oriented (Andrada et al. 2013; Andrada et al. 2014), this model is unable to reproduce the dynamics of such gaits and to address the problem of the trunk stabilization.

While walking upright poses advantages but also raises new challenges as two-thirds of our body mass is located two-thirds of body height above the ground (Winter 1995). A diminished base of support, as compared to the quadrupedal locomotion, and an elevated CoM in upright bipedal gait are two agents that may lead to an increased instability (Maus et al. 2010). Mechanically, such system which resembles an inverted pendulum might be intolerant to perturbation. One solution to enhance the postural stability may be sought through the virtual pendulum (VP) concept (Maus et al. 2010).

According to Maus et al. (2010) it seems that humans benefit from an external support by creating a virtual pivot point (VPP) above their CoM (Fig. 1-4A). The VPP— an emergent behavior of gait mechanics rather than a deliberate locomotion function— is an intersection point above the CoM along the long axis of body where the GRF redirected to by hip torques during stance. Based on this, such virtual support is likely adequate to achieve postural stability (Maus et al. 2010).

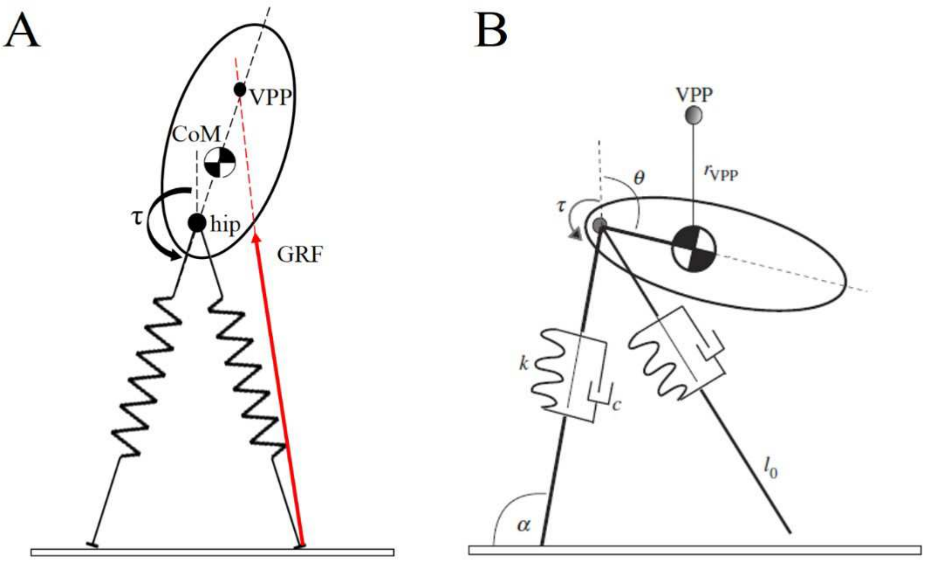

Fig. 1-4. The VPP model. (A). The VPP model consists of a rigid body above two massless leg springs. Hip torques (τ) are introduced to redirect the GRFs to a point located above the CoM. This intersection point is termed the virtual pivot point (VPP). (B) Modeling an asymmetric leg behavior as parallel spring and damper in a small bird (quail) by means of a VPP concept. Θ, angle between trunk and VPP; α, angle between ground and effective leg; k, leg stiffness; c, leg damping; l_0, rest length at touchdown; rVPP, distance CoM–VPP (modified from Andrada et al. (Andrada et al. 2014)).

As stated before the postural stability cannot be explored by means of a canonical SLIP model; therefore, incorporation of trunk (Maus et al. 2010; Andrada et al. 2014) instead of mass point into SLIP model may lead to a better understanding of balancing the trunk in legged locomotion. Furthermore, having observed an asymmetric leg function in bird experiments (i.e. quails), Andrada et al. (2014) modelled the axial leg behavior as parallel spring and damper elements (Fig. 1-4B).

Unlike upright bipedal gait in humans, birds' locomotion takes place with an almost horizontal trunk posture, i.e. a pronograde posture. Such frame is associated with an anteriorly located CoM with respect to the hip (Fig. 1-4B) (Gatesy 1991; Allen et al. 2013) compared with a vertically oriented CoM relative to the hip in humans. Under such circumstances, balancing the trunk against gravity leads to increased hip extension torques (Blickhan et al. 2015). Therefore, this poses constraints to the effective leg (connecting hip to CoP) function. The locomotion with a pronograde posture induces kinematic and kinetic asymmetries in leg function, as characterized by longer effective legs and higher forces in the early stance phase than lift-off. Such an asymmetric behavior is caused by the trunk orientation whose controlling entails damping in the leg (Andrada et al. 2014).

While the prediction of the axial leg function (the leg length and force in the leg direction) in pronograde locomotion of birds was accomplished by including axial damper parallel to the spring (Fig. 1-4B) to describe the compliant axial leg function (Andrada et al. 2014), no evidence is available in the literature regarding modelling of the leg using different configurations, e.g. the model of spring and damper in series. Given different leg models may give different predictions with respect to the gait stability, it is of research importance to find and examine novel models and theories of legged locomotion, essential to better predict a robustly stable legged locomotion of animals and some robots (Geyer et al. 2006; Maus et al. 2010; Shen and Seipel 2012; Andrada et al. 2014).

1.6 Implications of perturbation experiments

To further our understanding of human bipedal locomotion, our investigation must therefore not only cover the traditional clinical studies in healthy individuals while level walking, but also the adaptive and perturbation studies to examine the human morphology principally. Except under professional and certain circumstances (e.g. athletes, laborers, etc.), many of human beings rarely exploit their locomotor apparatus completely. Hence, there are still room to explore human frame experimentally. Given survival and evolution of living beings dependent on the ability to effectively deal with external and internal perturbations, the study of motion systems under perturbations can lead to a further identification of their properties (Blickhan et al. 2013).

Understanding changes in gait dynamics and associated compensatory mechanisms caused by both internal (posture) and/or external (surface) perturbations can provide insight into functional demands of bipedalism, and supply important information to a breadth of disciplines, ranging from morphology, physiology, ecology, and evolutionary biology to physics and engineering.

From biological perspective, different body frames can yield divergent dynamics or locomotor patterns. For example, although both ostriches and humans are bipeds, differences in body design allow ostriches to exert smaller braking forces than humans during turns (Qiao and Jindrich 2014). On the other hand, despite striking morphological disparities between human and avian, similar kinematic behaviours such as leg angle and leg length are shared among these species while running across uneven ground (Muller et al. 2016). Given such observations, we may therefore require a parallel investigation of many levels of biological systems and comparative data, and analyses from a broader range of locomotor environments to expand our understanding of the terrestrial bipedal locomotion. The study of human walking e.g. with a pitched posture proceeding to maximal trunk flexion in an attempt to mimic a pronograde locomotion of birds could be an example that provides relevant insights for the functional role of trunk in locomotion, and the influence of its orientation on gait dynamics.

Meanwhile, the experimental studies that permit testing the execution of human apparatus with different locomotor postures may shed some light into the evolution of human bipedal locomotion. Indeed, an exploration of gait features in a more complex setting, and in response to disturbances compared with quiet locomotion may also elicit the functional demands that have influenced the evolution of human bipedalism (Sockol et al. 2007; Pontzer et al. 2009; Blickhan et al. 2013).

One of the interesting subjects in engineering sciences is the design and development of human-inspired bipedal robots. In the artificial legged systems, the stability under a highly dynamic gait is still a challenging functional task (Merker et al. 2011). An advancement in the performance of such machines can be made by incorporating the knowledge obtained from the extensive analysis of human locomotion. More specifically, the compensatory adaptations that manifest in response to the disturbances during human gait can serve as a basis to identify the mechanisms underlying a robustly stable gait. Moreover, in the field of prosthetic engineering in addition to inter-limb asymmetries (Merker et al. 2011), a better understanding of the intra-limb leg operation in relation to the trunk geometry may help to guide the development of artificial limbs.

1.7 Interaction between posture and gait

1.7.1 Clinical perspective

It would be of clinical interest to identify the impact of variation in postural alignment on gait dynamics, given changes in the trunk orientation often occur with some pathological conditions or age. For instance, in patients with a lumbar flatback, a forward inclination of the trunk occurs (Potter et al. 2004). This in turn induces them to take resort to various forms of kinematic adaptations such as hyperextension of the spine and hips (Hasday et al. 1983; La Grone 1988) in order to maintain balance and align the trunk over the hip joints (Wasylenko et al. 1983). Such deformity in the trunk alignment is associated with a reduced walking capacity over level and uneven ground (Farcy and Schwab 1997). In contrast, an inadequate spine and/or hip extension often causes a crouched gait (Hasday et al. 1983), characterized by an increased knee and hip flexion during the stance phase of gait (Perry and Davids 1992). A decreased ability in balance control and a greater risk of fall are also common in patients exhibiting an abnormal increase in the anterior concavity of the thoracic spine in the sagittal plane, i.e. kyphosis (Sinaki et al. 2005).

Clinically, a swayback posture during stand and walk has been observed in patients with anterior hip pain. A swayback posture is a combination of posterior displacement of the upper trunk and an anterior displacement of the pelvis (posterior tilt). As compared to the normal posture in which the body's line of gravity passes roughly through the hip, in the swayback standing posture this line passes posterior to the hip (Somers, 2001). Thus, the swayback posture may be associated with a higher or longer hip flexor moment during walking. This, in turn, may lead to repetitive microtrauma and pain. On contrary, in individuals who habitually maintained a more forward inclined trunk posture, the hip extensor moment had a longer duration and the hip flexor moment had a lower magnitude (Leteneur et al., 2009). Patients with various knee pathologies have also been found to exhibit an alteration in the trunk kinematics (Asay et al. 2009; Oberländer et al. 2012). Individuals with severe knee osteoarthritis, for instance, demonstrate a more flexed trunk posture (6.3°) alongside a greater peak hip extensor moments and lower peak knee extensor moments during ascending stair than healthy controls (Asay et al. 2009).

The motor control of elderly patients may be affected by the impairment of posture — characterized by protrusion of the head and an increased thoracic kyphosis — and therefore are at an increased risk of falling and fractures (Ganz et al. 2007; de Groot et al. 2014). Perhaps, a forward shift of the body's CoM in patients with an increased thoracic kyphosis may require correcting responses which may limit the ability to cope with perturbations during walking. A prolonged sustaining of a bent posture as observed in some elderly females (Balzini et al. 2003) found to be associated with some negative clinical implications, such as the vertebral pain, muscular deterioration and a diminished motor function.

1.7.2 Walking on uneven surfaces

Daily locomotion involves walking and running on constantly changing ground surface properties and levels. Our locomotor system is required to continually cope with a variety of natural terrains, such as grass, sand or snow and uneven ground like holes, obstacles and curbs while maintaining the dynamic equilibrium. Since research focus has often been placed on human locomotion over smooth and level surfaces, thus our knowledge of biomechanics of gait on uneven ground is limited. However, such understanding could potentially guide the development of bio-inspired robots, exoskeletons, prostheses and clinical interventions during gait rehabilitation. Gait dynamics vary with environmentally induced perturbations.

The study by Muller et al. (2014) found walking across uneven ground, i.e. 10 cm drop, requires kinetic and kinematic adjustments not only in the perturbed step but also in the preceding step. The observed adjustments involved more crouched lower limb, more upright trunk posture and an attenuated GRF second peak, as approaching the drop (Muller et al. 2014). By obscuring the drop, they further investigated the role of the vision in negotiating uneven ground; they found that the visual perception of the perturbation allows feed-forward control mechanisms that are not available during the camouflaged drop scenario. This was further identified when human walkers demonstrated more pronounced changes in kinematic and kinetic behaviors in obscured perturbed steps than visible ones.

The biomechanics and energetics of walking on uneven terrain, with a continuous 2.5 cm height variability, represent an increased energy expenditure of ~28% as compared to walking on a smooth terrain (Voloshina et al. 2013). The findings of this study showed while contributions from step parameter adjustments and increased muscle activities were slight, such a greater energy cost was the result of an increased positive work at the hip and knee joints.

In a study (Höhne et al. 2011) aimed to examine the effect of impaired plantar cutaneous afferent feedback (by means of intradermal injections of an anaesthetic solution) on dynamic stability after an unexpected perturbation (a trackway covered by an exchangeable element allowing the surface alterations from hard to soft and vice versa) revealed that the loss of plantar sensation does not diminish the adaptational capacity of human locomotor system.

The other forms of environmental perturbations that can potentially challenge human traversing during daily locomotion are slippery surfaces such as wet, icy and soft terrains. Marigold and Patla (2002) investigated the reactive recovery responses that are employed to maintain balance during an unexpected slip. This study (Marigold and Patla 2002) found that the previous experience of the perturbations facilitates the adaptations, and the awareness of the surface properties leads to proactive adjustments, allowing a safe accommodation of the slippery surface.

Stepping down on an unexpected elevation during walking is a common task that can cause stumbles or falls. It is hypothesized that such a movement would be associated with the loss of control over the task and fall would occur, owing to buckling of the leg at landing. This assumption was examined in a study (van Dieen et al. 2007) which revealed that in healthy young male individuals buckling of the leg does not happen, most likely because of its more vertical orientation and thus momentum could not be adequately threatened at landing; however, a swift step of the trailing leg prevented the fall. Such mechanism was likely taken to counteract the forward linear and angular momentum of the trunk.

Walking can also be disturbed by an unexpected loss of footing due to a misstep into a hole. Impairment of rapid postural responses, key in restoring balance, may cause serious falls and injuries (Berg et al. 1997). Therefore, research on risk factors and mechanisms underlying falls and fall-prevention strategies is of importance for understanding the reactive responses to unexpected perturbations. To address this problem, Shinya et al. (2009) investigated the corrective postural responses after an unexpected complete loss of the ground support. Restoring balance in response to the perturbation was established using three strategies: (1) arousal of the reflexive muscle activities in the ankle plantar- and dorsi-flexors; (2) readjustment of the walking rhythm during the perturbed stance phase; (3) continuation of the adaptive locomotion to overcome the hole by bending both knees during the swing phase of the following steps prior to terminate walking (Shinya et al. 2009).

While previous studies have extensively addressed the human gait, involving mechanisms of the postural control in the context of expected and unexpected changes in the surface conditions, interaction of gait and posture, and the dynamics of gait during traversing uneven ground; however, our understanding of walking across uneven ground with an altered trunk orientation is limited (Fig. 1-5). An identification of challenges that stem from coping with such gait conditions as compared to upright bipedal gait may shed light on gait mechanics of individuals with an altered trunk posture with possible implications for identifying fall risk factors, and subsequently fall-prevention measures.

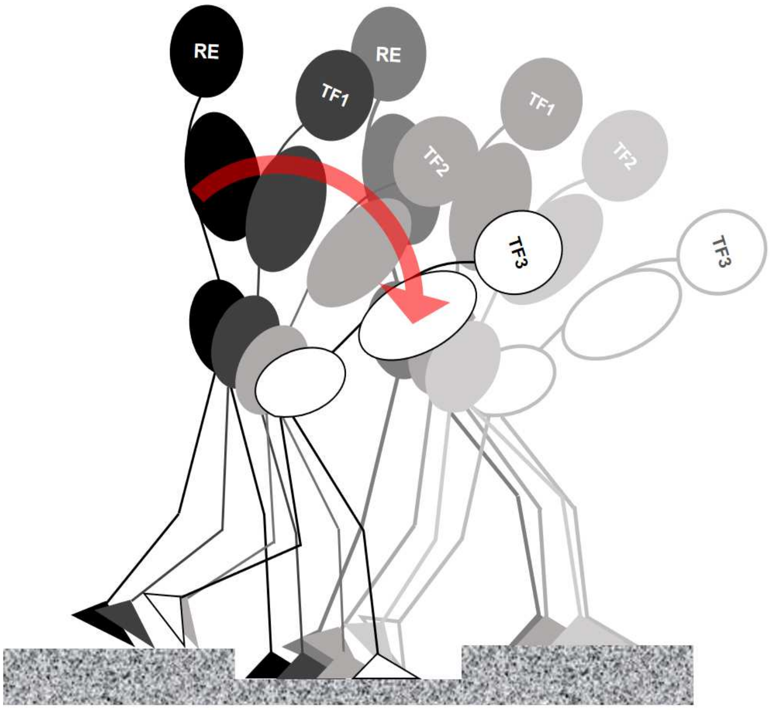

Fig. 1-5. Human walking across uneven ground while adopting various trunk flexion.

An alteration of the walking posture imposes certain mechanical constraints on the locomotor patterns. During the trunk-flexed gaits legs are more crouched and the pelvis is more posteriorly shifted (Saha et al. 2008), which contribute to offset an anterior shift of the CoM. These adjustments lead to changes in several kinematic and kinetic variables, as compared with a regular upright walking. For instance, a phase lag in the position of the hip relative to the ankle joint results in a phase lag in the CoM kinematics which, in turn, causes significant changes in the GRF parameters (Saha et al. 2008). Moreover, change in the walking posture, namely walking with bent trunk and bent knee, has been found to influence neither the segmental kinematic trajectories nor the planar constraint of intersegmental covariation (Grasso et al. 2000). However, such state is maintained through the compensatory adjustments in gait kinetic parameters, the temporal coupling across the oscillating body segments and the muscle synergies. Also, a reduced mechanical advantage of the flexed limbs (Biewener 1990) along with the energy absorption at the ankle and energy generation at the hip suggest an increased mean level of the muscle activity during trunk-flexed gaits. Build upon the relevant studies on interaction between posture and locomotion, it is convincible that increasing the sagittal trunk flexion during gait is associated with remarkable kinetic, kinematic and energetic changes in the lower limbs. However, our understanding of motor control of human gait in which trunk (36% of total body mass) is allowed to be bent fully, is very limited.

The stability of gait is subject to the trunk orientation and the CoM location. It is of research interest to investigate whether creating profound changes in our posture architecture would pose significant control challenges to our locomotor system. From control perspective, the stability of human bipedal gait is inherently a challenging functional task as two-thirds of body weight is centered at around two-thirds of body height above the ground (Winter 1995). The manipulation of this demanding task by changing the geometry of the trunk or/and subjecting to the external disturbances may add insult to injury. Compared to human upright trunk (orthograde), the trunk orientation in small birds is an almost horizontal (pronograde). For birds, the stabilization of the pronograde trunk during locomotion requires kinematic and kinetic asymmetries in leg function (Andrada et al. 2014). The location of the hip below the CoM facilitates a more elastic operation of the leg, leading to a more symmetric kinematic and kinetic behavior and the generation of hip extension and flexion moments in human gait. We expect mimicking birds' pronograde locomotion may reproduce the comparable kinematic and kinetic behavior in leg function, as a forward shift of the CoM relative to the hip would constraints such elastic operation of the leg (Blickhan et al. 2015). Although the shift in the placement of hip with respect to the CoM may increase the cost of locomotion since higher hip torques would be required to balance the trunk (Storer 1971); however, the pronograde posture may ease the problem of stabilization.

The compliant legs as in small birds is a matter of paradox in terms of economy and stability. Running with such compliant, crouched legs is associated with a lower muscle mechanical advantage and higher energy costs (McMahon et al. 1987; Biewener 1989; Gatesy 1991). On the other hand, as compared to the straight leg posture in human runners, the crouched leg posture in birds allow a greater robustness to ground height changes. One model that could explain why birds run with compliant legs, suggests the compromises in leg control for stability and economy (Daley and Usherwood 2010). Although our anatomy has not evolved for pitched postures, but the adaptive capacity of our locomotor apparatus allows maintaining bent postures during locomotion. This ability can be tested in experiments to shed new light on how crouched posture — biomechanically unfavorable and presumably metabolically expensive — derived from the bent trunk in the sagittal plane can influence the leg function and the capability of negotiating changes in ground level. Given a more forwardly bent trunk increasingly leads to a more crouched whole-body posture and thus the significant variations in kinematic behavior of walking as compared to regular upright walking, this may cause us to assume that the negotiation of changes in ground level with an altered trunk orientation may lead to frail unstable gaits. Little is known whether the able-bodied walkers are able to cope with postural and setting-derived perturbations through modulation of the kinetic and kinematic characteristics of gait. In other words, the literature does not provide any evidence if the able-bodied walkers have the capability of achieving robustly stable gaits while dealing with a hole in ground through dynamic adjustments in locomotor system prior, during and after perturbation. Such context-specific biomechanical regulations may involve different kinematic behavior between touchdown (TD) and toe-off (TO) moments, because an increase of the sagittal trunk flexion leads to a more asymmetric operation of legs. For instance, at TO a shorter effective leg with a steeper angle relative to TD would not allow adequate extension of legs. Having observed the capability of small birds in adjusting their zig-zag-like configured legs in order to cope with large disturbances in ground level (Blum et al. 2011), we hypothesize that adopting such crouched postures by human walkers may facilitate the traverse of uneven ground using compensatory adjustments in the trunk kinematics during the step-down. In this way, they may moderate variations in the CoM height.

1.8 Dissertation outline

The examination of locomotion in small birds has demonstrated that the pronograde trunk orientation induces prominent intra-limb asymmetries in the axial leg function, namely axial leg force and effective leg (connecting hip to Cop) length. However, it is not well understood whether these kinematic and kinetic asymmetries caused by the trunk represent general constraints on leg function regardless of the specific leg architecture or size of the species. *Chapter 2* of this work attempts to address this problem through examining: a) the effect of imposed trunk flexion on leg function with emphasis on the analogy between locomotion in small-bodied bipedal avian and human; and b) comparison between the ability of two simple models, namely spring and damper in series and parallel spring and damper, in prediction of the axial leg force. The findings of this chapter reveal that an experimentally prescribed pronograde posture in able-bodied walking induces asymmetries in effective leg function, as characterized by right-skewed vertical GRFs and shorter leg lengths at toe-off comparable with the asymmetries found in birds. These similarities between dynamics of locomotion in small birds and humans with flexed trunk indicate that the stabilization of the trunk constrains the basic leg function regardless the specific leg morphology, at least in the investigated taxa. Furthermore, while the parallel spring and damper model has been widely used in biomechanics and robotics to investigate legged locomotion, the model with a spring in series with the damper produces better predictions of the leg forces across gaits with various degrees of trunk flexion.

While human perturbation experiments have individually analysed either walking with natural and experimentally induced trunk configurations or adaptive and reactive kinematic and kinetic mechanisms in pre-perturbation and perturbation steps and have made comparisons with animal and avian locomotor behaviour, to our knowledge, kinetic and kinematic adaptations when stepping down (perturbation) alongside pre- and post-perturbation steps while maintaining different bent postures have not been investigated yet. It is convincible to assume that walking with an altered trunk configuration and negotiation of changes in ground levels lead to posture- and step-specific main effects on GRF parameters compared with the upright posture gait and level walking, respectively. Walking with altered trunk orientations yields different patterns of GRF (Grasso et al. 2000; Saha et al. 2008), however it is not given whether traversing uneven ground with trunk-flexed postures would demonstrate dissimilar gait dynamics than walking with a regular erect trunk. *Chapter 3* expands upon this notion by examining the interaction effects between changes in trunk posture and step types on walking kinetics. Hereto, we demonstrate that gaits with an increase of trunk flexion are increasingly associated with reduced kinetic adaptations across steps in uneven ground compared with the unperturbed level ground step. Altering the trunk angle is assumed to facilitate lower limb kinematic adaptations to changes in ground level. Healthy young participants in this experiment were found to exploit this mechanism to counteract e.g. the aligned effects of trunk flexed gait and step down on the first GRF peak in the perturbation step and on the second GRF peak in the pre-perturbation step to avoid excessive loads and falling, respectively.

Chapter 4 characterizes the adaptive kinematic behavior of able-bodied walking while negotiating uneven ground with altered trunk orientations as a complementary step to the Chapter 3. The contents of Chapter 4 indicate that the maintenance of dynamic stability while negotiating changes in ground level requires step-specific compensatory kinematic adaptations in lower limbs, regardless of the trunk orientation. As compared with regular upright walking, the trunk-flexed gaits across uneven ground exhibited: a) more crouched legs, characterized by sustained knee flexion during stance; b) a greater TD-TO kinematic discrepancy in effective leg (i.e. shorter legs at toe-off); c) a marginally flatter leg angle at TD. Moreover, backward rotation of the trunk during step-down seemed to be not only a preventive strategy employed by able-bodied participants, possibly, to control angular momentum of the body, but also to moderate changes in the CoM trajectory in trunk-flexed gaits. Finally, at the end of the step-up, participants demonstrated the restoration of the kinematic parameters to values of the unperturbed corresponding steps. These results suggest stability and robustness of the gait in able-bodied participants.

Finally, *Chapter 5* summarizes the separate findings of this thesis work to a more coherent picture of dynamics of human walking in response to the postural and environmental perturbations, and draws general biomechanical and clinical conclusions based on the results.

Chapter 2

2 Article I

Journal of Experimental Biology (2017) 220, 478-486
https://doi.org/10.1242/jeb.148312

Increasing trunk flexion transforms human leg function into that of birds despite different leg morphology

Soran Aminiaghdam[1]*, Christian Rode[2], Roy Müller[3] and Reinhard Blickhan[4]

* Correspondent author

Authorship contribution

Role	Contributor
Conceptualization	1; 3; 4
Methodology	1; 3; 4
Software	1; 2; 3; 4
Validation	1; 2; 3; 4
Formal analysis	1; 2; 4
Investigation	1; 3; 4
Resources	1; 3; 4
Data Curation	1; 2; 3; 4
Writing – original draft preparation	1
Writing – review and editing	1; 2; 4
Visualization	1
Supervision	2; 3; 4
Project administration	1
Funding acquisition	No funding

© 2017. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2017) 220, 478-486 doi:10.1242/jeb.148312

RESEARCH ARTICLE

Increasing trunk flexion transforms human leg function into that of birds despite different leg morphology

Soran Aminiaghdam*, Christian Rode, Roy Müller and Reinhard Blickhan

ABSTRACT

Pronograde trunk orientation in small birds causes prominent intra-limb asymmetries in the leg function. As yet, it is not clear whether these asymmetries induced by the trunk reflect general constraints on the leg function regardless of the specific leg architecture or size of the species. To address this, we instructed 12 human volunteers to walk at a self-selected velocity with four postures: regular erect, or with 30 deg, 50 deg and maximal trunk flexion. In addition, we simulated the axial leg force (along the line connecting hip and centre of pressure) using two simple models: spring and damper in series, and parallel spring and damper. As trunk flexion increases, lower limb joints become more flexed during stance. Similar to birds, the associated posterior shift of the hip relative to the centre of mass leads to a shorter leg at toe-off than at touchdown, and to a flatter angle of attack and a steeper leg angle at toe-off. Furthermore, walking with maximal trunk flexion induces right-skewed vertical and horizontal ground reaction force profiles comparable to those in birds. Interestingly, the spring and damper in series model provides a superior prediction of the axial leg force across trunk–flexed gaits compared with the parallel spring and damper model; in regular erect gait, the damper does not substantially improve the reproduction of the human axial leg force. In conclusion, mimicking the pronograde locomotion of birds by bending the trunk forward in humans causes a leg function similar to that of birds despite the different morphology of the segmented legs.

KEY WORDS: Trunk orientation, Asymmetry, Able-bodied walking, Posture, Leg model

INTRODUCTION

Bipedal walking and running are the common human gaits. Humans, birds, and sometimes apes and monkeys use bipedal locomotion (Alexander, 2004; Hirasaki et al., 2004). In contrast to most animals, human walking is characterized by an erect trunk (Grasso et al., 2000), extended limbs during the stance phase (Foster et al., 2013) and two-peaked vertical ground reaction force (GRF) patterns (Alexander, 2004; Winiarski and Rutkowska-Kucharska, 2009; Toda et al., 2015). The dynamics of locomotion can be affected by altering specific gait requirements. For example, running with flexed knee decreases the vertical stiffness of the legs relative to normal human running (McMahon et al., 1987).

Although bipedal locomotion in birds and humans seems to be highly adapted (Alexander, 2004; Müller et al., 2016), the design of their locomotor systems is drastically different, not only in terms of segmentation but also for their hip placement with respect to the centre of mass (CoM) (Gatesy and Biewener, 1991). Unlike human CoM, which is situated above the hip, owing to a horizontal upper body orientation (pronograde) in birds, the hip is located posterior to the CoM (Hutchinson and Allen, 2009). Birds with horizontal trunk orientation achieve steady-state locomotion using two leg strategies (throughout the article, 'leg' refers to the segment connecting the hip and the centre of pressure, CoP). The first is a kinematic asymmetry, i.e. longer legs at touchdown (TD) and shorter legs at toe-off (TO); the second is a kinetic asymmetry i.e. exertion of greater forces in the early stance phase and attenuated forces during the rest of stance phase (a right-skewed GRF pattern) (Andrada et al., 2014).

The human trunk accounts for more than 50% of total body mass; hence, trunk orientation has a significant effect on the position of the CoM and human locomotion (de Leva, 1996; Gillet et al., 2003; Leteneur et al., 2009). The trunk stabilization, basically the task of balancing an unstable inverted pendulum standing on the hip (Maus et al., 2010), is an important task in human locomotion. Humans are able to adopt pitched positions on command, but certainly, our locomotor system is not tuned to such postures. This ability can be exploited in experiments using different postures to shed new light on how trunk orientation can influence the leg function or on the biomechanically unfavourable, probably metabolically expensive, posterior position of the hip with respect to the upper body CoM in birds (Alexander, 1991; Blickhan et al., 2015).

Despite the different morphology of human and bird legs, in both walking and running, the function of the virtual leg can be described with surprisingly simple phenomenological gait models (Maus et al., 2010; Andrada et al., 2014). In a system including a trunk with inertia, the human leg function could be approximated with a spring-like telescopic leg and hip torques that keep the trunk upright (Maus et al., 2010). A spring-like axial leg function may result from compliant muscles and properly adjusted muscle activation (Geyer et al., 2003). However, when modelling the pronograde locomotion of birds, the spring describing the compliant axial leg function (leg length and force in leg direction) was complemented by axial damping to successfully explain the axial kinetic and kinematic asymmetries induced by trunk orientation (Andrada et al., 2014).

Following the principle of parsimony, it is important to find simple yet well-fitting models of the leg function because they are convenient and transparent in systematic studies on the influence of basic parameters on performance. Moreover, such models can be applied to the investigation of the locomotion stability (Geyer et al., 2006; Maus et al., 2010; Andrada et al., 2014) or in virtual model control of complex machines (Sreenath et al., 2011). Dissimilar leg models may yield different predictions with respect to gait stability. Although it is common to use a spring and a damper in parallel to describe the axial leg function (Shen and Seipel, 2012; Andrada et al., 2014), to the best of our knowledge, a model with a damper in series with a spring using the same number of parameters has not yet been employed to investigate the asymmetric axial leg function.

Department of Motion Science, Institute of Sport Sciences, Friedrich Schiller University Jena, Seidelstraße 20, Jena 07740, Germany.

*Author for correspondence (soran.aminiaghdam@uni-jena.de)

S.A., 0000-0001-9310-6768

Received 14 August 2016; Accepted 17 November 2016

List of symbols and abbreviations

α_{TD}, α_{TO}	leg orientation at touchdown and at toe-off
BW	body weight
CoM	centre of mass
CoP	centre of pressure
c_p, c_s	damping parameter (parallel spring and serial spring)
F_a	axial force
GRF	ground reaction force
H_{GRFb}, H_{GRFp}	peak horizontal force (braking and propulsive)
I_S	vertical or support impulses
k_p, k_s	stiffness parameter (parallel spring and serial spring)
L	instantaneous leg length
l_0	rest length of the leg
l_d, l_{s0}	rest length (serial damper and serial spring)
$\dot{l}$, $\dot{l}_d$	rate of length change (leg and serial damper)
PSD	parallel-spring damper
RE	regular erect trunk alignment
RMS	root mean square
SSD	series-spring damper
TD, TO	touchdown, toe-off
TF1	30 deg of trunk flexion
TF2	50 deg of trunk flexion
TF3	maximal trunk flexion
V_{GRF1}, V_{GRF2}	vertical ground reaction force (first and second peak)

Gait asymmetries are the key traits of human locomotion (Dingwell et al., 2010). This is evident in a left–right asymmetrical behaviour during locomotion in able-bodied participants, even with equal leg masses (Sadeghi et al., 2000), in temporal and kinematic parameters (Gundersen et al., 1989), in GRF (Herzog et al., 1989) and in joint moments (Leteneur et al., 2009). While such inter-limb asymmetries have been extensively studied in human walking and also in technical walking systems (e.g. legged robots, prosthetic legs) (Merker et al., 2011), the intra-limb asymmetries in leg function are not well understood. In spite of a considerable number of studies on the potential effect of trunk posture on the human walkers whether as an imposed trunk posture (Grasso et al., 2000; Saha et al., 2008; Kluger et al., 2014), the natural inclination of the trunk (Leteneur et al., 2009, 2013) or age-related flexed posture (McGibbon and Krebs, 2001; de Groot et al., 2014), little is known about the effects of trunk orientation on the axial leg function, specifically when trunk posture is varied across a wide range of angles in the sagittal plane.

We hypothesize that humans increasingly approximate asymmetries observed in the axial leg function of birds during the stance phase, characterized by a right-skewed GRF profile and increased TD and TO kinematic asymmetries when proceeding from the orthograde to pronograde trunk orientation. This would indicate that the trunk posture imposes specific constraints on bipedal terrestrial locomotion in terms of leg function despite considerable differences in the detailed morphology of the leg or the size of the biological systems. We test this hypothesis in able-bodied participants walking with various trunk orientations. Furthermore, we investigate whether either leg model, the parallel spring and damper system or the model with spring and damper in series, gives a superior prediction of the axial leg function.

MATERIALS AND METHODS

Human subjects

Twelve able-bodied adults (six females, six male) aged 26±3.35 years (mean±s.d.) with average height of 169.75±7.41 cm and average mass of 65.08±8.07 kg participated in this study. Participants had no known musculoskeletal or neurological disorders that could affect their walking pattern or trunk motion. An informed consent form was signed by each participant before participation. The experimental protocol was approved by the local Ethics Committee of the University of Jena (3532-08/12) and carried out according to the Declaration of Helsinki.

Instrumentation

Data collection was conducted at the Biomechanics Laboratory at the Sports Institute within University of Jena. All trials were recorded with eight cameras (240 Hz) by a 3D infrared system (MCU1000, Qualisys, Gothenburg, Sweden) and synchronized with force acquisition by using the trigger of the Kistler software and hardware. Three consecutive force platforms (9285BA, 9281B, 9287BA; Kistler, Winterthur, Switzerland) embedded in the middle portion of a 12 m walkway sampled force at 1000 Hz.

A 13 body segment model was defined by 21 markers (spherical retro-reflective surface, 14 mm). The markers were placed on the following bony landmarks: fifth metatarsal heads, lateral malleoli, lateral epicondyles of femurs, greater trochanters, anterior superior iliac spines, posterior superior iliac spines, L5–S1 junction, lateral humeral epicondyles, wrists, acromioclavicular joints, seventh cervical spinous process and middle of the forehead.

Procedure

Participants were asked to walk at self-selected normal walking speed for each of the four conditions: with their regular erect trunk alignment (RE), with 30 deg of trunk flexion (TF1), with 50 deg of trunk flexion (TF2), and with maximal trunk flexion (TF3) (Fig. 1, Fig. 2A). To produce the most consistent trunk posture across participants, trunk flexion was achieved by bending from the hips (Saha et al., 2008). Considering this criterion, the TF3 constituted the maximum amount of trunk flexion that the participants could sustain while walking. Trunk angle was defined by the angle sustained by the line connecting the midpoint between the L5–S1 junction (L5) and the seventh cervical spinous process (C7) with respect to the vertical (Fig. 1A) (Müller et al., 2014). Practice trials were permitted to allow participants to accommodate to the locomotion conditions and secure step onto the force plates in left–right–left sequence. Trunk angles were compared visually with adjustable-height cardboard templates by a second examiner prior to performing of each trial and during gait along the walkway for TF1 and TF2. For TF3, there was no comparison. The templates, drawn with angles displaying target trunk flexion angles TF1 and TF2, were hung on a wall parallel to the walkway: one at the beginning and the other one in the middle of walkway. The participants accomplished eight trials per condition in which each foot stepped on a single force plate.

Selected variables and parameters

Gait parameters comprised velocity, stance time, step length, swing time and cadence. We determined the mean angles of trunk, hip, knee and ankle throughout the gait cycle (Fig. 1A). The vertical displacement of CoM was determined by body segmental analysis using the anthropometric tables of Zatsiorsky–Seluyanov modified by De Leva relative to the laboratory coordinate system throughout the stance phase (de Leva, 1996; Gard et al., 2004). Related parameters were the values of the kinematic variables at the instants of TD and TO, their range of motion, and their maximal values (ankle: dorsiflexion and plantarflexion).

We assessed the first peak of the vertical ground reaction force (V_{GRF1}), the second peak of the vertical ground reaction force (V_{GRF2}), the peak horizontal braking force (H_{GRFb}) and the peak

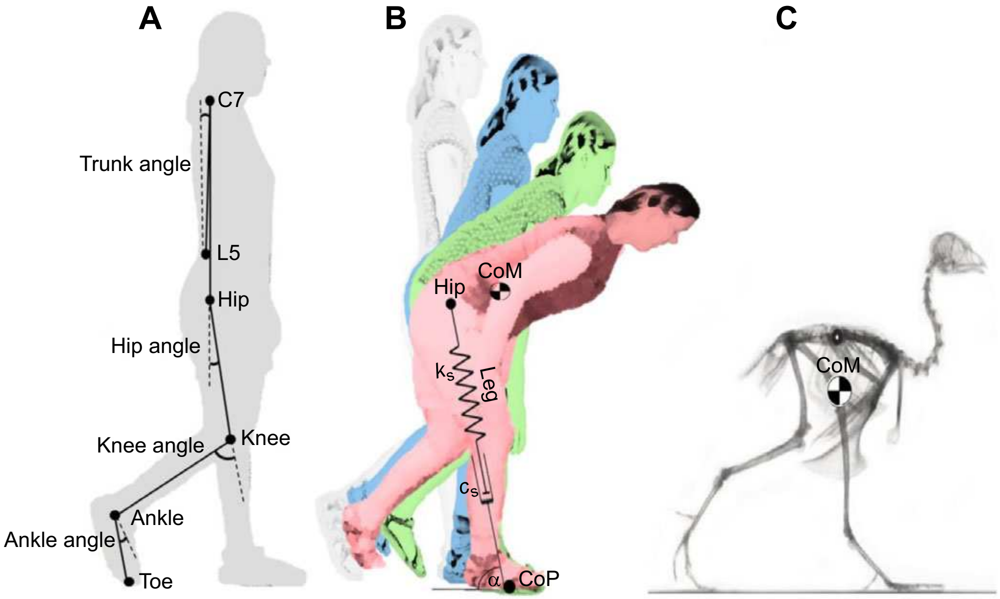

Fig. 1. Human and bird locomotion. (A) Illustration of the definitions of hip, knee and ankle joints as used in this study. (B) Side view of one participant while adopting regular erect (RE, grey), 30 deg trunk flexion (TF1, blue), 50 deg trunk flexion (TF2, green), maximal trunk flexion (TF3, red) postures during level walking gaits and modelling asymmetric leg function as spring and damper in series (SSD). CoM, centre of mass; k_s, stiffness parameter of serial spring; c_s, damping parameter of serial spring; α, leg orientation; CoP, centre of pressure. Consent to publish images was obtained. (C) Lateral X-ray projection of a quail enlarged for comparison (courtesy of Prof. Martin S. Fischer, Institute of Systematic Zoology and Evolutionary Biology with Phyletic Museum, Friedrich Schiller University Jena).

horizontal propulsive force (H_{GRFp}). For kinetic analysis, GRF was normalized to the participant body weight (BW). A vertical GRF threshold of 0.03 BW was used to determine the instants of TD and TO at each contact. Furthermore, we determined the duration of the braking phase relative to the duration of the stance time and calculated the vertical or support impulses (I_S) by integrating the according force–time curves and the normalized I_S to the product of body weight and the square root of the quotient of leg length and gravity (Hof, 1996). Leg (Fig. 1B) was normalized to the distance between the greater trochanter marker and the lateral malleoli marker at the instant of TD. Leg orientation, angle between leg and ground, at the instants of TD (α_{TD}, angle of attack) and TO (α_{TO}) was calculated with respect to the negative x-axis (Fig. 1B).

Data processing and statistics

Kinetic and kinematic data of all successful trials were analysed using custom written MATLAB (MathWorks) code. The raw coordinate data were filtered using a fourth-order low-pass, zero-lag Butterworth filter with 12 Hz cut-off frequency.

The effects of trunk orientation on joint kinematics and kinetics were evaluated using SPSS (SPSS Inc., Chicago, IL) with a statistical significance level of 0.05. For all participants, eight trials were analysed for each trunk posture. The data were categorized based on the trunk posture (RE, TF1, TF2 and TF3). Prior to analysis Levene's test and Kolmogorov–Smirnov test were performed to examine the equality of variance and normality of distribution, respectively. If data were parametric, a one-way ANOVA and paired *t*-test were used to examine the differences across gait conditions and in case of a significant difference, *post hoc* Bonferroni testing was employed; otherwise, a Wilcoxon signed-rank test was performed.

Leg models

To determine the axial leg function (Andrada et al., 2014), the sagittal plane GRF of the leg was projected onto the leg axis. Axial leg force was modelled in two different ways: parallel spring and damper elements (PSD), and spring and damper elements in series (SSD) (Fig. 1B). For the parallel arrangement, the axial force F_a is

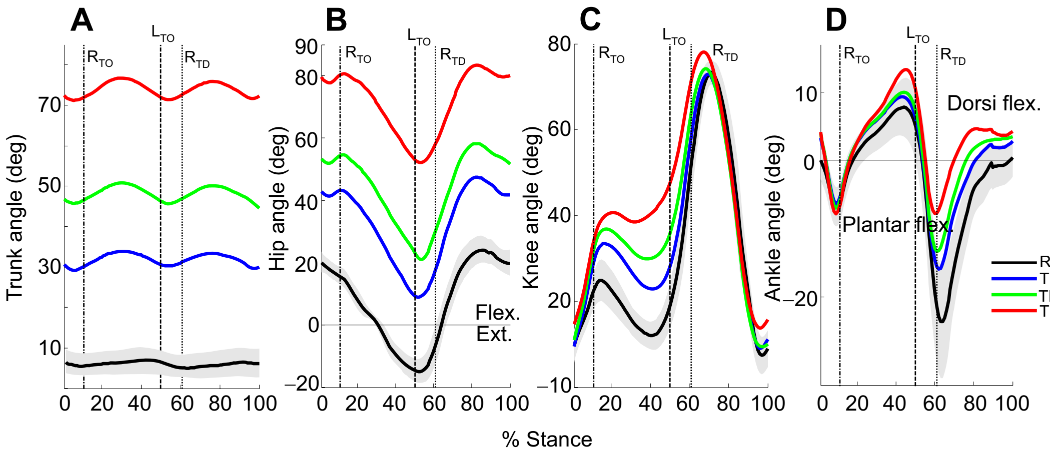

Fig. 2. Trunk and lower limb kinematics. Averaged (A) trunk, (B) hip, (C) knee and (D) ankle angles pertaining to the left limb in the sagittal plane during the gait cycle for RE (black), TF1 (blue), TF2 (green) and TF3 (red) level walking gaits (N=12). The grey shaded area represents s.d. of RE gait. RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion; R_{TO}, right toe-off; R_{TD}, right touchdown; L_{TO}, left toe-off.

Table 1. Spatiotemporal gait parameters

	RE	TF1	TF2	TF3
Velocity (m s^{-1})	1.49±0.10	1.60±0.12^{a}	1.65±0.13^{a}	1.63±0.14^{a}
Stance time (s)	0.60±0.04	0.57±0.05^{a}	0.54±0.04^{a,b}	0.54±0.04^{a,b}
Swing time (s)	0.40±0.01	0.39±0.03^{a}	0.38±0.02^{a}	0.38±0.03^{a}
Normalized step length (step length/leg length)	0.96±0.09	0.96±0.08	0.96±0.09	0.96±0.09
Cadence (steps min^{-1})	118.3±7.29	124.6±10.5^{a}	128.4±10.1^{a,b}	128.4±10.6^{a,b}
Braking phase (% stance phase)	52.1±4.46	44.3±4.98^{a}	41.5±2.93^{a,b}	38.3±2.92^{a,b,c}

Values expressed as means±s.d. ^{a,b,c}Significant differences ($P<0.05$). RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion.

governed simply by:

$$F_a = k_p(l_0 - l) + c_p\dot{l}, \tag{1}$$

where l and $\dot{l}$ are the instantaneous length and the rate of length change of the leg, respectively, k_p is the stiffness of the parallel spring, l_0 the rest length of the leg and $c_p<0$ the damping parameter of the parallel damper. The first term of the sum is the contribution of the spring and the right term is the contribution of the damper to axial force.

For the serial arrangement, F_a is equal in the spring and the damper, and the sum of the length of the spring l_s and the distance the damper travelled l_d equals l. Thus, the force is given by:

$$F_a = k_s(l_{s0} - l_s) = c_s\dot{l}_d\,, \tag{2}$$

where k_s and l_{s0} are the stiffness and rest length of the serial spring, $c_s<0$ and $\dot{l}_d$ are the damping parameter and the rate of length change of the serial damper, respectively. Hence, l_d can be obtained by integration of:

$$\dot{l}_d = \frac{k_s}{c_s}\cdot(l_{s0} - l + l_d). \tag{3}$$

In simulations, the initial length of the damper was set to zero.

Optimization

We minimized the sum of squared differences between the axial force that our leg models produced and the measured axial force by varying the independent spring and damper parameters with the MATLAB algorithm GlobalSearch. The leg length–time data were used as input. In both leg models, the rest lengths of the springs were dependent parameters. They were chosen such that the models reproduced the force at TD. We set lower bounds and upper bounds for stiffness and damping values. Stiffness values did not reach boundaries, yet damping values did reach upper (0 Ns m^{-1}) and lower bounds (−100,000 Ns m^{-1}) in some cases (especially in upright walking) for the PSD and the SSD model, respectively. For the PSD model, a damping value of 0 Ns m^{-1} indicates that the

Table 2. Kinetic and kinematic parameters

	RE	TF1	TF2	TF3
Kinematics				
Trunk$_{TD}$ (deg)	7.70±3.08	32.4±7.20^{a}	47.2±6.30^{a,b}	71.7±7.80^{a,b,c}
Trunk$_{TO}$ (deg)	5.70±2.90	30.9±6.47^{a}	47.6±7.54^{a,b}	71.3±7.16^{a,b,c}
Trunk$_{RoM}$ (deg)	3.37±1.49	7.37±3.75^{a}	9.09±2.90^{a,b}	7.28±2.04^{a,c}
Trunk$_{max}$ (deg)	8.25±3.09	34.5±6.76^{a}	51.5±7.23^{a,b}	77.1±7.03^{a,b,c}
Hip$_{TD}$ (deg)	20.7±4.38	41.7±8.08^{a}	55.0±8.16^{a,b}	77.1±7.27^{a,b,c}
Hip$_{TO}$ (deg)	−14.4±6.13	10.9±10.8^{a}	23.5±9.50^{a,b}	49.8±9.11^{a,b,c}
Hip$_{RoM}$ (deg)	41.2±3.24	39.4±4.14	37.5±4.95^{a}	33.9±5.79^{a,b,c}
Hip$_{max}$ (deg)	24.9±5.12	47.6±7.81^{a}	60.1±7.92^{a,b}	83.1±5.73^{a,b,c}
Knee$_{TD}$ (deg)	9.32±4.24	10.1±3.87	10.9±5.24	13.6±6.23^{a,b,c}
Knee$_{TO}$ (deg)	35.1±5.49	40.2±6.20^{a}	45.2±6.51^{a,b}	54.02±8.31^{a,b,c}
Knee$_{RoM}$ (deg)	68.3±3.56	66.6±2.78^{a}	67.1±3.07	67.4±3.71
Knee$_{max}$ (deg)	74.8±3.11	74.4±4.03	75.4±4.99	79.4±8.03^{a,b,c}
Ankle$_{TD}$ (deg)	−1.17±2.13	2.16±2.29^{a}	2.15±2.97^{a}	2.42±3.36^{a}
Ankle$_{TO}$ (deg)	−11.2±5.69	−6.81±5.11^{a}	−4.46±5.18^{a,b}	−2.67±6.41^{a,b}
Ankle$_{RoM}$ (deg)	36.3±6.54	29.9±4.77^{a}	27.8±4.62^{a}	28.7±4.63^{a}
Ankle dorsiflexion (deg)	7.25±4.43	8.45±4.25	9.68±4.57^{a}	12.6±5.17^{a,b,c}
Ankle plantarflexion (deg)	−29.1±7.76	−21.5±5.76^{a}	−18.1±4.90^{a,b}	−21.2±7.69^{a,b}
CoM$_{TD}$ (m)	0.87±0.47	0.84±0.39	0.84±0.44^{a}	0.78±0.66^{a,b,c}
CoM$_{TO}$ (m)	0.87±0.43	0.84±0.36^{a}	0.83±0.48^{a}	0.79±0.61^{a,b,c}
CoM$_{RoM}$* (m)	0.03±0.01	0.04±0.01^{a}	0.03±0.01^{b}	0.03±0.01
CoM$_{max}$* (m)	0.89±0.04	0.87±0.03^{a}	0.86±0.04^{a}	0.8±0.05^{a,b,c}
Kinetic data				
V_{GRF1} (N BW^{-1})	1.21±0.82	1.33±0.14^{a}	1.39±0.40^{a,b}	1.38±0.15^{a}
V_{GRF2} (N BW^{-1})	1.15±0.07	0.97±0.10^{a}	0.89±0.11^{a,b}	0.87±0.09^{a,b}
H_{GRFb} (N BW^{-1})	−0.21±0.05	−0.25±0.08^{a}	−0.28±0.09^{a}	−0.31±0.10^{a,b}
H_{GRFp} (N BW^{-1})	0.26±0.03	0.24±0.03^{a}	0.22±0.04^{a,b}	0.21±0.04^{a,b}
I_S	1.86±0.12	1.76±0.15^{a}	1.70±0.14^{a,b}	1.71±0.14^{a,b}

Values are expressed as means±s.d. ^{a,b,c}Significant differences ($P<0.05$). RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion; TD, touchdown; TO, toe-off; RoM, range of motion; max, maximal; V_{GRF1}, 1st peak of vertical ground reaction force; V_{GRF2}, 2nd peak of vertical ground reaction force; H_{GRFb}, peak horizontal braking force; H_{GRFp}, peak horizontal propulsive force; I_S, dimensionless vertical or support impulse.
*: measured during stance phase.

Table 3. Leg parameters obtained from experimental data

	RE	TF1	TF2	TF3
Normalized leg length (TD)	1.14±0.35	1.15±0.03	1.15±0.03	1.14±0.03
Normalized leg length (TO)	1.11±0.07	1.1±0.35	1.09±0.35^{a}	1.06±0.35^{a,b,c}
α_{TD}	66.1±4.67	63.6±4.49^{a}	63.4±4.58^{a}	62.9±4.74^{a}
α_{TO}	116.3±3.38	113.9±3.25^{a}	113.9±3.31^{a}	112.5±3.62^{a,b}

α_{TD}, angle of attack; α_{TO}, leg orientation at TO. Values expressed as means±s.d. ^{a,b,c}Significant differences (P<0.05). RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion.

damper produces no force, and for the SSD model, a damping value of −100,000 Ns m^{-1} means that the damper barely moved. In both cases, the PSD and the SSD leg models are in effect reduced to a spring. To compare the quality of the fit between PSD and SSD models, we used the root mean square (RMS) values that were normalized to the maximal axial force of each trial.

RESULTS

Spatiotemporal parameters

Group means and standard deviations for spatiotemporal gait parameters are listed in Table 1. Except for normalized step length, significant differences (P<0.05) were found across gait conditions for the entire gait parameters. As trunk flexion angle increased, an upward trend can be observed in the velocity and cadence, and a downward trend in the stance time and swing time. Between TF2 and TF3, there were no significant differences in parameters.

Joint kinematics

Fig. 2A shows the mean pattern of the trunk angle across gait conditions throughout the gait cycle. The joint kinematics parameters are shown in Table 2 (classified by postures). When clustering by posture, differences (P<0.05) among groups were found for all parameters of interest. Not surprisingly, the greater the trunk flexion, the larger the hip flexion angle at TD and TO, and the greater the peak hip flexion angle during the gait cycle. The hip range of motion decreased with trunk flexion (Fig. 2B, Table 2).

Knee flexion at TD and TO as well as peak knee flexion increased with trunk flexion. In contrast, the knee range of motion decreased marginally with trunk flexion (Fig. 2C, Table 2).

With increased trunk flexion, the ankle tended to be significantly more dorsiflexed at TD and less plantarflexed at TO (Table 2). Also, the peak ankle dorsiflexion during stance increased while the peak ankle plantarflexion during swing was lower for gaits with a trunk-flexed posture.

The vertical position of the CoM at TO was nearly the same as that at TD within each gait condition (Fig. 3). However, compared with RE, the vertical position of CoM at TD and TO decreased significantly by ∼10% in TF3 (Fig. 3C, Table 2).

Kinetic parameters

Fig. 3 shows the average normalized vertical (A) and anterior–posterior (B) GRFs at the preferred walking speed for the different trunk-flexed postures. Although the magnitude of V_{GRF1} was significantly higher for trunk-flexed postures, V_{GRF2} decreased with trunk flexion by up to 24% in TI3 gait (Table 2). In comparison to regular erect trunk (RE) gait, H_{GRFb} amplitude increased by up to 47% and H_{GRFp} amplitude decreased by up to 19% in TF3 (Fig. 3A, Table 2). These resulted in a more asymmetric profile of vertical GRFs, with the second peaks and valley much less pronounced for trunk-flexed postures and asymmetric profile of horizontal GRFs, with higher H_{GRFb} and lower H_{GRFp} (Fig. 3). Moreover, with increased trunk flexion, the braking phase was systematically decreased by ∼26% in TF3 gait (Table 2). The support impulse

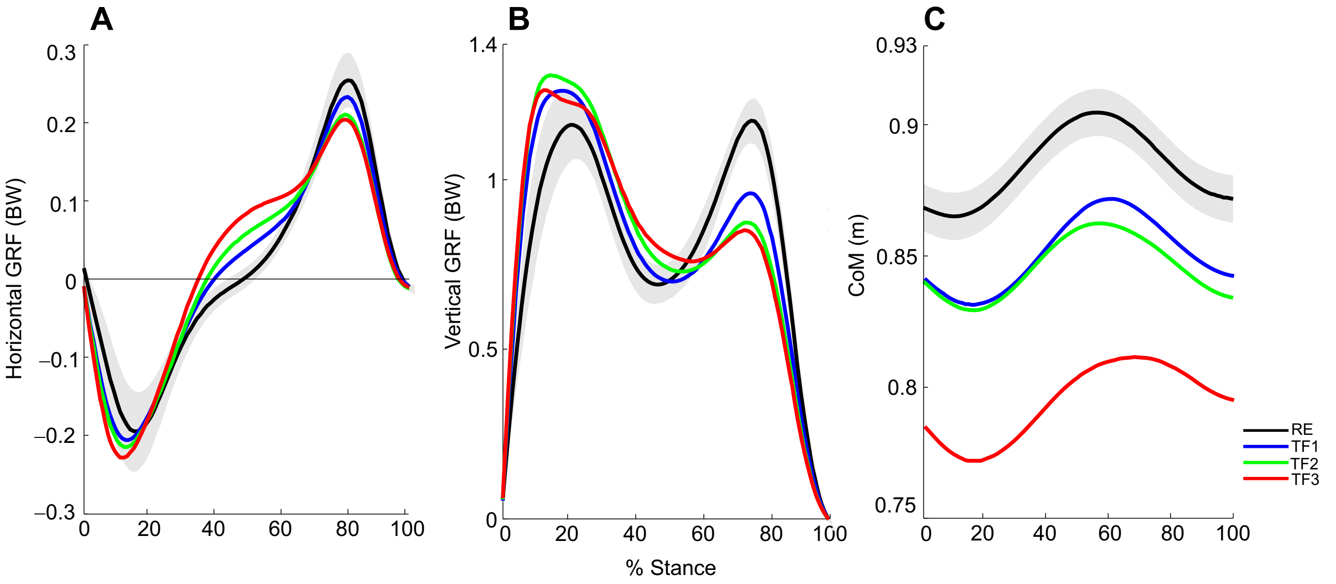

Fig. 3. Ground reaction forces (GRF) and CoM waveforms for different walking conditions. Shown are ensemble-averaged horizontal GRF (A), vertical GRF (B) [normalized to participant body weight (BW)] and centre of mass (CoM) (C) for RE, TF1, TF2 and TF3 level walking gaits during the stance phase (N=12). The contact time is normalized to 100%. The grey shaded area represents the corresponding s.d. RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion.

decreased significantly from 1.86±0.12 in RE by ~5% to 1.76±0.12 in TF1 and 8% to 1.7±0.14 in TF2 and TF3, respectively (Table 2).

Properties of the leg

Table 3 lists the group mean±s.d. values pertaining to the properties of the leg across gait postures. Participants showed adaptations in the leg angle at TD (α_{TD}) and TO (α_{TO}) for the different trunk angles (Table 3). The leg angle decreased significantly by 4.8% from 66.1±4.67 deg (RE) to 62.9±4.74 deg(TF3) at TD and by 3.2% from 116.3±3.38 deg (RE) to 112.5±3.62 deg (TF3) at TO. In other words, during maximal trunk-flexed gait, the leg displayed a flatter angle at TD and a steeper angle at TO.

The leg length at TD remained almost unaffected (P=0.514), whereas the leg length at TO significantly decreased across postures with increased trunk flexion angle (P<0.001). The leg length exhibited a strong asymmetry during the stance phase (longer at TD and shorter at TO; Fig. 4A, Table 3).

The SSD model produced significantly better predictions of leg axial forces than the PSD model for trunk-flexed gaits (Fig. 5, Fig. 6). The SSD model fitted axial force in TF2 better than in other gait conditions (Fig. 5C). The average deviation of the SSD model force from axial force was 0.16 (RE), 0.11 (TF1), 0.1 (TF2) and 0.13 (TF3) of the maximal force.

DISCUSSION

An increase of sagittal trunk flexion led to greater kinetic and kinematic intra-limb asymmetries (Figs 3 and 4). Despite the considerable differences in leg morphology and size between humans and birds, able-bodied walking with maximum trunk flexion (TF3) produces a leg function similar to that found in birds. Moreover, for all trunk angles, the leg model with spring and damper in series gives a superior prediction of the axial leg function (Figs 5 and 6).

The findings of the current study support the hypothesis that the sagittal trunk posture leads to altered gait parameters and leg function. Specifically, it was hypothesized that changes in trunk orientation would result in right-skewed vertical GRF profiles and in shorter duration of braking relative to the propulsion phase. Compared with RE gait, vertical GRF tended to be more asymmetric with increasing trunk flexion (Fig. 3B). In contrast to the symmetric, M-shaped vertical GRF pattern during RE gait in humans, vertical GRF approximated the right-skewed profile found in birds with pronograde trunk orientation (Andrada et al., 2014). Furthermore, the duration of the braking phase decreased significantly with trunk flexion (Fig. 3A, Table 2) towards values found in birds (Andrada et al., 2014). These dynamic similarities between bird and human trunk-flexed locomotion suggest that the trunk configuration causes these dynamic asymmetries and that the leg (connecting hip and CoP) operation is independent of the specific leg morphology.

While the normalized length of the leg remained unchanged at TD, with increasing trunk flexion it underwent a significant decrease at TO. Together with the posterior shift of the pelvis, the unchanged leg length at TD led to a decrease in the distance between the CoM and the CoP. In order to prevent toppling or falling over, TO occurred at a steeper angle in the trunk-flexed gait. To maintain a sufficient step length, the posterior shift of the pelvis is compensated in part by choosing a flatter angle of attack (leading to a ~0.02 m gain in TD position). Still, step time in trunk-flexed walking remained shorter than in the RE gait, which is also reflected in a significant decrease of support impulse (Table 2). Consequently, the braking phase became shorter relative to the propulsion phase with an increase of trunk flexion, suggesting that the average braking force must be larger than the average propulsive force to yield zero impulse in horizontal direction, i.e. to keep locomotion speed constant. Assuming that an increase in propulsive force is associated with increased axial leg force, the reduced braking time (Table 2) leads to the right-skewed vertical GRF profile.

Walking with bent postures was associated with a crouched gait pattern, characterized by a sustained knee flexion throughout the stance phase, and an increase in hip flexion and ankle dorsiflexion (Wren et al., 2005; Saha et al., 2008). This can be explained with a flatter angle of attack that leads to a decreased height of the hip above the ground, which in turn yields more flexed limb joints during trunk-flexed walking. In addition, with increasing trunk flexion, the angular range of motion decreased across lower limb joints (Table 2) because in more flexed limbs, smaller angular

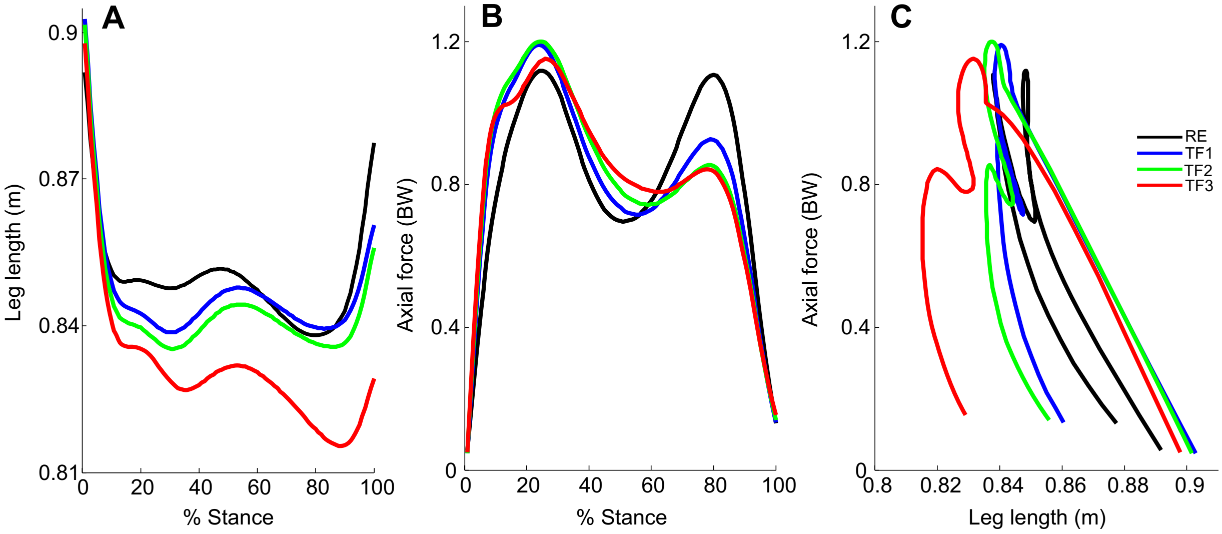

Fig. 4. Axial leg function. Averaged (A) leg length, (B) axial leg force and (C) axial loop (axial force versus leg length) for RE and, TF1, TF2 and TF3 gaits (N=12). Axial loops start at long length and end with a shorter leg length (counterclockwise loop). The contact time is normalized to 100%. RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion.

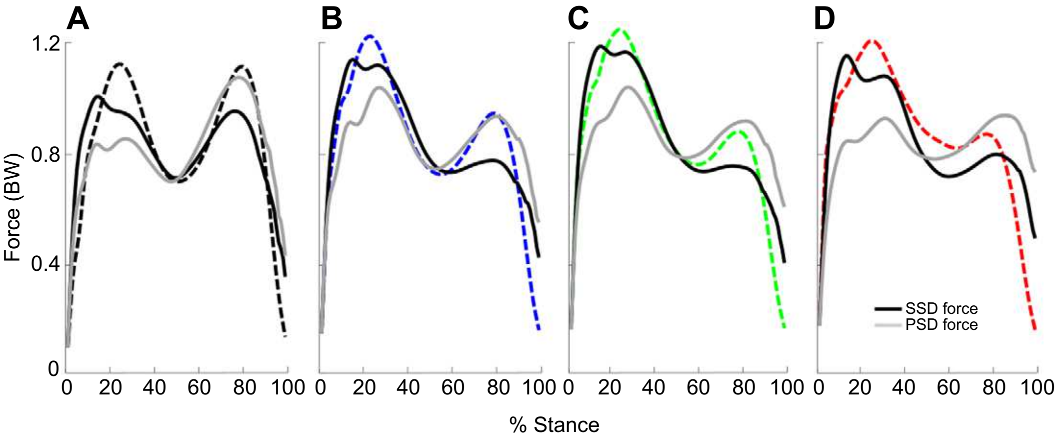

Fig. 5. Model forces versus experimental axial force for different walking conditions. (A) RE, (B) TF1, (C) TF2 and (D) TF3 gaits (*N*=12). Shown are normalized ensemble-averaged leg axial force (dashed lines), fit from SSD model (series-spring-damper, solid black curve) and fit from PSD model (parallel-spring-damper, solid grey curve). SSD model produces better predictions of leg axial forces in response to trunk-flexed postures than the PSD model across all gait conditions (Fig. 6). RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion.

changes are required to achieve similar leg length changes to those measured in upright walking with extended legs. Since locomotion with trunk-flexed postures was achieved by bending over at the waist, the hip joint showed the greatest extent of flexion throughout the gait cycle in comparison to RE gait (Table 2). With increasing sagittal trunk flexion, all leg joints were flexed more at TO owing to the earlier TO at a steeper angle (Table 2). The kinematic asymmetries in trunk-flexed gait (TD and TO angles and leg lengths) are in agreement with those found in birds (Andrada et al., 2014).

Compared with RE walking, in our study, walking with maximal trunk flexion (TF3) led to ∼10% greater self-selected gait velocity and cadence, ∼10% shorter stance time and ∼5% shorter swing duration while the normalized step length remained unchanged. In our experiment, the task of foot strikes in left–right–left sequence on three equidistant force plates embedded in the walkway may have prompted the participants to maintain constant step lengths. With the same step lengths and lower vertical impulse per step, a higher cadence is necessary to support the body weight. This in turn enforces higher speed. Such increased walking speed is not in agreement with the result observed by Saha et al. (2008), who found that walking speed does not significantly vary during walking with trunk-flexed postures. The reason for this inconsistency may be attributed to different approaches employed to control the trunk postures. They used a program that allows continuous, real time estimation of the trunk flexion angle via provision of auditory cues, which may have required participants to walk slower in order to maintain their trunk close to the desired angle. In contrast, in our experiments the trunk angle was checked visually by an independent examiner, which may have led to less constrained walking conditions.

It may be speculated that the imposed trunk flexion in TF1 and TF2 would limit the range of angular excursion throughout the gait. In contrast, trunk excursions were increased in trunk-flexed gaits compared with RE gait (Fig. 2A, Table 2). Owing to the posterior shift of the hip in the forward bent posture, the horizontal leverage of the CoM with respect to the hip is increased. After TD, the zig-zag configuration of the leg and body responds with bending (Fig. 2). In addition, an increased first peak of the ground reaction force increases the impulse in the first half of the contact. This is accompanied by increased hip muscle forces necessary to balance trunk weight in a more bent posture. These increased forces can, in part, be achieved by a stronger recruitment and by higher passive forces due to elongation of hip muscles that would contribute to muscular compliance and hence to oscillations. This argument can, however, not explain the relatively similar range of motion of the trunk angle for all trunk-flexed gaits (Table 2).

Kluger et al. (2014) analysed in detail the kinetics and energetics of lower limb joints in the context of trunk-flexed walking. They reported increased hip extension torques and hip work, and

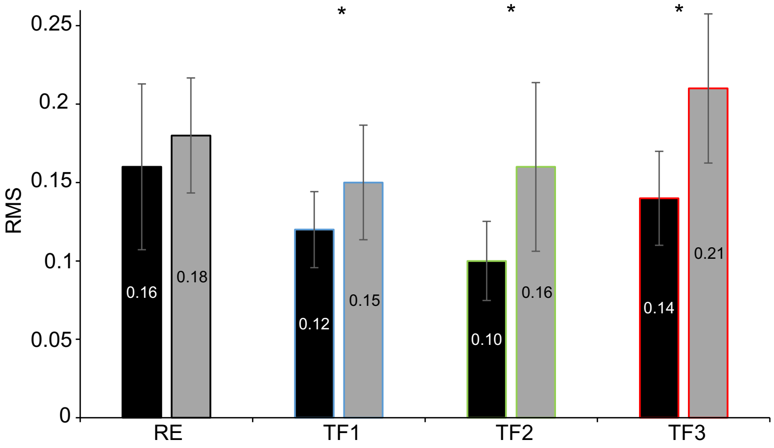

Fig. 6. Root mean square (RMS) difference between model forces and experimental axial force. Shown are ensemble-averaged RMS obtained by nonlinear curve fitting using SSD model (series-spring damper, black) and PSD model (parallel-spring damper, grey) for the gait conditions RE, TF1, TF2 and TF3. Error bars denote s.d.; asterisks denote statistically significant differences across conditions. Mean RMS values for SSD model were significantly lower than those for SSD model across all gait conditions except for RE gait (RE: t_{11}=1.54, *P*=0.174; TF1: t_{11}=3.21, *P*=0.008; TF2: t_{11}=3.69, *P*=0.004; TF3: t_{11}=4.95, *P*<0.001). RE, regular erect trunk; TF1, 30 deg trunk flexion; TF2, 50 deg trunk flexion; TF3, maximal trunk flexion.

decreased plantarflexion torques and negative work at the ankle joint during stance phase. In a recent work, Blickhan et al. (2015) investigated the effect of the hip placement directly below, at, or above the virtual pivot point (intersection of GRFs above CoM). They revealed that shifting the hip far posteriorly, as observed in some birds, can lead to the production of pure extension torques throughout the stance phase. These results are consistent with large hip torques and positive work at the hip and negative work at the tarsometatarsal–phalangeal joint – the functional equivalent of the ankle joint – in birds (Cavagna et al., 1963). In accordance with the increased energy dissipation in the ankle joint, our results show that energy dissipation in the leg in the axial direction increases with the increase of trunk flexion angle (Fig. 4C). Therefore, the relative placement of the hip with respect to the CoM is proposed to be an important measure in the modifications of leg function, and consequently, for balancing the trunk in legged motion systems (Blickhan et al., 2015).

The model with a spring in series with the damper produced better predictions of the leg forces than the parallel spring-damper model across all trunk-flexed gaits (Figs 5 and 6). Interestingly, in the case of RE walking, for both models, in many cases the optimization yielded parameters that corresponded to spring-like leg behaviour with negligible energy dissipation, and the model predictions were not significantly different (Fig. 6). This indicates that the damper does not substantially improve the reproduction of the human leg forces in walking with upright trunk, which corroborates the assumption of spring-like leg behaviour in conceptual models of human walking (Geyer et al., 2006). Although the parallel spring and damper model has been widely used in biomechanics and robotics to describe and investigate legged locomotion (Shen and Seipel, 2012; Andrada et al., 2014), our results highlight that the serial spring and damper model is superior in predictions of axial leg force of trunk-flexed walking. Because the leg models differ in their dynamic responses, we argue that employing the spring in series with the damper model may yield altered predictions of the locomotion stability in birds.

Understanding the interaction between posture and hip arrangement and their relation to axial leg function may be relevant in the medical field, in engineering and in explaining the evolution of a bipedal gait. For example, the observed intra-limb asymmetries as a consequence of trunk-flexed posture and associated compensatory mechanisms may be of clinical relevance for patients exhibiting a disordered gait (Saha et al., 2008; Doherty et al., 2011; de Groot et al., 2014). Engineers designing not merely androids but also robot birds and other creatures (Hyon et al., 2003; Hugel et al., 2011; Zhou and Bi, 2012) may benefit from the characterization of the axial leg function and its modelling e.g. for trajectory planning in virtual model control of bipedal robotic locomotion (Sreenath et al., 2011). Last, but not least, based on the differences in body size and limb morphology, the comparison of living avian and human bipeds may facilitate the interpretation of the evolution of bipedal locomotion (Gatesy and Biewener, 1991; Hirasaki et al., 2004; Schwartz, 2007; Thorpe et al., 2007; Foster et al., 2013).

The results of this study highlight the effects of sagittal trunk orientation on leg function in bipeds and reveals that the spring and damper in series model is superior in the reproduction of axial leg function in trunk-flexed gaits. An experimentally prescribed pronograde posture in able-bodied walking induces asymmetries in leg function characterized by a right-skewed vertical GRF and a shorter leg length at TO, which are similar to the asymmetries found in birds. Considering these similarities in locomotion between bird and human with trunk flexed, we conclude that the necessity to stabilize the trunk constrains the basic leg function independent of the specific leg morphology, at least in the investigated species.

Acknowledgements
Authors thank Johanna Vielemeyer for her valuable contribution to collecting experimental data.

Competing interests
The authors declare no competing or financial interests.

Author contributions
The experiments were planned by R.B., supervised by R.M., and carried out by S.A. The data were analysed by S.A. and C.R. All authors contributed to the interpretation of the results and revised the manuscript.

Funding
This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

References

Alexander, R. M. N. (1991). Energy-saving mechanisms in walking and running. *J. Exp. Biol.* **160**, 55-69.

Alexander, R. M. N. (2004). Bipedal animals, and their differences from humans. *J. Anat.* **204**, 321-330.

Andrada, E., Rode, C., Sutedja, Y., Nyakatura, J. A. and Blickhan, R. (2014). Trunk orientation causes asymmetries in leg function in small bird terrestrial locomotion. *Proc. Biol. Sci.* **281**.

Blickhan, R., Andrada, E., Müller, R., Rode, C. and Ogihara, N. (2015). Positioning the hip with respect to the COM: Consequences for leg operation. *J. Theor. Biol.* **382**, 187-197.

Cavagna, G. A., Saibene, F. P., Santi, G. F. and Margaria, R. (1963). Analysis of the mechanics of locomotion. *Exp. Med. Surg.* **21**, 117-126.

de Groot, M. H., van der Jagt-Willems, H. C., van Campen, J. P. C. M., Lems, W. F., Beijnen, J. H. and Lamoth, C. J. C. (2014). A flexed posture in elderly patients is associated with impairments in postural control during walking. *Gait Posture* **39**, 767-772.

de Leva, P. (1996). Adjustments to Zatsiorsky-Seluyanov's segment inertia parameters. *J. Biomech.* **29**, 1223-1230.

Dingwell, J. B., John, J. and Cusumano, J. P. (2010). Do humans optimally exploit redundancy to control step variability in walking? *PLoS Comput. Biol.* **6**, e1000856.

Doherty, K. M., van de Warrenburg, B. P., Peralta, M. C., Silveira-Moriyama, L., Azulay, J.-P., Gershanik, O. S. and Bloem, B. R. (2011). Postural deformities in Parkinson's disease. *Lancet Neurol.* **10**, 538-549.

Foster, A. D., Raichlen, D. A. and Pontzer, H. (2013). Muscle force production during bent-knee, bent-hip walking in humans. *J. Hum. Evol.* **65**, 294-302.

Gard, S. A., Miff, S. C. and Kuo, A. D. (2004). Comparison of kinematic and kinetic methods for computing the vertical motion of the body center of mass during walking. *Hum. Mov. Sci.* **22**, 597-610.

Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* **224**, 127-147.

Geyer, H., Seyfarth, A. and Blickhan, R. (2003). Positive force feedback in bouncing gaits? *Proc. Biol. Sci.* **270**, 2173-2183.

Geyer, H., Seyfarth, A. and Blickhan, R. (2006). Compliant leg behaviour explains basic dynamics of walking and running. *Proc. R. Soc. B Biol. Sci.* **273**, 2861-2867.

Gillet, C., Duboy, J., Barbier, F., Armand, S., Jeddi, R., Lepoutre, F.-X. and Allard, P. (2003). Contribution of accelerated body masses to able-bodied gait. *Am. J. Phys. Med. Rehabil.* **82**, 101-109.

Grasso, R., Zago, M. and Lacquaniti, F. (2000). Interactions between posture and locomotion: motor patterns in humans walking with bent posture versus erect posture. *J. Neurophysiol.* **83**, 288-300.

Gundersen, L. A., Valle, D. R., Barr, A. E., Danoff, J. V., Stanhope, S. J. and Snyder-Mackler, L. (1989). Bilateral analysis of the knee and ankle during gait: an examination of the relationship between lateral dominance and symmetry. *Phys. Ther.* **69**, 640-650.

Herzog, W., Nigg, B. M., Read, L. J. and Olsson, E. (1989). Asymmetries in ground reaction force patterns in normal human gait. *Med. Sci. Sports Exerc.* **21**, 110-114.

Hirasaki, E., Ogihara, N., Hamada, Y., Kumakura, H. and Nakatsukasa, M. (2004). Do highly trained monkeys walk like humans? A kinematic study of bipedal locomotion in bipedally trained Japanese macaques. *J. Hum. Evol.* **46**, 739-750.

Hof, A. L. (1996). Scaling gait data to body size. *Gait Posture* **4**, 222-223.

Hugel, V., Hackert, R. and Abourachid, H. (2011). Kinematic modeling of bird locomotion from experimental data. *IEEE Trans. Robot.* **27**, 185-200.

Hutchinson, J. R. and Allen, V. (2009). The evolutionary continuum of limb function from early theropods to birds. *Naturwissenschaften* **96**, 423-448.

Hyon, S., Emura, T. and Mita, T. (2003). Dynamics-based control of a one-legged hopping robot. *J. Syst. Control Eng.* **217**, 83-98.

Kluger, D., Major, M. J., Fatone, S. and Gard, S. A. (2014). The effect of trunk flexion on lower-limb kinetics of able-bodied gait. *Hum. Mov. Sci.* **33**, 395-403.

Leteneur, S., Gillet, C., Sadeghi, H., Allard, P. and Barbier, F. (2009). Effect of trunk inclination on lower limb joint and lumbar moments in able men during the stance phase of gait. *Clin. Biomech.* **24**, 190-195.

Leteneur, S., Simoneau, E., Gillet, C., Dessery, Y. and Barbier, F. (2013). Trunk's natural inclination influences stance limb kinetics, but not body kinematics, during gait initiation in able men. *PLoS ONE* **8**, e55256.

Maus, H. M., Lipfert, S. W., Gross, M., Rummel, J. and Seyfarth, A. (2010). Upright human gait did not provide a major mechanical challenge for our ancestors. *Nat. Commun.* **1**, 70.

McGibbon, C. A. and Krebs, D. E. (2001). Age-related changes in lower trunk coordination and energy transfer during gait. *J. Neurophysiol.* **85**, 1923-1931.

McMahon, T. A., Valiant, G. and Frederick, E. C. (1987). Groucho running. *J Appl Physiol. (1985)* **62**, 2326-2337.

Merker, A., Rummel, J. and Seyfarth, A. (2011). Stable walking with asymmetric legs. *Bioinspir. Biomim.* **6**, 045004.

Müller, R., Tschiesche, K. and Blickhan, R. (2014). Kinetic and kinematic adjustments during perturbed walking across visible and camouflaged drops in ground level. *J. Biomech.* **47**, 2286-2291.

Müller, R., Birn-Jeffery, A. V. and Blum, Y. (2016). Human and avian running on uneven ground: a model-based comparison. *J R Soc. Interface* **13**.

Sadeghi, H., Allard, P., Prince, F. and Labelle, H. (2000). Symmetry and limb dominance in able-bodied gait: a review. *Gait Posture* **12**, 34-45.

Saha, D., Gard, S. and Fatone, S. (2008). The effect of trunk flexion on able-bodied gait. *Gait Posture* **27**, 653-660.

Schwartz, J. H. (2007). The origins of human bipedalism. *Science* **318**, 1065; author reply 1065.

Shen, Z. H. and Seipel, J. E. (2012). A fundamental mechanism of legged locomotion with hip torque and leg damping. *Bioinspir. Biomim.* **7**, 046010.

Sreenath, K., Park, H.-W., Poulakakis, I. and Grizzle, J. W. (2011). A compliant hybrid zero dynamics controller for stable, efficient and fast bipedal walking on MABEL. *Int. J. Robot. Res.* **30**, 1170-1193.

Thorpe, S. K. S., Holder, R. L. and Crompton, R. H. (2007). Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* **316**, 1328-1331.

Toda, H., Nagano, A. and Luo, Z. (2015). Age and gender differences in the control of vertical ground reaction force by the hip, knee and ankle joints. *J. Phys. Ther. Sci.* **27**, 1833-1838.

Winiarski, S. and Rutkowska-Kucharska, A. (2009). Estimated ground reaction force in normal and pathological gait. *Acta Bioeng. Biomech.* **11**, 53-60.

Wren, T. A., Rethlefsen, S. and Kay, R. M. (2005). Prevalence of specific gait abnormalities in children with cerebral palsy: influence of cerebral palsy subtype, age, and previous surgery. *J. Pediatr. Orthop.* **25**, 79-83.

Zhou, X. and Bi, S. (2012). A survey of bio-inspired compliant legged robot designs. *Bioinspir. Biomim.* **7**, 041001.

Chapter 3

3 Article II

Biology Open (2017) 6, 1000-1007 https://doi.org/10.1242/bio.025239

Effects of altered sagittal trunk orientation on kinetic pattern in able-bodied walking on uneven ground

Soran Aminiaghdam[1]*, Christian Rode[2]

* Correspondent author

Authorship contribution

Role	Contributor
Conceptualization	1
Methodology	1
Software	1
Validation	1; 2
Formal analysis	1; 2
Investigation	1
Resources	3*
Data Curation	1; 2
Writing – original draft preparation	1
Writing – review and editing	1; 2
Visualization	1
Supervision	1
Project administration	1
Funding acquisition	No funding

© 2017. Published by The Company of Biologists Ltd | Biology Open (2017) 6, 1000-1007 doi:10.1242/bio.025239

RESEARCH ARTICLE

Effects of altered sagittal trunk orientation on kinetic pattern in able-bodied walking on uneven ground

Soran Aminiaghdam* and Christian Rode

ABSTRACT

Studies of disturbed human locomotion often focus on the dynamics of the gait when either posture, movement or surface is perturbed. Yet, the interaction effects of variation of trunk posture and ground level on kinetic behaviour of able-bodied gait have not been explored. For 12 participants we investigated the kinetic behaviour, as well as velocity and contact time, across four steps including an unperturbed step on level ground, pre-perturbation, perturbation (10-cm drop) and post-perturbation steps while walking with normal speed with four postures: regular erect, with 30°, 50° and maximal sagittal trunk flexion (70°). Two-way repeated measures ANOVAs detected significant interactions of posture×step for the second peak of the vertical ground reaction force (GRF), propulsive impulse, contact time and velocity. An increased trunk flexion was associated with a systematic decrease of the second GRF peak during all steps and with a decreased contact time and an increased velocity across steps, except for the perturbation step. Pre-adaptations were more pronounced in the approach step to the drop in regular erect gait. With increased trunk flexion, walking on uneven ground exhibited reduced changes in GRF kinetic parameters relative to upright walking. It seems that in trunk-flexed gaits the trunk is used in a compensatory way during the step-down to accommodate changes in ground level by adjusting its angle leading to lower variations in centre of mass height. Exploitation of this mechanism resembles the ability of small birds in adjusting their zig-zag-like configured legs to cope with changes in ground level.

KEY WORDS: Locomotion, Posture, Kinetics, Ground reaction force

INTRODUCTION

On the one hand, the negotiation of changes in the surface such as compliance, slip, obstacle or drop during walking challenges the human locomotor system and requires continuous adaptations (Tang et al., 1998; Marigold and Patla, 2002, 2005, 2008; van Dieen et al., 2007; Shinya et al., 2009; Müller et al., 2014). On the other hand, the generation of the ground reaction force (GRF) in human walking is strongly influenced by the orientation of the trunk (50% of total human body mass) owing to its significant effect on the displacement and acceleration of the body centre of mass (CoM) (Grasso et al., 2000; Gillet et al., 2003; Marigold and Patla, 2005; Saha et al., 2008; Leteneur et al., 2009; Kluger et al., 2014; Aminiaghdam et al., 2017).

Understanding changes in gait dynamics and accompanying compensatory techniques under both internal (posture) and/or external (surface) perturbations can shed light into functional demands of bipedalism in various scientific areas. For example, improved knowledge of the role of the trunk orientation in gait is of clinical interest as age or some pathological conditions alter trunk posture and adaptive capacity of the locomotor system (Farcy and Schwab, 1997; Lin et al., 2000; Sarwahi et al., 2002; Potter et al., 2004; Malone et al., 2015). Furthermore, the study of human gait with a crouched posture, i.e. mimicking pronograde locomotion of birds is of interest for comparative biologists (Gatesy and Biewener, 1991; Hirasaki et al., 2004; Schwartz, 2007; Thorpe et al., 2007; Foster et al., 2013; Aminiaghdam et al., 2017). In addition, experimental studies focused on investigating how human anatomy performs in different locomotor postures may provide further explanation for interpretation of the evolution of human bipedal locomotion. In general, exploration of gait features in a setting with greater variations of posture or ground level may also elicit the functional demands that have influenced the evolution of human bipedalism better than walking on uniform surfaces (Sockol et al., 2007; Pontzer et al., 2009).

Balancing the trunk, basically the functional task of stabilising an unstable inverted pendulum standing on the hip (Maus et al., 2010), plays an important role in human locomotion. The trunk has been suggested to serve as a reference in the control of posture and movement (Mouchnino et al., 1993; Darling and Miller, 1995; Massion et al., 1997). Furthermore, a forwardly bent trunk induces a gravitational moment that can be utilised to generate greater forward propulsion through the hip (Leroux et al., 2002) which in turn facilitates walking uphill/climbing stairs or to accelerate. At the same time, because the trunk is heavy, a forward bent trunk allows vertical alteration of CoM height (Aminiaghdam et al., 2017; Saha et al., 2008) when changing the hip angle. For example, when approaching a drop in ground level during walking, an upward rotation of the trunk during the step-down would increase the distance between CoM and foot and thus limit changes in CoM height which in turn would likely lead to reduced changes in kinetic behaviour. Humans might exploit this mechanism that in some way resembles the ability of small birds to adjust their zig-zag-like configured legs when coping with ground level perturbations (Birn-Jeffery and Daley, 2012; Birn-Jeffery et al., 2014; Müller et al., 2016). In this sense, we expect that the upper body might be transformed into an active component of the human locomotor system in trunk-flexed walking.

Studies of perturbed human locomotion often focus on gait dynamics when either posture, surface or movement is individually perturbed. A study by Saha et al. (2008) revealed that dynamic balance during walking with 25° and 50° sagittal trunk flexion in able-bodied participants is achieved by adjusting lower limb kinematics to more crouched configurations. They reported a higher GRF and loading rate during weight acceptance phase and a lower GRF during pre-swing phase. In a recent study, Aminiaghdam, et al. (2017) found that proceeding to a horizontal

Department of Motion Science, Institute of Sport Sciences, Friedrich Schiller University Jena, Seidelstraße 20, Jena 07740, Germany.

*Author for correspondence (soran.aminiaghdam@uni-jena.de)

S.A., 0000-0001-9310-6768

Received 25 May 2017; Accepted 27 May 2017

trunk configuration in humans caused similar dynamic intra-limb asymmetries in leg function as compared with birds. Such asymmetries, found to be necessary for maintaining dynamic balance in pronograde gait (Andrada, et al., 2014), were characterised by a reduction of the effective leg (connecting hip to centre of pressure) length and the GRF in the pre-swing phase as compared to the weight acceptance phase (Andrada et al., 2014; Aminiaghdam et al., 2017). Comparing human and avian running on uneven ground, Müller et al. (2016) reported that despite striking morphological disparities these species share some common kinematic behaviour (i.e. leg angle and leg length) while negotiating changes in ground level. For walking on uneven ground, when human walkers encounter a drop, they modulate their GRF kinetics proportional with the drop height not only in the perturbation step, but also in the approach step to the perturbation (Müller, et al., 2014). However, the quality and quantity of the kinetic and kinematic adaptations or reactions to external perturbations are context-specific (Müller, et al., 2014; van der Linden, et al. 2009, 2007). While these studies have analysed human walking with various trunk configurations or adaptive and reactive kinetic mechanisms in pre-perturbation and perturbation contacts and made comparisons with avian locomotor behaviour, to our knowledge, kinetic and kinematic adaptations when stepping down (perturbation) and in pre- and post-perturbation steps with different bent postures have not been investigated yet.

In this study, we investigate kinetic characteristics of the GRF during the stance phase across three steps in uneven ground, i.e. in the perturbation and pre- and post-perturbation steps, as a function of trunk orientation compared with unperturbed step in level ground. Trunk-flexed gaits and accommodation of changes in ground levels are expected to lead to posture- and step-specific main effects on GRF characteristics as compared to the upright walking and level walking, respectively. We hypothesise a systematic change in patterns of GRF as a function of walking posture within each step, however walking with bent postures would demonstrate reduced kinetic adaptations across steps in uneven ground relative to the unperturbed level ground step as altering the trunk angle might facilitate kinematic adaptations to changes in ground level. For example, we expect that the aligned effects of trunk flexed gait and step down on the first GRF peak in the perturbation step and on the second GRF peak in the pre-perturbation step do not simply add up to avoid excessive loads and falling down, respectively.

RESULTS

The data analyzed comprises 768 trials with a total of 2304 step cycles. All healthy young participants on every trial were successful in maintaining their stability (no falls) while traversing the travel path with and without drop. Table 1 summarises posture×step interactions and the main effects of posture and step.

Main effects of posture

With more sagittal trunk flexion (averaging over the steps), the unloading rate (UR) decreased and, less clearly, the first peak in the GRF ($VGRF_{1P}$) increased, while the vertical impulse (VIMP) decreased (Fig. 1 and Fig. 2A, Table 1). More specifically, comparing TF3 gait with regular erect (RE) gait, UR decreased by 21% [to 9.19±0.88 (mean±standard deviation)], $VGRF_{1P}$ increased by 14% (to 1.48±0.18), and VIMP decreased by 8% (to 1.77±0.16) (Fig. 1 and Fig. 2A). For trunk-flexed gaits the loading rate (LR) was generally higher than in RE gait, and the highest LR was observed during walking with 30° sagittal trunk flexion (TF1) gait (13.8±2.17) with an increase of ∼19% relative to RE gait (Fig. 2A). By contrast, increased sagittal trunk flexion did not lead to a change in the braking impulse across gaits (Fig. 2A).

Main effects of step

Only $VGRF_{1P}$, UR and VIMP showed main effects (Table 1) when averaging over the postures, and most effects occurred in the perturbation step (Fig. 2B). Relative to the level step ‘L’, VIMP increased by 4% (to 1.82±0.15), 7% (to 1.87±0.16) and 9% (to 1.90±0.15) for pre-perturbation step ‘U-1’, perturbation step ‘U0’, and post-perturbation step ‘U+1’, respectively, $VGRF_{1P}$ increased by 23% (to 1.63±0.10) for ‘U0’, and UR increased by 9% (to 8.13±1.29) and 10% (to 8.21±1.20) for ‘U0’ and ‘U+1’, respectively (Fig. 2B).

Interaction effects posture by step

Step-dependent effects of posture were detected for the second peak of the vertical GRF ($VGRF_{2P}$), propulsive impulse (PIMP), contact time (T_C) and velocity (Table 1). While in RE gait, $VGRF_{2P}$ first decreased in ‘U-1’ and then increased in ‘U0’, this pattern gradually reversed with increasing trunk flexion (Fig. 3A). Moreover, the pronounced differences in propulsive impulse between steps for RE gait diminished with increasing trunk flexion (Fig. 3B), and differences in contact time decreased in ‘U0’ (Fig. 3C). While velocity remained constant in steps ‘L’ and ‘U-1’ in RE gait, it decreased in trunk-flexed gaits (Fig. 3D).

RE gait showed step-dependent effects for all variables exhibiting interaction except for velocity (Table 1). In contrast, trunk-flexed gaits demonstrated step-dependent effects only for T_C (Table 1). No posture-dependent effects were observed for PIMP and only two for velocity (Table 1). Trunk-flexed gaits consistently showed posture-dependent effects compared with RE gait for $VGRF_{2P}$ (decrease) and less consistently for T_C (decrease, no effect for TF1) (Fig. 3A,C, Table 1). Notably, except for two posture-dependent effects on $VGRF_{2P}$ during steps ‘U0’ and ‘U+1’ in TF3 gait, no effects were found within trunk-flexed gaits (Table 1). T_C and velocity did not show posture-dependent effects in the perturbation step ‘U0’ (Fig. 3C,D, Table 1).

DISCUSSION

In this study, the adaptive kinetic behaviour of able-bodied walking while negotiating uneven ground with altered trunk orientations was investigated. A systematic change of the patterns of GRF as a function of walking posture and step type was observed (Fig. 1). We found step-dependent effects of posture for the second peak of the vertical GRF, propulsive impulse, contact time and velocity (Fig. 3, Table 1). For these variables, simple main effect analysis showed that walking with trunk-flexed gait was associated with reduced changes across steps in uneven ground (perturbation, pre- and post-perturbation steps) compared with upright walking (Table 1). Main effects of posture and step categories on able-bodied walking were observed in the majority of cases, indicating posture- and step-specific GRF characteristics (Fig. 2). In the following paragraphs, the individual main effects of posture and step as well as their interaction effects on the gait kinetics will be discussed in detail.

Posture-dependent kinetic behaviour

Studies on level walking with a trunk-flexed gait have shown that the alteration of trunk kinematics in sagittal plane leads to compensatory kinematic adjustments in lower limbs, which in turn causes changes in the gait kinetics (Saha et al., 2008; Aminiaghdam et al., 2017). Accordingly, our results highlight that the GRF profile varies with an increase of sagittal trunk flexion,

Table 1. Means and standard deviations of kinetic and gait parameters

		Posture				*P*-value/*F*-value		
	Step	RE	TF1	TF2	TF3	Posture	Step	Posture×Step
VGRF_{1P} (BW)	L	1.19±0.08	1.33±0.12	1.38±0.13	1.38±0.14	0.00/17.1	0.00/52.1	0.50/0.76
	U-1	1.24±0.08	1.34±0.11	1.40±0.14	1.40±0.14			
	U0	1.53±0.13	1.63±0.17	1.66±0.20	1.72±0.30			
	U+1	1.25±0.08	1.36±0.12	1.40±0.14	1.41±0.16			
VGRF_{2P} (BW)	L	1.15±0.06	0.96±0.10[a]	0.89±0.10[a]	0.87±0.07[a]	0.00/86.6	0.19/1.65	0.00/8.97
	U-1	*1.06±0.07*	0.96±0.11	0.93±0.13[a]	0.90±0.10[a]			
	U0	**1.19±0.10**	1.01±0.09[a]	0.92±0.12[a]	0.86±0.11[a,b]			
	U+1	**1.20±0.07**	1.00±0.08[a]	0.93±0.10[a]	0.89±0.09[a,b]			
LR (BW/s)	L	10.6±1.70	12.8±1.91	13.5±1.90	12.9±1.72	0.00/9.19	0.13/2.11	0.07/2.37
	U-1	12.3±1.46	14.8±2.11	14.4±3.25	12.6±1.80			
	U0	11.5±1.43	13.5±2.19	12.7±2.63	11.1±1.60			
	U+1	12.0±2.89	14.7±2.70	14.0±3.34	13.2±2.45			
UR (BW/s)	L	9.21±1.25	7.87±1.02	6.94±1.16	6.60±1.17	0.00/22.1	0.00/6.06	0.06/3.11
	U-1	8.89±1.10	8.47±1.44	7.95±1.39	7.65±1.14			
	U0	9.90±0.98	9.11±2.61	7.94±1.72	7.20±0.83			
	U+1	10.0±1.21	8.97±2.67	8.04±1.68	7.51±0.98			
VIMP	L	1.84±0.12	1.75±0.15	1.70±0.14	1.70±0.13	0.00/23.0	0.00/20.9	0.10/2.04
	U-1	1.89±0.13	1.84±0.15	1.80±0.13	1.74±0.15			
	U0	1.96±0.11	1.88±0.16	1.84±0.15	1.80±0.19			
	U+1	2.01±0.12	1.91±0.14	1.87±0.13	1.82±0.16			
BIMP	L	−0.10±0.02	−0.10±0.03	−0.09±0.03	−0.09±0.03	0.55/0.71	0.06/3.33	0.07/2.28
	U-1	−0.11±0.03	−0.11±0.04	−0.12±0.04	−0.11±0.03			
	U0	−0.12±0.02	−0.11±0.02	−0.10±0.02	−0.11±0.02			
	U+1	−0.11±0.02	−0.11±0.02	−0.11±0.02	−0.11±0.02			
PIMP	L	0.13±0.01	0.12±0.01	0.12±0.02	0.13±0.02	0.30/1.26	0.00/8.13	0.00/6.91
	U-1	*0.16±0.02*	0.15±0.02	0.14±0.02	0.14±0.02			
	U0	**0.11±0.02**	0.12±0.02	0.12±0.02	0.13±0.02			
	U+1	**0.13±0.02**	0.13±0.02	0.13±0.02	0.13±0.03			
T_C (s)	L	0.62±0.03	0.59±0.03	0.56±0.03[a]	0.56±0.04[a]	0.00/28/0	0.00/77.9	0.00/4.55
	U-1	0.66±0.03	0.63±0.03	*0.61±0.03*[a]	0.59±0.04[a]			
	U0	**0.59±0.03**	**0.57±0.04**	**0.56±0.03**	0.55±0.05			
	U+1	*0.67±0.03*	*0.64±0.04*	*0.62±0.04*[a]	0.61±0.04[a]			
Velocity (m/s)	L	1.49±0.13	1.61±0.15	1.66±0.17[a]	1.63±0.16	0.00/7.94	0.00/9.14	0.01/3.58
	U-1	1.49±0.11	1.50±0.13	1.53±0.16	1.58±0.16			
	U0	1.59±0.10	1.62±0.11	1.64±0.15	1.65±0.17			
	U+1	1.48±0.08	1.52±0.10	1.59±0.12	1.62±0.15[a]			

The last three columns show the *P*-values/*F*-values for the main effects of posture and step and for the posture×step interaction, respectively. In case of interaction effect, significant differences from RE, TF1 and TF2 across each step are indicated with ‘a’, ‘b’, and ‘c’, respectively ($P<0.05$; one-way ANOVA). Accordingly, italic values indicate significant difference from the unperturbed step ‘L’, bold values from the pre-perturbation step ‘U-1’ and underlined values from the perturbation step ‘U0’ ($P<0.05$) for each walking posture ($N=12$). RE, regular erect trunk; TF1, 30° trunk flexion; TF2, 50° trunk flexion; TF3, maximal trunk flexion; U+1, post-perturbation step.

regardless of ground condition (Fig. 1). The vertical GRF profile tended to be more asymmetric, i.e. greater forces during weight acceptance and attenuated forces during push-off as the trunk leans far forward (Fig. 1). Such right-skewed profiles of vertical GRF exhibited higher weight acceptance loads associated with higher loading rates, a lower push-off associated with lower unloading rates and lower vertical impulses (Figs 1 and 3, Table 1). Such behaviour is consistent with a simple effective leg model of spring-and-damper-in-series (Aminiaghdam et al., 2017). In that study, we have shown that the damper right-skews the GRF by increasing forces after touchdown and decreasing the forces at toe-off leading to an earlier lift-off. Surprisingly, despite remarkable disparities in the morphology of segmented legs between human and bird, experimentally induced pronograde locomotion in human yields kinematic and kinetic effective leg behaviour comparable to those found in birds (Aminiaghdam et al., 2017).

Increased loading rates and lower unloading rates have been found in dysfunctional gait in many studies, for example in patients with Down syndrome (Wu and Ajisafe, 2014), with knee osteoarthritis (Farrokhi et al., 2015; Silva Dde et al., 2015), in elderly female individuals during stair ascent (Hamel et al., 2005) or obese individuals (Pamukoff et al., 2016), and in loaded gait while carrying a back pack (Park et al., 2016). Trunk orientation causes similar effects (Fig. 2A). These changes reflect adaptations of the gait pattern. For example, in both animals and humans, a swift transition from stance to swing is actuated by unloading at higher rates during pre-swing phase (Grillner, 1985; Pearson et al., 1992; Pang and Yang, 2000). Furthermore, the active ankle push-off is responsible for initiating the leg swing in humans (Lipfert et al., 2014). In trunk-flexed walking, this push-off is impaired as judged from the lower VGRF_{2P}, and the unloading rate is lower (Figs 1 and 3A) than in RE gait. Trunk kinematics therefore may be considered as a significant criterion for clinicians not only in the assessment of dysfunctional gait, but also in the design, development and monitoring of the progression of rehabilitation regimes.

Owing to a shorter contact time, the vertical impulse is diminished in the trunk-flexed gaits compared with RE gait (Fig. 2A). This requires a faster swing phase and a higher cadence to support body weight. Such a decrease in vertical impulse has also been observed during level walking while adopting the same bent postures (Aminiaghdam et al., 2017). Moreover, in accordance with our previous study on trunk-flexed level walking, altered trunk

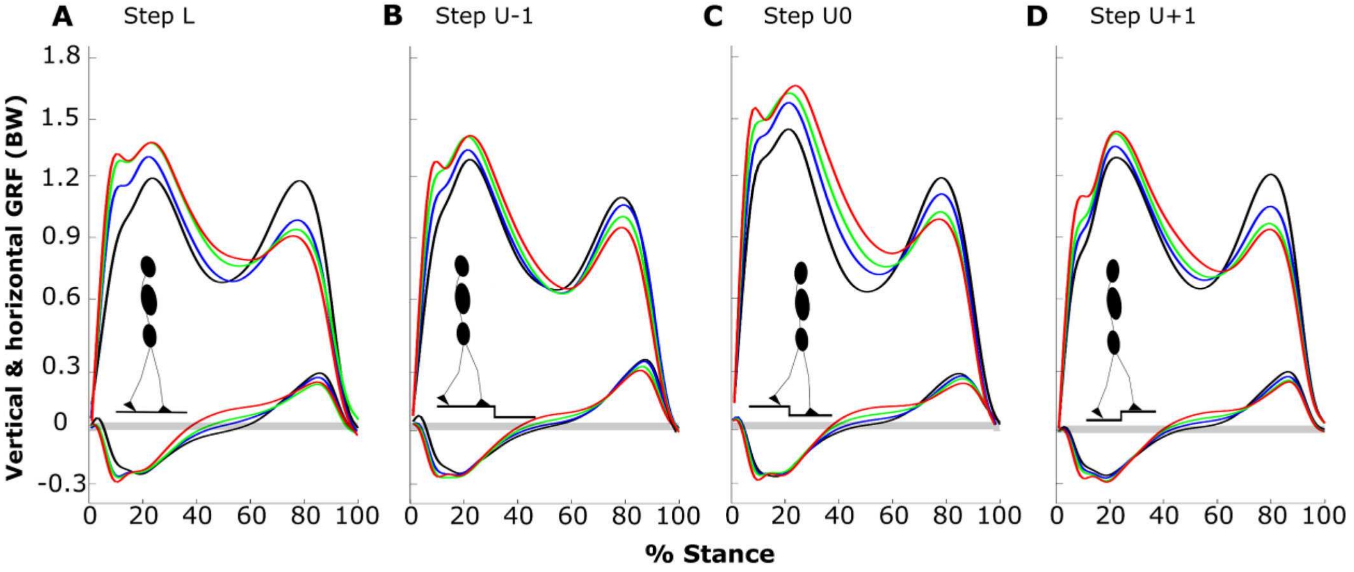

Fig. 1. Ground reaction forces (GRF) for different walking conditions. Shown are ensemble-averaged horizontal and vertical GRFs [normalized to participant body weight (BW)] during unperturbed level step (L, A), pre-perturbation step (U-1, B), perturbation step (U0, C) and post-perturbation step (U+1, D) for RE (black), TF1 (blue), TF2 (green) and TF3 (red) gaits during the stance phase (*N*=12). The contact time is normalized to 100%.

kinematics yielded no change in braking impulse (Fig. 2A, Table 1). There, we demonstrated that an increased sagittal trunk flexion leads to a shorter braking phase relative to the propulsive phase and a greater braking peak force (Aminiaghdam et al., 2017). Hence, the unchanged braking impulse in uneven walking might be the consequence of a combination of a rapid deceleration of the body mass and a greater braking force.

Step-dependent kinetic behaviour

When human walkers become aware of changes in the ground level, e.g. a drop, they adjust their locomotor strategies in the step before the perturbation (Müller and Blickhan, 2010; Müller et al., 2012, 2014, 2016). For the main effect of the step type, our results revealed a significant effect in the pre-perturbation step only in case of the vertical impulse (4% increase relative to level step, Fig. 2B).

The longer flight time associated with the step down led to a greater $VGRF_{1P}$ (16% increase relative to level step) in the perturbation step 'U0'. The greater vertical impulse (9% increase relative to level step) in this step is largely due to a greater vertical GRF as contact time did not significantly extend relative to the level step (Fig. 2B, Table 1). Human walkers with regular upright posture negotiate visible and camouflaged drops in ground using the same strategy, i.e. a shorter contact time and a longer double support (Müller et al., 2014). The observed higher unloading rate in 'U0' (7% increase relative to level step, Fig. 2B) may be due to an earlier landing after a shorter swing phase of the contralateral limb on an elevated surface in the subsequent step along with a slight increase of the vertical GRF at the end of the stance phase (Table 1).

A greater vertical impulse (9% increase relative to level step, Fig. 2B) in post-perturbation step 'U+1' is the result of a significantly longer contact time which is required for the elevation and propulsion of the CoM after the drop (Fig. 2B, Table 1). Moreover, participants were able to produce a greater push-off at the end of the stance phase reflected in increased second peak of the vertical GRF, which led to higher unloading rates (10% increase relative to level step, Fig. 2B).

Interaction of posture and step

Step-specific effects of gaits with different trunk orientations were observed for $VGRF_{2P}$, propulsive impulse, contact time and velocity (Table 1). As hypothesised, among these variables we found reduced kinetic adaptations in trunk-flexed gaits across steps in uneven ground when compared with RE gait (Table 1). This was in agreement with our hypothesis that, in trunk-flexed gaits, the trunk could be utilised to negotiate changes in ground level by straightening during step down. In fact, such straightening is evident in Fig. 4A. In contrast with one of our hypotheses that aligned effects of trunk-flexed gait and step-down on the first GRF peak in the perturbation step do not simply add up to avoid excessive loads, interaction was not strong enough to yield a significant effect across all steps.

As for the two kinetic parameters exhibiting interaction, an increase of trunk flexion led to a decrease in the $VGRF_{2P}$ but no changes in propulsive impulse across gait postures. In comparison to RE gait in the step 'U0', for example, TF3 gait exhibited 28% decrease in the $VGRF_{2P}$ (Figs 1 and 3A, Table 1). Owing to an earlier toe-off at a steeper effective leg angle, the trunk-flexed gait in human and birds is associated with more flexed leg joints and decreased effective leg length at toe-off compared with touchdown (Grillner, 1985; Pearson et al., 1992; Pang and Yang, 2000; Andrada et al., 2014; Aminiaghdam et al., 2017). In fact, such kinematic behaviour yields an inefficient push-off reflected in low $VGRF_{2P}$. Furthermore, a combination of a longer propulsive phase and a lower magnitude of the propulsive force in trunk-flexed gaits resulted in no significant difference in propulsive impulse from normal walking (Fig. 3B, Table 1). In contrast with RE gait, step-dependent effects of posture in trunk-flexed gaits on $VGRF_{2P}$ and propulsive impulse were not observed (Table 1).

For the gait parameters, i.e. contact time and velocity, simple main effects showed that with increasing deviation of the trunk from upright, they become shorter and faster, respectively. Surprisingly, adaptations in the pre-perturbation step led to approximately the same contact time and speed regardless of trunk orientation in the perturbation step (Fig. 3C,D, Table 1). Moreover, walking with different trunk orientations yielded no significant change in velocity

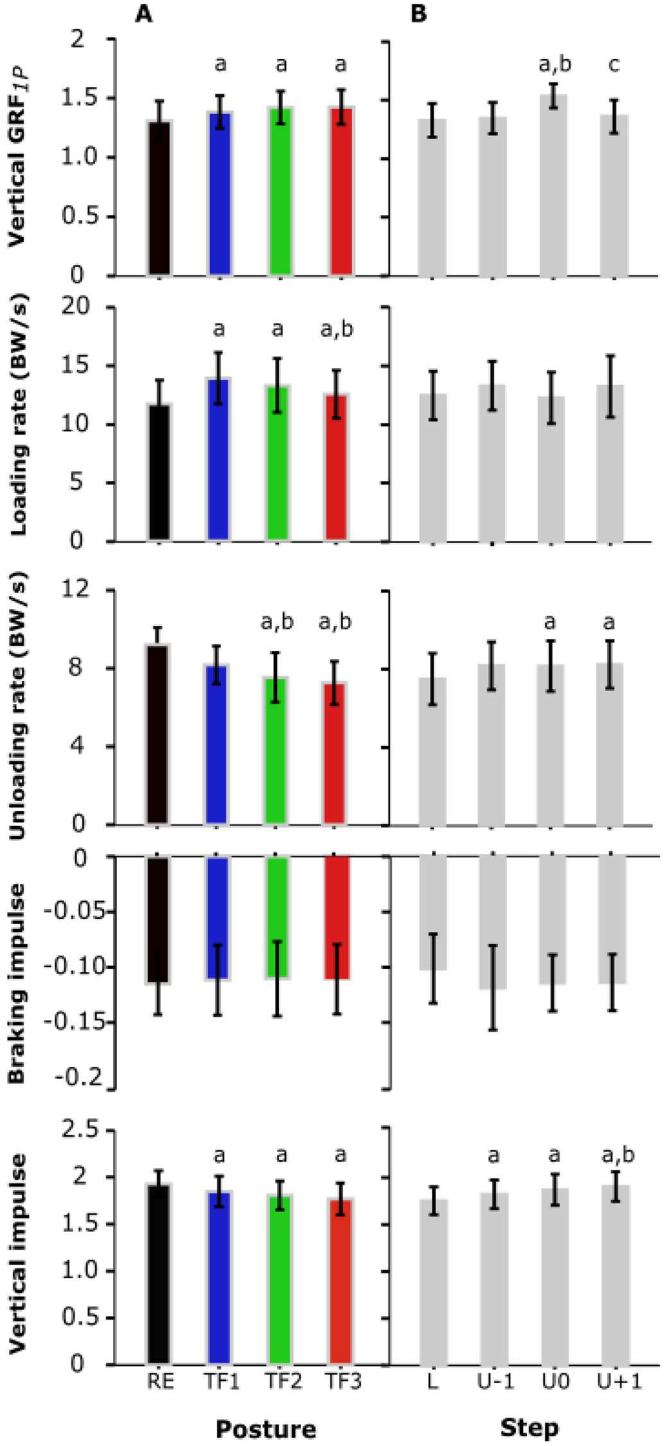

Fig. 2. Main effects of posture and step. Shown are the mean and standard deviations (error bars) for the main effects of posture (A) and step type (B) on the first peak of the vertical GRF, loading rate, unloading rate, braking impulse and vertical impulse (*N*=12). Significant differences from RE, TF1 and TF2 as well as from 'L', 'U-1', and 'U0' are indicated with 'a', 'b', and 'c', respectively ($P<0.05$; one-way ANOVA). RE (black), regular erect trunk; TF1 (blue), 30° trunk flexion; TF2 (green), 50° trunk flexion; TF3 (red), maximal trunk flexion; L, unperturbed level step; U-1, pre-perturbation step; U0, perturbation step; U+1, post-perturbation step.

across steps. This was reflected in braking and propulsive impulses where also no changes were observed during various gait conditions across steps, except in the approach step to the drop where propulsive impulse increased in RE gait (Fig. 3B, Table 1). As a result, individuals performed steady state gaits at each trunk posture. However, except for TF3, in other gaits human walkers performed the post-perturbation step with a longer contact time.

Conclusion

Expanded analysis of walking across uneven ground revealed that GRF parameters were more consistent for trunk-flexed gaits. Pre-adaptations were more pronounced in the approach step to the drop in regular erect gait. This observation is tentatively explained with the role of the trunk. In contrast with walking with upright trunk, in trunk-flexed gaits the trunk may be used in a compensatory way during the step-down to accommodate changes in ground level by adjusting its angle leading to reduced variations in CoM height during traversing uneven ground. Exploitation of this mechanism would resemble the ability of small birds in adjusting their zig-zag-like configured legs to cope with large ground level perturbations.

MATERIALS AND METHODS

Participants

Six males and six females (mean±s.d.; age 26±3.35 years, height 169.75±7.41 cm, mass 65.08±8.07 kg), free from health problems that could affect their walking pattern and trunk motion, were recruited for this study. A consent form was signed by each participant before participation. The experimental protocol was approved by the local Ethics Committee of the Friedrich Schiller University Jena (3532-08/12) and carried out in accordance with the Declaration of Helsinki.

Experimental design and measurements

Data collection was conducted at the Biomechanical Laboratory of the Sports Institute within Friedrich Schiller University Jena. All trials were recorded with eight cameras (240 Hz) by a 3D infrared system (MCU1000, Qualisys, Gothenburg, Sweden) and synchronised by using the trigger of Kistler soft- and hardware. Three consecutive force platforms (9285BA, 9281B, 9287BA, Kistler, Winterthur, Switzerland) embedded in the middle portion of a 12 m-long walkway and sampled at 1000 Hz. 21 markers (spherical retro-reflective surface, 14 mm) defined a 13-body segment model. The markers were placed on the following bony landmarks: fifth metatarsal heads, lateral malleoli, lateral epicondyles of femurs, greater trochanters, anterior superior iliac spines, posterior superior iliac spines, L5-S1 junction, lateral humeral epicondyles, wrists, acromioclavicular joints, seventh cervical spinous process and middle of the forehead (Aminiaghdam et al., 2017).

Participants were asked to walk at their self-selected normal walking speed under four trunk flexion conditions (with no restriction on the arm movements) across two experimental ground conditions involving a level walkway and a walkway with a 10-cm drop: self-selected regular erect trunk alignment (RE), 30° (TF1), 50° (TF2), and maximal trunk flexion (TF3) (Fig. 4A). One height-variable force plate at the site of the second step and two ground-level force plates at the site of the first and third steps were set (Fig. 4B). After walking on the unperturbed uniform track, the variable-height force plate was lowered by 10 cm and participants walked along the uneven walkway. Trunk flexion was achieved by bending from the hips, which allows the most consistent trunk posture among participants (Saha et al., 2008; Aminiaghdam et al., 2017). Under such definition, the TF3 constituted the maximum amount of trunk flexion that the participants could adopt while walking (Fig. 4). Trunk angle was defined by the angle sustained by the line connecting the midpoint between the L5–S1 junction (L5) and the seventh cervical spinous process (C7) with respect to the vertical axis of the lab coordinate system (Müller et al., 2014; Aminiaghdam et al., 2017). Trunk angles were compared visually with adjustable-height cardboard templates by a second examiner prior to performing of each trial and during gait along the walkway for TF1 and TF2. For TF3, there was no comparison. The templates, drawn with angles displaying target trunk flexion angles TF1 and TF2, were hung on a wall parallel to the walkway:

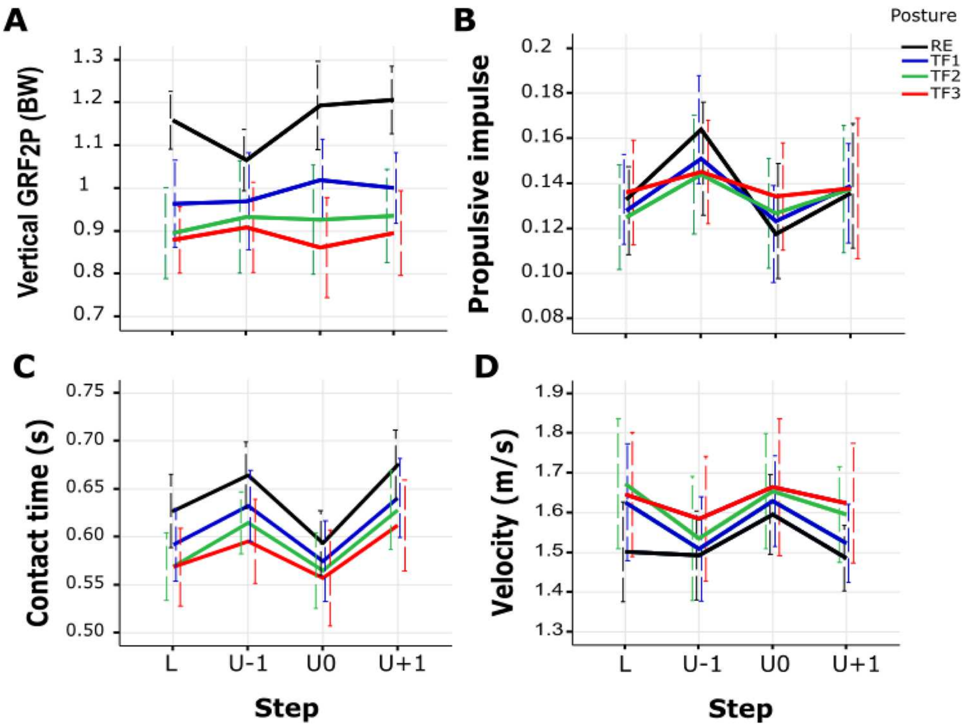

Fig. 3. Posture×step interaction. Shown are posture×step interactions on the second peak of vertical GRF (A), propulsive impulse (B), contact time (C) and velocity (D) (*N*=12). Error bars indicate ±standard deviation. RE, regular erect trunk; TF1, 30° trunk flexion; TF2, 50° trunk flexion; TF3, maximal trunk flexion; L, unperturbed level step; U-1, pre-perturbation step; U0, perturbation step; U +1, post-perturbation step.

one at the beginning and the other one in the middle of the walkway (Saha et al., 2008; Aminiaghdam et al., 2017). Practice trials were permitted to allow participants to accommodate to the locomotion conditions and to secure step onto the force plates. Five out of twelve participants were identified to have a dominant left leg. To eliminate the influence of the dominant leg (Sadeghi et al., 2000), we instructed all participants to hit force plates in left-right-left sequence (Müller et al., 2014). Due to organisational reasons, level and uneven setups as well as repetitions of trunk orientations were not randomised, but the sequence of flexed trunk orientations were randomised per participant. The participants accomplished eight trials per condition in which each foot stepped on a single force plate.

The following parameters of interest were determined across each step: the first peak of the vertical GRF ($VGRF_{1P}$) and the second peak of the vertical GRF ($VGRF_{2P}$); loading rate (LR) and unloading rate (UR) as the slope of vertical GRF between initial heel strike and the $VGRF_{1P}$ and between the $VGRF_{2P}$ and toe-off, respectively; vertical impulse (VIMP) by integrating the vertical GRF, braking impulse (BIMP) and propulsive impulse (PIMP) by integrating the anterior–posterior GRF over the time that the force was oriented in the posterior and anterior directions, respectively, and normalised to the product of body weight and the square root of the quotient of leg length and gravity (Hof, 1996); contact time (T_C) as the time duration between the initial heel strike and toe-off; gait velocity as mean of horizontal velocity of the L5 marker between the initial heel strike and toe-off. For kinetic analysis, GRF was normalised to participant body weight (BW). A vertical GRF threshold of 0.03 BW was used to determine the instants of the initial heel strike and the toe-off at each step.

Data processing and statistics

Kinetic and kinematic data of all successful trials were analysed using custom written Matlab (Mathworks Inc., MA, USA) code. The raw coordinate data were filtered using a fourth-order low-pass, zero-lag Butterworth filter with 12 Hz cut-off frequency (Aminiaghdam et al., 2017). For our normally distributed data, two-way repeated-measures ANOVAs were implemented with SPSS (IBM SPSS Statistics 22, Armonk, NY, USA)

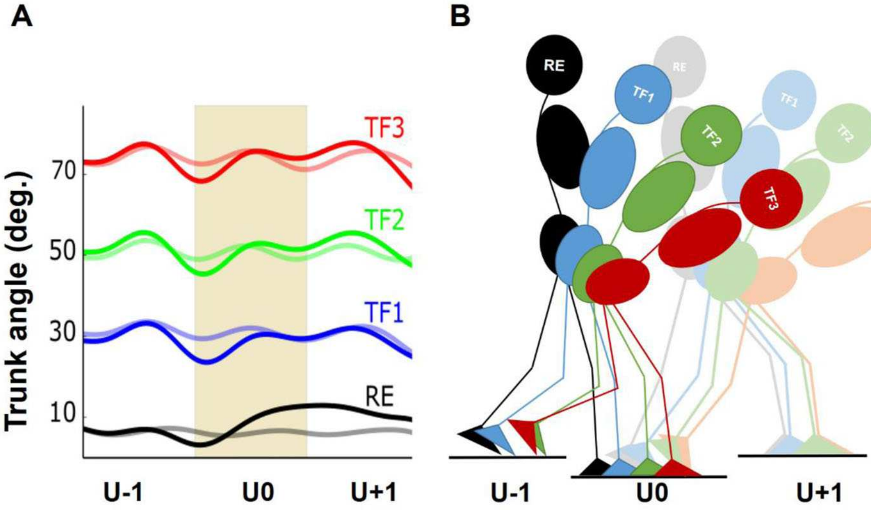

Fig. 4. Trunk kinematics and human locomotion diagram. (A) The trunk kinematics in the sagittal plane across three level (pale lines) and three uneven steps (solid lines) with regular erect (RE, black), 30° trunk flexion (TF1, blue), 50° trunk flexion (TF2, green), maximal trunk flexion (TF3, red) postures. The shaded area, the second step across two setups, separates pre- and post-perturbation steps. (B) Side view of the instrumented walkway with three consecutive force plates denoted by U-1 (pre-perturbation step), U0 (perturbation step) and U+1 (post-perturbation step). The second force plate (drop) was lower by 10 cm in walking on uneven ground.

using two within-participants factors: (1) step category (unperturbed step 'L' during level walking; pre-perturbed 'U-1', perturbed 'U0' and post-perturbation 'U+1' steps during uneven walking), and (2) postures (RE, TF1, TF2 and TF3). The posture×step interaction was evaluated for each dependent variable of interest. Post hoc comparisons were performed using Bonferroni. A *P*-value of $P<0.05$ was considered as statistically significant in all cases. In case of a significant interaction, simple main effects were used to compare walking postures across each step and steps while walking with each posture. In case of a non-significant interaction, the main effects of the posture (averaging across the steps) and the step (averaging across the postures) were evaluated for each variable of interest using one-way ANOVA and post hoc comparisons.

Acknowledgements
The authors thank Reinhard Blickhan for his support in developing the research concept as well as Roy Müller and Johanna Vielemeyer for their valuable contribution in collecting experimental data.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: S.A., C.R.; Methodology: S.A., C.R.; Software: S.A.; Validation: S.A., C.R.; Formal analysis: S.A., C.R.; Investigation: S.A.; Resources: S.A.; Data curation: S.A.; Writing - original draft: S.A.; Writing - review & editing: S.A., C.R.; Visualization: S.A., C.R.; Supervision: S.A., C.R.; Project administration: S.A.

Funding
This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

Data availability
The relevant data associated with our paper has been deposited in Figshare online repository (doi: 10.6084/m9.figshare.5017076).

References

Aminiaghdam, S., Rode, C., Müller, R. and Blickhan, R. (2017). Increasing trunk flexion transforms human leg function into that of birds despite different leg morphology. *J. Exp. Biol.* **220**, 478-486.

Andrada, E., Rode, C., Sutedja, Y., Nyakatura, J. A. and Blickhan, R. (2014). Trunk orientation causes asymmetries in leg function in small bird terrestrial locomotion. *Proc. Biol. Sci.* **281**.

Birn-Jeffery, A. V. and Daley, M. A. (2012). Birds achieve high robustness in uneven terrain through active control of landing conditions. *J. Exp. Biol.* **215**, 2117-2127.

Birn-Jeffery, A. V., Hubicki, C. M., Blum, Y., Renjewski, D., Hurst, J. W. and Daley, M. A. (2014). Don't break a leg: running birds from quail to ostrich prioritise leg safety and economy on uneven terrain. *J. Exp. Biol.* **217**, 3786-3796.

Darling, W. G. and Miller, G. F. (1995). Perception of arm orientation in three-dimensional space. *Exp. Brain Res.* **102**, 495-502.

Farcy, J.-P. C. and Schwab, F. J. (1997). Management of flatback and related kyphotic decompensation syndromes. *Spine* **22**, 2452-2457.

Farrokhi, S., O'Connell, M. and Fitzgerald, G. K. (2015). Altered gait biomechanics and increased knee-specific impairments in patients with coexisting tibiofemoral and patellofemoral osteoarthritis. *Gait Posture* **41**, 81-85.

Foster, A. D., Raichlen, D. A. and Pontzer, H. (2013). Muscle force production during bent-knee, bent-hip walking in humans. *J. Hum. Evol.* **65**, 294-302.

Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* **224**, 127-147.

Gillet, C., Duboy, J., Barbier, F., Armand, S., Jeddi, R., Lepoutre, F.-X. and Allard, P. (2003). Contribution of accelerated body masses to able-bodied gait. *Am. J. Phys. Med. Rehabil.* **82**, 101-109.

Grasso, R., Zago, M. and Lacquaniti, F. (2000). Interactions between posture and locomotion: Motor patterns in humans walking with bent posture versus erect posture. *J. Neurophysiol.* **83**, 288-300.

Grillner, S. (1985). Neurobiological bases of rhythmic motor acts in vertebrates. *Science* **228**, 143-149.

Hamel, K. A., Okita, N., Bus, S. A. and Cavanagh, P. R. (2005). A comparison of foot/ground interaction during stair negotiation and level walking in young and older women. *Ergonomics* **48**, 1047-1056.

Hirasaki, E., Ogihara, N., Hamada, Y., Kumakura, H. and Nakatsukasa, M. (2004). Do highly trained monkeys walk like humans? A kinematic study of bipedal locomotion in bipedally trained Japanese macaques. *J. Hum. Evol.* **46**, 739-750.

Hof, A. L. (1996). Scaling gait data to body size. *Gait Posture* **4**, 222-223.

Kluger, D., Major, M. J., Fatone, S. and Gard, S. A. (2014). The effect of trunk flexion on lower-limb kinetics of able-bodied gait. *Hum. Mov. Sci.* **33**, 395-403.

Leroux, A., Fung, J. and Barbeau, H. (2002). Postural adaptation to walking on inclined surfaces: I. Normal strategies. *Gait Posture* **15**, 64-74.

Leteneur, S., Gillet, C., Sadeghi, H., Allard, P. and Barbier, F. (2009). Effect of trunk inclination on lower limb joint and lumbar moments in able men during the stance phase of gait. *Clin. Biomech.* **24**, 190-195.

Lin, C. J., Guo, L.-Y., Su, F.-C., Chou, Y.-L. and Cherng, R.-J. (2000). Common abnormal kinetic patterns of the knee in gait in spastic diplegia of cerebral palsy. *Gait Posture* **11**, 224-232.

Lipfert, S. W., Gunther, M., Renjewski, D. and Seyfarth, A. (2014). Impulsive ankle push-off powers leg swing in human walking. *J. Exp. Biol.* **217**, 1218-1228.

Malone, A., Kiernan, D., French, H., Saunders, V. and O'Brien, T. (2015). Do children with cerebral palsy change their gait when walking over uneven ground? *Gait Posture* **41**, 716-721.

Marigold, D. S. and Patla, A. E. (2002). Strategies for dynamic stability during locomotion on a slippery surface: effects of prior experience and knowledge. *J. Neurophysiol.* **88**, 339-353.

Marigold, D. S. and Patla, A. E. (2005). Adapting locomotion to different surface compliances: neuromuscular responses and changes in movement dynamics. *J. Neurophysiol.* **94**, 1733-1750.

Marigold, D. S. and Patla, A. E. (2008). Age-related changes in gait for multi-surface terrain. *Gait Posture* **27**, 689-696.

Massion, J., Popov, K., Fabre, J.-C., Rage, P. and Gurfinkel, V. (1997). Is the erect posture in microgravity based on the control of trunk orientation or center of mass position? *Exp. Brain Res.* **114**, 384-389.

Maus, H. M., Lipfert, S. W., Gross, M., Rummel, J. and Seyfarth, A. (2010). Upright human gait did not provide a major mechanical challenge for our ancestors. *Nat. Commun.* **1**, 70.

Mouchnino, L., Aurenty, R., Massion, J. and Pedotti, A. (1993). Is the trunk a reference frame for calculating leg position? *Neuroreport* **4**, 125-127.

Müller, R. and Blickhan, R. (2010). Running on uneven ground: leg adjustments to altered ground level. *Hum. Mov. Sci.* **29**, 578-589.

Müller, R., Ernst, M. and Blickhan, R. (2012). Leg adjustments during running across visible and camouflaged incidental changes in ground level. *J. Exp. Biol.* **215**, 3072-3079.

Müller, R., Tschiesche, K. and Blickhan, R. (2014). Kinetic and kinematic adjustments during perturbed walking across visible and camouflaged drops in ground level. *J. Biomech.* **47**, 2286-2291.

Müller, R., Birn-Jeffery, A. V. and Blum, Y. (2016). Human and avian running on uneven ground: a model-based comparison. *J. R Soc. Interface* **13**.

Pamukoff, D. N., Lewek, M. D. and Blackburn, J. T. (2016). Greater vertical loading rate in obese compared to normal weight young adults. *Clin. Biomech.* **33**, 61-65.

Pang, M. Y. and Yang, J. F. (2000). The initiation of the swing phase in human infant stepping: importance of hip position and leg loading. *J. Physiol.* **528**, 389-404.

Park, J. H., Stegall, P., Zhang, H. and Agrawal, S. (2016). Walking with a backpack using load distribution and dynamic load compensation reduces metabolic cost and adaptations to loads. *IEEE Trans. Neural Syst. Rehabil. Eng*.

Pearson, K. G., Ramirez, J. M. and Jiang, W. (1992). Entrainment of the locomotor rhythm by group Ib afferents from ankle extensor muscles in spinal cats. *Exp. Brain Res.* **90**, 557-566.

Pontzer, H., Raichlen, D. A. and Sockol, M. D. (2009). The metabolic cost of walking in humans, chimpanzees, and early hominins. *J. Hum. Evol.* **56**, 43-54.

Potter, B. K., Lenke, L. G. and Kuklo, T. R. (2004). Prevention and management of iatrogenic flatback deformity. *J. Bone Joint Surg. Am.* **86-A**, 1793-1808.

Sadeghi, H., Allard, P., Prince, F. and Labelle, H. (2000). Symmetry and limb dominance in able-bodied gait: a review. *Gait Posture* **12**, 34-45.

Saha, D., Gard, S. and Fatone, S. (2008). The effect of trunk flexion on able-bodied gait. *Gait Posture* **27**, 653-660.

Sarwahi, V., Boachie-Adjei, O., Backus, S. I. and Taira, G. (2002). Characterization of gait function in patients with postsurgical sagittal (flatback) deformity: a prospective study of 21 patients. *Spine* **27**, 2328-2337.

Schwartz, J. H. (2007). The origins of human bipedalism. *Science* **318**, 1065; author reply 1065.

Shinya, M., Fujii, S. and Oda, S. (2009). Corrective postural responses evoked by completely unexpected loss of ground support during human walking. *Gait Posture* **29**, 483-487.

Silva Dde, O., Briani, R. V., Pazzinatto, M. F., Ferrari, D., Aragão, F. A. and de Azevedo, F. M. (2015). Reduced knee flexion is a possible cause of increased loading rates in individuals with patellofemoral pain. *Clin. Biomech.* **30**, 971-975.

Sockol, M. D., Raichlen, D. A. and Pontzer, H. (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc. Natl. Acad. Sci. USA* **104**, 12265-12269.

Tang, P.-F., Woollacott, M. H. and Chong, R. K. Y. (1998). Control of reactive balance adjustments in perturbed human walking: roles of proximal and distal postural muscle activity. *Exp. Brain Res.* **119**, 141-152.

Thorpe, S. K., Holder, R. L. and Crompton, R. H. (2007). Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* **316**, 1328-1331.

van der Linden, M. H. et al. (2007). Muscle reflexes and synergies triggered by an unexpected support surface height during walking. *J. Neurophysiol.* **97**, 3639-3650.

van der Linden, M. H. et al. (2009). Hitting a support surface at unexpected height during walking induces loading transients. *Gait & Posture* **29**, 255-260.

Van Dieen, J. H., Spanjaard, M., Konemann, R., Bron, L. and Pijnappels, M. (2007). Balance control in stepping down expected and unexpected level changes. *J. Biomech.* **40**, 3641-3649.

Wu, J. and Ajisafe, T. (2014). Kinetic patterns of treadmill walking in preadolescents with and without Down syndrome. *Gait Posture* **39**, 241-246.

Chapter 4

4 Article III

PLoS ONE 12(12): e0190135. https://doi.org/10.1371/journal.pone.0190135

Posture alteration as a measure to accommodate uneven ground in able-bodied gait

Soran Aminiaghdam[1]*, Reinhard Blickhan[2], Roy Müller[3] and Christian Rode[4]

* Correspondent author

Authorship contribution

Role	Contributor
Conceptualization	1; 2; 3
Methodology	1; 2; 3
Software	1
Validation	1; 2; 3; 4
Formal analysis	1
Investigation	1; 2; 4
Resources	2
Data Curation	1; 2; 4
Writing – original draft preparation	1
Writing – review and editing	1; 2; 4
Visualization	1
Supervision	2; 4
Project administration	1
Funding acquisition	No funding

PLOS | ONE

RESEARCH ARTICLE

Posture alteration as a measure to accommodate uneven ground in able-bodied gait

Soran Aminiaghdam*, Reinhard Blickhan, Roy Muller, Christian Rode

Department of Motion Science, Institute of Sport Sciences, Friedrich Schiller University Jena, Jena, Thuringia, Germany

* soran.aminiaghdam@uni-jena.de

Citation: Aminiaghdam S, Blickhan R, Muller R, Rode C (2017) Posture alteration as a measure to accommodate uneven ground in able-bodied gait. PLoS ONE 12(12): e0190135. https://doi.org/10.1371/journal.pone.0190135

Editor: Yury P. Ivanenko, Fondazione Santa Lucia Istituto di Ricovero e Cura a Carattere Scientifico, ITALY

Received: June 2, 2017

Accepted: December 9, 2017

Published: December 27, 2017

Data Availability Statement: Data are available from the figshare repository: https://figshare.com/articles/Posture_alteration_as_a_measure_to_accommodate_uneven_ground_in_able-bodied_gait/5692006 (DOI: 10.6084/m9.figshare.5692006).

Funding: The authors received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist.

Abstract

Though the effects of imposed trunk posture on human walking have been studied, less is known about such locomotion while accommodating changes in ground level. For twelve able participants, we analyzed kinematic parameters mainly at touchdown and toe-off in walking across a 10-cm visible drop in ground level (level step, pre-perturbation step, step-down, step-up) with three postures (regular erect, ~30˚ and ~50˚ of trunk flexion from the vertical). Two-way repeated measures ANOVAs revealed step-specific effects of posture on the kinematic behavior of gait mostly at toe-off of the pre-perturbation step and the step-down as well as at touchdown of the step-up. In preparation to step-down, with increasing trunk flexion the discrepancy in hip−center of pressure distance, i.e. effective leg length, (shorter at toe-off versus touchdown), compared with level steps increased largely due to a greater knee flexion at toe-off. Participants rotated their trunk backwards during step-down (2- to 3-fold backwards rotation compared with level steps regardless of trunk posture) likely to control the angular momentum of their whole body. The more pronounced trunk backwards rotation in trunk-flexed walking contributed to the observed elevated center of mass (CoM) trajectories during the step-down which may have facilitated drop negotiation. Able-bodied individuals were found to recover almost all assessed kinematic parameters comprising the vertical position of the CoM, effective leg length and angle as well as hip, knee and ankle joint angles at the end of the step-up, suggesting an adaptive capacity and hence a robustness of human walking with respect to imposed trunk orientations. Our findings may provide clinicians with insight into a kinematic interaction between posture and locomotion in uneven ground. Moreover, a backward rotation of the trunk for negotiating step-down may be incorporated into exercise-based interventions to enhance gait stability in individuals who exhibit trunk-flexed postures during walking.

Introduction

In addition to investigating a locomotor system operating in steady-state conditions, the study of its behavior when coping with perturbations can lead to further identification of the system

Abbreviations: CoM, centre of mass; CoP, centre of pressure; GRF, ground reaction force; L, unperturbed step in level ground; RE, regular erect trunk; TD, touchdown; TF1, ~30° of trunk flexion; TF2, ~50° of trunk flexion; TO, toe-off; U-1, pre-perturbation step in uneven ground; U0, step-down in uneven ground; U+1, step-up in uneven ground.

properties [1]. During locomotion, human must not only ensure a forward progression in accordance with dynamic equilibrium, but is also required to continuously cope with perturbations—such as postural changes, terrain variations, obstacles, drops, etc.—in an anticipatory fashion through coordinated interactions between different body segments [2, 3]. Maintaining dynamic stability across uneven ground can be a critical issue to locomotion. The gait is assumed stable if it returns to a periodic trajectory after being exposed to a perturbation and it can be considered robustly stable if it can recover from large perturbations [4]. Experimentally imposed trunk flexion [5–7] and changing ground level [8, 9] have been proposed as two types of perturbations to human locomotion.

The trunk plays a key role in human locomotion. It may perform as a reference in the control of posture and movement in upright gait [10, 11]. Stabilizing the trunk, an unstable inverted-pendulum positioned over the hips [12, 13], is a crucial locomotor task. Due to its large mass, the trunk orientation has considerable effects on the ground reaction force (GRF) [14] and the center of mass (CoM) trajectory [5, 7]. The relative position of the hip with respect to the CoM determines the effective leg (connecting the hip and the center of pressure [CoP]) function [5, 15]. A forward inclination of the trunk can be utilized to generate a greater forward propulsion through the hip in various forms of locomotion involving fast walking, uphill gait [16] and stepping up [17]. Furthermore, a backward rotation of the trunk has been observed during step-down, possibly to regulate the whole-body angular momentum [9]. In [5], we speculated that a dynamic backward trunk rotation during trunk-flexed walking may reduce the vertical CoM oscillation in walking across uneven ground. If this speculation can be confirmed, it may find clinical applications benefitting individuals exhibiting trunk-flexed posture and impaired postural control [18, 19].

Bending the trunk forward in level walking leads to an anterior shift of the CoM with respect to the hip. This causes a shorter effective leg at toe-off (TO) than at touchdown (TD; heel strike) [5, 20], and this intra-limb asymmetry increases with trunk flexion [5]. Despite an unchanged effective leg length [5], trunk-flexed gait is associated with a posterior shift of the pelvis relative to the CoP [5, 20], together with crouched legs during the stance phase [5, 7].

While many aspects of human locomotion involving the mechanisms of postural control in the context of unexpected changes in surface conditions [21–26], the effect of trunk posture on gait [5–7, 18, 27–31], and the kinematic and kinetic adjustments during crossing uneven ground [8, 9, 32–36] have been extensively studied, little is known about kinetic and kinematic adaptions in human locomotion over uneven ground with altered trunk orientation. In a recent study [37] focusing on kinetic adjustments in walking across uneven ground, we found reduced between-step variations in the GRF patterns with increasing trunk flexion. We expect the compensatory kinematic strategies that enable the observed reduced between-step kinetic effects when walking with trunk-flexed gaits across uneven ground. Coping with such gait conditions is likely to present different challenges compared to upright postures. Understanding these challenges is of clinical interest as age or some pathological conditions can alter the trunk posture and the adaptive capacity of human locomotor system [38–42].

Considering an altered dynamics of the trunk-flexed gaits from regular upright walking [5–7, 18, 27, 28, 31], the context-specific kinetic and kinematic adaptations during walking and the intra-limb kinetic and kinematic asymmetries in leg function at TD and TO as a result of an increased sagittal trunk flexion [5], this study aims at examining the adaptive locomotor kinematic behavior in perturbed steps (10 cm visible drop; level step, pre-perturbation step, step-down, step-up) while walking with three postures (regular erect, with ~30° and ~50° trunk flexion from the vertical). We expect step-specific effects of imposed trunk posture on kinematic parameters of human walking, with more pronounced adaptations at TO since a posterior shift of the hip relative to the CoM during trunk-flexed gaits leads to a shorter effective leg at TO than at TD and correspondingly to a flatter leg angle at TD and a steeper one at TO. Furthermore, we hypothesize that the kinematic adaptations across steps would be posture-dependent, i.e. more pronounced kinematic adjustments during trunk-flexed gaits that may be necessary for maintaining balance, and that these adaptations would affect the vertical oscillation of the CoM. Specifically, we hypothesize that participants exploit a backward rotation of the trunk during step-down to reduce effects of the step-down on the CoM height. Finally, we expect a robustly stable walking, i.e. an immediate restoration of the kinematic parameters at the end of the step-up following the step-down, despite alteration in the trunk posture owing to the adaptive capacity of the locomotor system in young healthy participants.

Materials and methods

Participants

Twelve (six males, six females) healthy volunteers (mean ± SD; age = 26 ± 3.35 years, height = 169.75 ± 7.41 cm, mass = 65.08 ± 8.07 kg) with no history of orthopedic (leg length discrepancy, joint fracture, joint laxity, arthritis), musculoskeletal and neurologic disorders participated in this study. Lower limb range of motion was not assessed. A consent form was signed by each participant before participation. The experimental protocol was approved by the local Ethics Committee of the Friedrich Schiller University Jena (3532-08/12) and carried out in accordance with the Declaration of Helsinki.

Experimental design and measurements

Kinematic data was collected using eight infra-red Qualisys motion capture cameras (MCU1000, Qualisys, Gothenburg, Sweden) sampling at 240 Hz. GRFs during walking were measured at 1000 Hz using three consecutive force platforms (9285BA, 9281B, 9287BA, Kistler, Winterthur, Switzerland), embedded in the middle portion of a 12 m-long walkway. Kinematics and GRF data were synchronized by using the Kistler's external trigger and BioWare data acquisition software (Kistler Instrument AG, Winterthur, Switzerland). Data collection was conducted at the Biomechanical Laboratory of the Sports Institute within Friedrich Schiller University Jena. Spherical retro-reflective surface markers (14 mm) were used to track the motion of the body. A thirteen-body segment model [5] was defined using 21 markers. The markers were placed on the following bony landmarks: fifth metatarsal heads, lateral malleoli, lateral epicondyles of femurs, greater trochanters, anterior superior iliac spines, posterior superior iliac spines, L5-S1 junction, lateral humeral epicondyles, wrists, acromioclavicular joints, seventh cervical spinous process and middle of the forehead.

Participants were instructed to walk at their self-selected normal walking speed (Fig 1) (with no restriction on the arm movements) across two experimental ground conditions involving a level walkway and a walkway with a 10 cm drop for each of the three conditions: self-selected regular erect trunk alignment (RE), 30° (TF1) and 50° (TF2) (Fig 2). One height-variable force plate at the site of the second contact and two ground-level force plates at the site of the first and third contacts were set (Fig 2A). After walking on the unperturbed level track, the variable-height force plate was lowered by 10 cm and participants walked along the uneven walkway. To determine the most consistent trunk posture across participants, trunk flexion was achieved by bending from the hips [5, 7, 37]. Trunk angle was defined by the angle sustained by the line connecting the L5 marker (midpoint between the L5–S1 junction) and the C7 marker (seventh cervical spinous process) with respect to the vertical axis of the lab coordinate system (Fig 2B) [5, 9, 37]. A co-examiner compared trunk angles (TF1 and TF2) visually with adjustable-height cardboard templates prior to performing of each trial and during gait along the walkway. The templates, drawn with lines displaying target trunk flexion

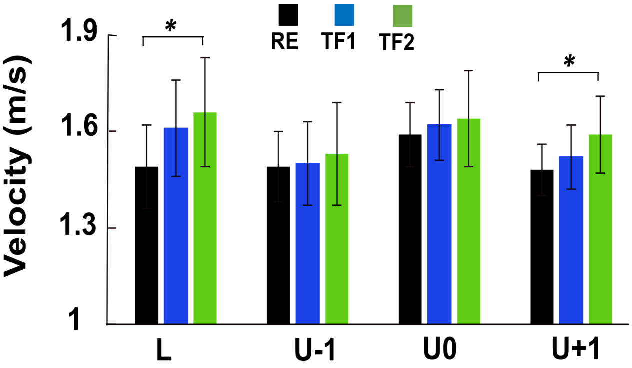

Fig 1. Gait velocity across steps and postures. Simple main effect analysis showed that participants walked with an increased velocity during gait with 50˚ of trunk flexion (TF2) in unperturbed step (p = 0.02) and step-up (p = 0.03) as compared to the gait with regular upright posture (RE); however, there were no between step differences when walking with RE (p = 0.51), TF1 (p = 0.55) and TF2 (p = 0.11). Error bars denote standard deviation. RE, regular erect trunk; TF1, ~30˚ trunk flexion; TF2, ~50˚ trunk flexion; L, unperturbed level step; U-1, pre-perturbation step; U0, step-down; U+1, step-up.

https://doi.org/10.1371/journal.pone.0190135.g001

angles TF1 and TF2, were hung on a wall parallel to the walkway: one at the beginning and the other one in the middle of walkway [5, 7, 37]. Participants were encouraged to walk along the walkway to accommodate to the locomotion conditions and secure step onto the force plates. The dominant lower limb was defined based on participants' verbal report of which limb they use to kick a soccer ball [43]. To simulate the natural situation of arbitrary step-down with respect to limb dominance [44], we defined a left-right-left sequence thus making sure that some participants stepped down with the dominant limb (n = 7), some not (n = 5) [9]. Due to

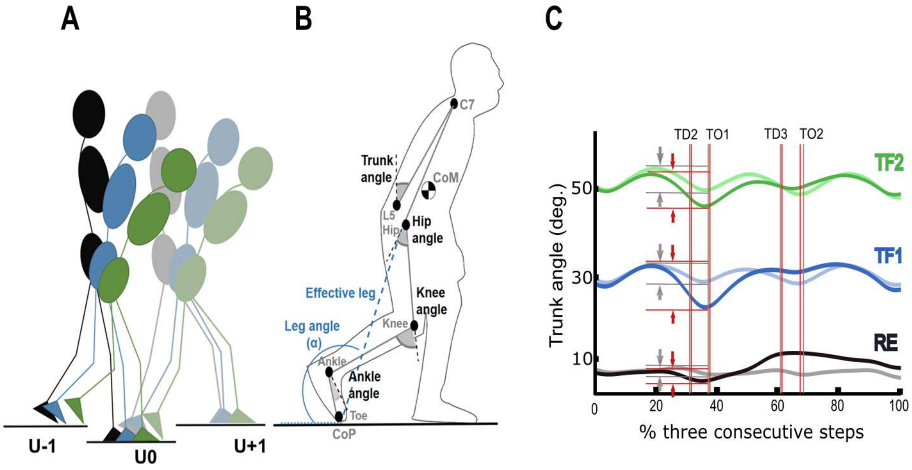

Fig 2. Human locomotion diagram and trunk angle trajectories. (A) Side view of the instrumented walkway with three consecutive force plates. The second force plate (step-down) was lowered 10 cm during uneven walking with RE, TF1 and TF2 conditions. (B) Illustration of the definitions of the trunk angle as well as hip, knee, and ankle joint angles, the effective leg and the leg angle as used in this study. (C) The trunk kinematics in the sagittal plane across three level steps (blurred curves) and three uneven steps (solid curves) with regular erect (RE, black), ~30˚ of trunk flexion (TF1, blue) and ~50˚ of trunk flexion (TF2, green) during walking. The vertical grey and red lines represent TD and TO instants pertaining to the three consecutive steps during level and uneven walking, respectively. The horizontal grey and red lines highlight the maximum of the trunk angle in the step 'U-1' and the minimum of the trunk angle in the step 'U0' for each walking postures, respectively. L, unperturbed level step; U-1, pre-perturbation step; U0, step-down; U+1, step-up; CoM, center of mass; α, leg angle; CoP, center of pressure; TD, touchdown; TO, toe-off.

https://doi.org/10.1371/journal.pone.0190135.g002

organizational reasons, level and uneven setups as well as repetitions of trunk orientations were not randomized, but the sequence of flexed trunk orientations were randomized per participant. While maintaining each gait posture, the participants performed eight successful trials in which each single force plate was cleanly struck by one foot.

Parameters of interest

The ensemble average of following parameters of interest, in addition to their angular trajectories throughout stance phase of each individual step, were determined in the sagittal plane: 1) hip, knee and ankle joint angles (Fig 2B) at the instants of TD and TO; 2) effective leg length, defined as the length between the hip and CoP (Fig 2B), at the instants of TD (EL_{TD}) and TO (EL_{TO}); 3) vertical position of the CoM at the instants of TD (CoM_{TD}) and TO (CoM_{TO}) relative to the ground determined by the body segmental analysis method relative to the laboratory coordinate system [45, 46]; 4) leg angle, angle between effective leg and ground (Fig 2B), at the instants of TD (α_{TD}, angle of attack) and TO (α_{TO}) was calculated with respect to the negative x-axis. A vertical GRF threshold of 0.03 body weight was used to determine the instants of TD and TO at each contact [5]. The effective leg length and CoM were both normalized to the distance between the greater trochanter marker and the lateral malleoli marker at the instant of TD. Backward rotation during step-down was calculated as the difference of the maximum of the trunk angle in 'U-1' and the minimal trunk angle in 'U-0' (Fig 2C).

Data processing and statistics

Kinetic and kinematic data of all successful trials were analyzed using custom written Matlab (Mathworks Inc., MA, USA) code. The raw coordinate data were filtered using a fourth-order low-pass, zero-lag Butterworth filter with 12 Hz cutoff frequency [5, 37].

Prior to analysis Levene's test and Shapiro-Wilk test were performed to examine equality of variance and normality of distribution, respectively. We analyzed all data sets using a two-way repeated measures ANOVA to examine the effects of the posture (RE, TF1 and TF2) and step (unperturbed step 'L' in level ground; pre-perturbation step 'U-1', step-down 'U0' and step-up 'U+1' across uneven ground) on the vertical position of the CoM, the effective leg length and angle, and the lower limb joints (hip, knee and ankle) at TD and TO instants. In case of a significant interaction, simple main effects were used to compare walking postures across each step, as well as across steps while walking with each individual posture using one-way ANOVA and post-hoc comparisons with Bonferroni adjustments for multiple comparisons. In case of a non-significant interaction, the main effects of the posture and step were evaluated on each dependent variable of interest. Where Mauchly's test indicated a violation of sphericity, p-values and degrees of freedom were corrected using the Greenhouse–Geisser correction factor. Furthermore, paired t-tests (using mean values per subject) were used to compare backward rotation of the trunk in level and perturbed (step-down) walking for each trunk inclination. All statistical analyses were performed with SPSS Statistics 21 (IBM Corporation, New York, NY, USA). The statistical significance level of all tests was set to $p = 0.05$.

Results

The data analyzed includes 576 trials with a total of 1728 step cycles. Participants were successful in maintaining their stability (no falls) on every trial while crossing the level and uneven ground. Table 1 shows the mean trunk angles at TD and TO across steps while maintaining trunk postures. Mean trunk backward rotations during step down were significantly higher than those for level steps across all gait conditions (Fig 2C). The backward rotation in RE gait increased from 3.5 ± 0.8° during level walking to 5.7 ± 1.9° during step-down (t = 3.89,

Table 1. Means and standard deviations of kinematic parameters.

	Step	Posture			p-value/F-value		
					ES		
		RE	TF1	TF2	Posture	Step	Posture × Step
Trunk$_{TD}$ (deg)	L	6.2±3.4	30.4±6.2	47.3±6.9			
	U-1	6.1±3.3	29.8±6.3	46.6±5.2			
	U0	5.2±5.6	26.2±6.5	43.8±5.9			
	U+1	12.6±4.4	32.6±6.7	48.9±3.9			
Trunk$_{TO}$ (deg)	L	5.0±3.4	29.7±5.1	45.9±7.6			
	U-1	5.2±5.4	23.9±10.1	43.1±3.9			
	U0	11.5±5.0	24.2±13.1	49.1±6.2			
	U+1	7.5±5.4	27.0±11.3	46.2±4.0			
Normalized CoM$_{TD}$	L	1.12±0.02	1.10±0.02	1.08±0.02	0.00/120	0.00/144	0.00/5.96
	U-1	1.12±0.02	1.07±0.08	1.07±0.02			
	U0	1.16±0.03	**1.14±0.03**	**1.11±0.03^{a}**	0.95	0.96	0.49
	U+1	**1.06±0.02**	1.05±0.02	**1.04±0.03**			
Normalized CoM$_{TO}$	L	1.12±0.02	1.10±0.02	1.08±0.02	0.00/42.5	0.00/105	0.69/0.64
	U-1	1.05±0.03	1.02±0.03	1.01±0.03			
	U0	1.17±0.02	1.15±0.03	1.13±0.03	0.87	0.94	0.09
	U+1	1.11±0.04	1.11±0.06	1.08±0.06			
Normalized EL$_{TD}$	L	1.14±0.03	1.16±0.03	1.16±0.03	0.01/6.24	0.00/15.1	0.04/3.97
	U-1	1.14±0.04	1.15±0.04	1.15±0.03			
	U0	1.14±0.02	1.14±0.03	1.13±0.03	0.51	0.71	0.39
	U+1	**1.08±0.02**	**1.10±0.03**	**1.10±0.02**			
Normalized EL$_{TO}$	L	1.12±0.03	1.10±0.02	1.09±0.03	0.00/7.16	0.00/37.3	0.00/5.69
	U-1	1.07±0.02	1.04±0.01^{a}	1.01±0.02^{a,b}			
	U0	**1.15±0.03**	**1.15±0.03**	**1.14±0.03**	0.54	0.86	0.48
	U+1	1.10±0.03	**1.09±0.04**	**1.07±0.05**			
Hip$_{TD}$ (deg)	L	19.9±3.4	43.3±4.0^{a}	53.5±8.2^{a,b}	0.00/458	0.00/19.5	0.00/28.6
	U-1	20.4±3.9	37.4±8.7^{a}	53.5±8.2^{a,b}			
	U0	15.9±3.4	39.1±8.3^{a}	51.0±6.9^{a,b}	0.99	0.83	0.87
	U+1	**37.7±4.9**	42.7±4.4	53.4±7.2^{a}			
Hip$_{TO}$ (deg)	L	-12.4±5.0	11.9±7.4^{a}	24.6±9.9^{a,b}	0.00/145	0.33/1.24	0.00/7.89
	U-1	-13.0±8.0	11.0±9.2^{a}	24.9±9.6^{a,b}			
	U0	-8.0±4.1	11.3±8.9^{a}	20.6±8.5^{a}	0.97	0.23	0.66
	U+1	-13.1±6.7	11.7±8.4^{a}	22.9±9.2^{a}			
Knee$_{TD}$ (deg)	L	9.6±4.0	10.8±3.5	10.7±5.3	0.00/9.37	0.00/31.7	0.00/12.9
	U-1	9.7±5.3	10.7±5.6	12.2±5.7			
	U0	14.1±5.6	15.6±6.0	16.3±5.8	0.70	0.88	0.76
	U+1	**29.2±5.4**	**22.8±8.4**	**21.1±8.1**			
Knee$_{TO}$ (deg)	L	40.5±6.3	45.7±6.5	50.4±6.1^{a}	0.00/9.67	0.00/31.1	0.00/5.27
	U-1	51.5±10.6	61.4±9.2	70.6±7.0^{a}			
	U0	**30.7±3.6**	**30.2±4.5**	**32.9±4.0**	0.70	0.88	0.56
	U+1	**37.2±10.4**	**43.6±12.6**	**50.2±7.0^{a}**			
Ankle$_{TD}$ (deg)	L	-1.6±2.3	2.1±2.2^{a}	2.7±1.9^{a}	0.15/2.41	0.88/0.21	0.00/3.72
	U-1	-1.5±3.0	1.4±2.5	2.6±2.5^{a}			
	U0	-2.0±10.9	-4.7±15.2	**-8.5±17.3**	0.37	0.05	0.48
	U+1	1.4±3.1	3.3±2.9	3.1±3.3			

(*Continued*)

Table 1. (*Continued*)

	Step	Posture			p-value/F-value		
					ES		
		RE	TF1	TF2	Posture	Step	Posture × Step
Ankle$_{TO}$ (deg)	L	-14.9±6.2	-11.5±2.5	-9.8±4.3	0.29/1.42	0.00/12.3	0.13/1.85
	U-1	-2.5±7.2	-2.1±4.4	-2.3±4.6			
	U0	-18.5±3.0	-16.6±3.2	-13.3±5.5	0.26	0.75	0.31
	U+1	-13.7±7.6	-11.8±3.0	-9.5±4.2			
α_{TD} (deg)	L	66.5±4.6	62.6±5.1	62.2±6.3	0.01/6.52	0.55/0.71	0.37/1.12
	U-1	65.0±4.7	63.1±4.4	59.9±7.9			
	U0	65.6±2.5	63.9±4.4	63.9±3.2	0.52	0.10	0.15
	U+1	64.6±2.9	64.0±2.8	63.4±2.7			
α_{TO} (deg)	L	117±2.7	116±5.9	116±7.3	0.09/2.92	0.00/33.0	0.84/0.44
	U-1	119±2.1	120±2.4	120±5.1			
	U0	120±2.8	119±4.6	120±3.0	0.32	0.84	0.06
	U+1	116±2.9	111±3.1	110±2.9			

The last three columns show the p-values/F-values and effect size (ES, partial eta squared) of the main effects of posture and step and, the posture×step interaction, respectively. In case of interaction effect, significant differences from RE and TF1 across each step are indicated with 'a' and 'b', respectively ($p<0.05$). Accordingly, shaded, bold and underlined values indicate the significant difference from the unperturbed step 'L', from the pre-perturbation step 'U-1' and from the step-down 'U0' ($p<0.05$), respectively, for each walking posture (N = 12). CoM, center of mass; TD, touchdown; TO, toe-off; EL_{TD}, normalized effective leg length at TD; EL_{TO}, normalized effective leg length at TO; α_{TD}, leg angle at TD; α_{TO}, leg angle at TO; RE, regular erect trunk; TF1, ~30° trunk flexion; TF2, ~50° trunk flexion; U+1, step-up.

https://doi.org/10.1371/journal.pone.0190135.t001

p = 0.003), in TF1 from 4.8 ± 3.4° to 14.9 ± 10.9° (t = 2.95, p = 0.01) and in TF2 gait from 5.6 ± 2.4° to 9.9 ± 3.4° (t = 4.62, p = 0.001).

Table 1 summarizes posture×step interactions and the main effects of posture and step on kinematic parameters. Two-way repeated measures ANOVAs indicated step-specific effects of the trunk orientation on normalized vertical position of the CoM at TD (CoM_{TD}) (Fig 3H), normalized effective leg length at TD (EL_{TD}) (Fig 3A) and TO (EL_{TO}) (Fig 3B), hip angle at TD (Hip_{TD}) (Fig 3C) and TO (Hip_{TO}) (Fig 3D), knee angle at TD ($Knee_{TD}$) (Fig 3E) and TO ($Knee_{TO}$) (Fig 3F) and ankle joint at TD ($Ankle_{TD}$) (Fig 3G).

Post-hoc tests revealed no significant differences of EL_{TD} and EL_{TO} between gait postures during unperturbed level step 'L' (Figs 3A, 3B and 4A, Table 1). In the pre-perturbation step 'U-1', while EL_{TD} exhibited no significant changes across gait postures and compared to the corresponding level steps, significantly lower EL_{TO} compared to the level steps was found in all gait postures with a decreased EL_{TO} by ~3% and ~6% from RE gait to 1.04 ± 0.02 and 1.01 ± 0.02 in TF1 and TF2 gaits, respectively (Figs 3A, 3B and 4B, Table 1). During the step-down 'U0', EL_{TD} remained relatively unchanged as compared to the corresponding level steps and showed no between gait posture differences. Trunk-flexed gaits (TF1 and TF2) demonstrated a significantly elongated effective leg at TO (EL_{TO}) after step-down compared with corresponding values of both 'L' and 'U-1' steps with no between gait posture differences (Figs 3A, 3B and 4C, Table 1). Significantly shortened EL_{TD} in the step-up 'U+1'compared to all preceding steps in all gait postures with no between gait posture differences was found (Figs 3A and 4D, Table 1). EL_{TO} demonstrated a significant increase in trunk-flexed gaits relative to the step 'U-1' and a significant decrease compared to the step 'U0' regardless of the trunk orientation (Figs 3B and 4D, Table 1).

The tests of simple main effects revealed that trunk-flexed gaits demonstrated an increased Hip_{TD} and Hip_{TO} across all steps with no between step differences except for the RE gait in the

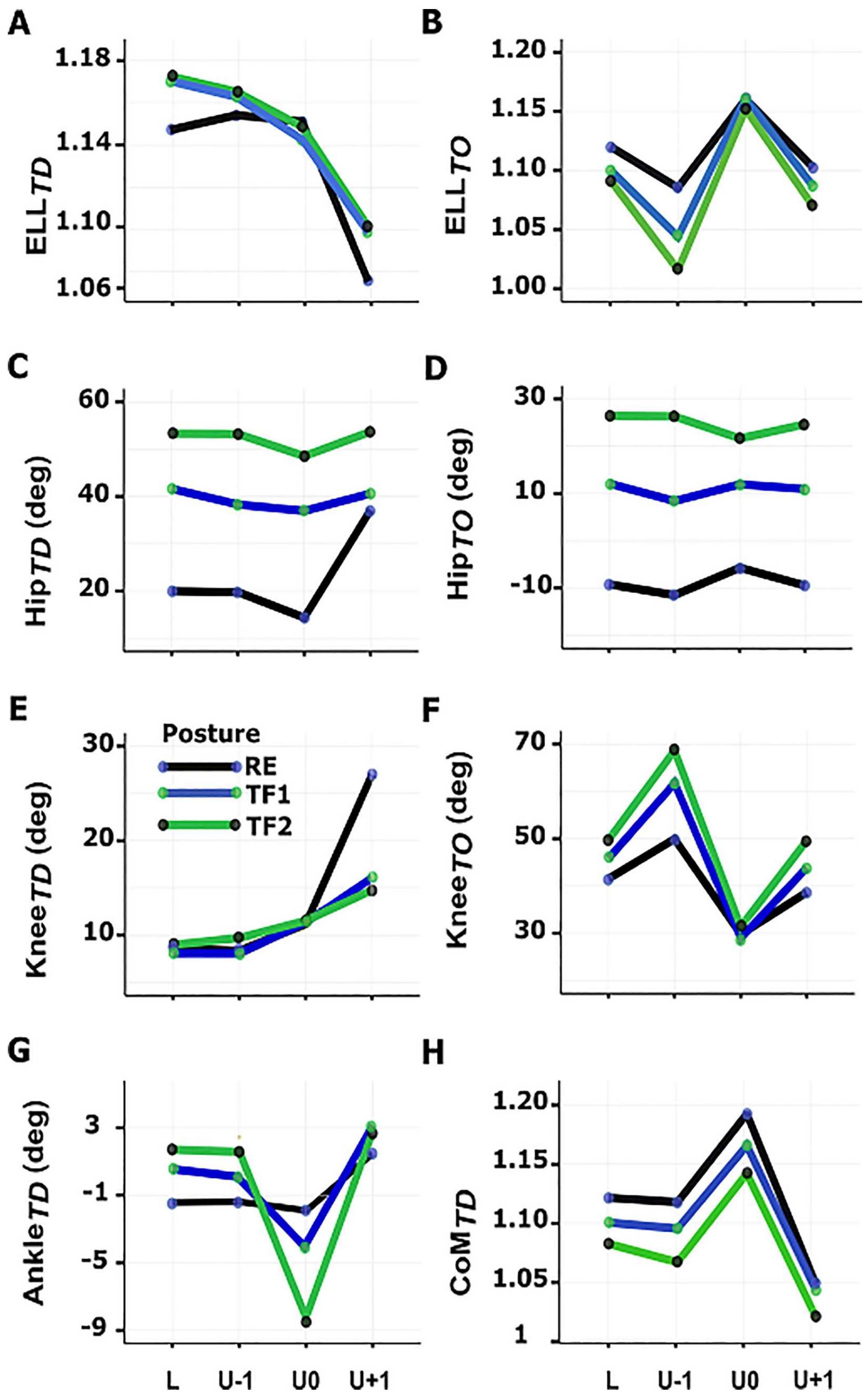
A
ELL*TD*
1.18
1.14
1.10
1.06
B
ELL*TO*
1.20
1.15
1.10
1.05
1.00
C
Hip*TD* (deg)
60
40
20
D
Hip*TO* (deg)
30
10
-10
E
Knee*TD* (deg)
30
20
10
Posture
RE
TF1
TF2
F
Knee*TO* (deg)
70
50
30
G
Ankle*TD* (deg)
3
-1
-5
-9
H
CoM*TD*
1.20
1.15
1.10
1.05
1
L
U-1
U0
U+1
L
U-1
U0
U+1

Fig 3. Posture×step interaction. (A)Normalized effective leg length at TD, (B) normalized effective leg length at TO, (C) hip position at TD, (D) hip position at TO, (E) knee position at TD, (F) knee position at TO, (G) ankle position at TD and (H) normalized CoM position at TD. (N = 12). RE, regular erect trunk; TF1, ~30˚ trunk flexion; TF2, ~50˚ trunk flexion; L, unperturbed level step; U-1, pre-perturbation step; U0, step-down; U+1, step-up.

https://doi.org/10.1371/journal.pone.0190135.g003

step 'U+1' where the hip flexion increased by ~18˚ compared to the step 'L' (Figs 3C, 3D and 4, Table 1).

For the Knee$_{TD}$, no between step and between posture differences were found except for the step 'U+1' where the knee flexion dramatically increased in all gait postures compared to the preceding corresponding steps with no between posture differences (Figs 3E and 4, Table 1). In the step 'L', TF2 gait led to a significant increase of ~10˚ in Knee$_{TO}$ compared to the RE gait (Figs 3F and 4A, Table 1). Significantly increased Knee$_{TO}$ in the step 'U-1' compared to the corresponding level steps was found regardless of the gait posture with a significant increase of the ~20˚ in TF2 gait relative to the step 'L' (Figs 3F and 4B, Table 1). In the step 'U0', the Knee$_{TO}$ decreased across gait postures. Trunk-flexed gaits demonstrated a significantly decreased knee flexion compared to the both steps 'L' and 'U-1' with no between posture differences (Figs 3F and 4C, Table 1). During the step 'U+1', participants increased their Knee$_{TO}$ which was found to be significantly lower from those during 'U-1' and significantly higher from that of step 'U0' in trunk-flexed gaits. In this step, TF2 gait was associated with an increase of ~13˚ in Knee$_{TO}$ compared with RE gait (Figs 3F and 4D, Table 1).

In the step 'L', trunk-flexed gaits demonstrated an increased Ankle$_{TD}$ (Figs 3G and 4A, Table 1). Significantly increased ankle flexion (dorsiflexion) was observed in TF2 gait compared with RE gait in the step 'U-1'(Figs 3G and 4B, Table 1). TF2 gait was associated with a significant increase of plantarflexion relative to the steps 'L' and 'U-1' but not significantly different from RE and TF1 gaits during the step 'U0'(Figs 3G and 4C, Table 1). In the step 'U+1', Ankle$_{TD}$ showed a significant increase only with respect to the step 'U-1' with no between posture differences (Figs 3G and 4D, Table 1).

As indicated by the analysis of simple main effects, during steps 'L' and 'U-1', no between step and between gait posture differences for CoM$_{TD}$ were found (Figs 3H, 4A and 4B, Table 1). In the step 'U0', trunk-flexed gaits compared with step 'U-1' represented a significant increase of CoM$_{TD}$ with a significant decrease of ~4% to 1.11 ± 0.03 from RE gait to TF2 gait (Figs 3H and 4C, Table 1). CoM$_{TD}$ demonstrated a significant decrease in the step 'U+1' in all gait postures relative to the preceding corresponding steps with no between gait posture differences (Figs 3H and 4D, Table 1).

Significant main effects of posture for the normalized vertical position of the CoM at TO (CoM$_{TO}$) and the leg angle at TD (α_{TD}) and of step for the CoM$_{TO}$, the leg angle at TO (α_{TO}) and the ankle joint at TO (Ankle$_{TO}$) were found (Fig 5, Table 1). For posture factor, as compared to the RE gait, CoM$_{TO}$ was decreased by ~2% in TF1 and by ~3% in TF2 (Fig 5A, Table 1), and leg angle at TD (α_{TD}) was decreased by ~3˚ in TF2 (Fig 5B, Table 1). For the main effect of step, compared to the step 'L', while CoM$_{TO}$ did not significantly change in the step 'U+1', in the step 'U-1' decreased by ~7% and increased by ~5% in the step 'U0' (Fig 5C, Table 1). α_{TO} was increased by 6˚ in the steps 'U-1' and 'U0'. In the step 'U+1', α_{TO} was decreased by 10˚ relative to the steps 'U-1' and 'U0' and not significantly different from the step 'L' (Fig 5D, Table 1). Ankle$_{TO}$ was decreased by ~9˚ in the step 'U-1' and was increased by ~14˚ and ~8˚ in the steps 'U0' and 'U+1', respectively, relative to the step 'U-1' (Fig 5E, Table 1).

Discussion

Considering the frequent occurrence of trunk-flexed locomotion (e.g. in elderly and patients with spinal pathologies) and its detrimental effect on gait stability, understanding the role of

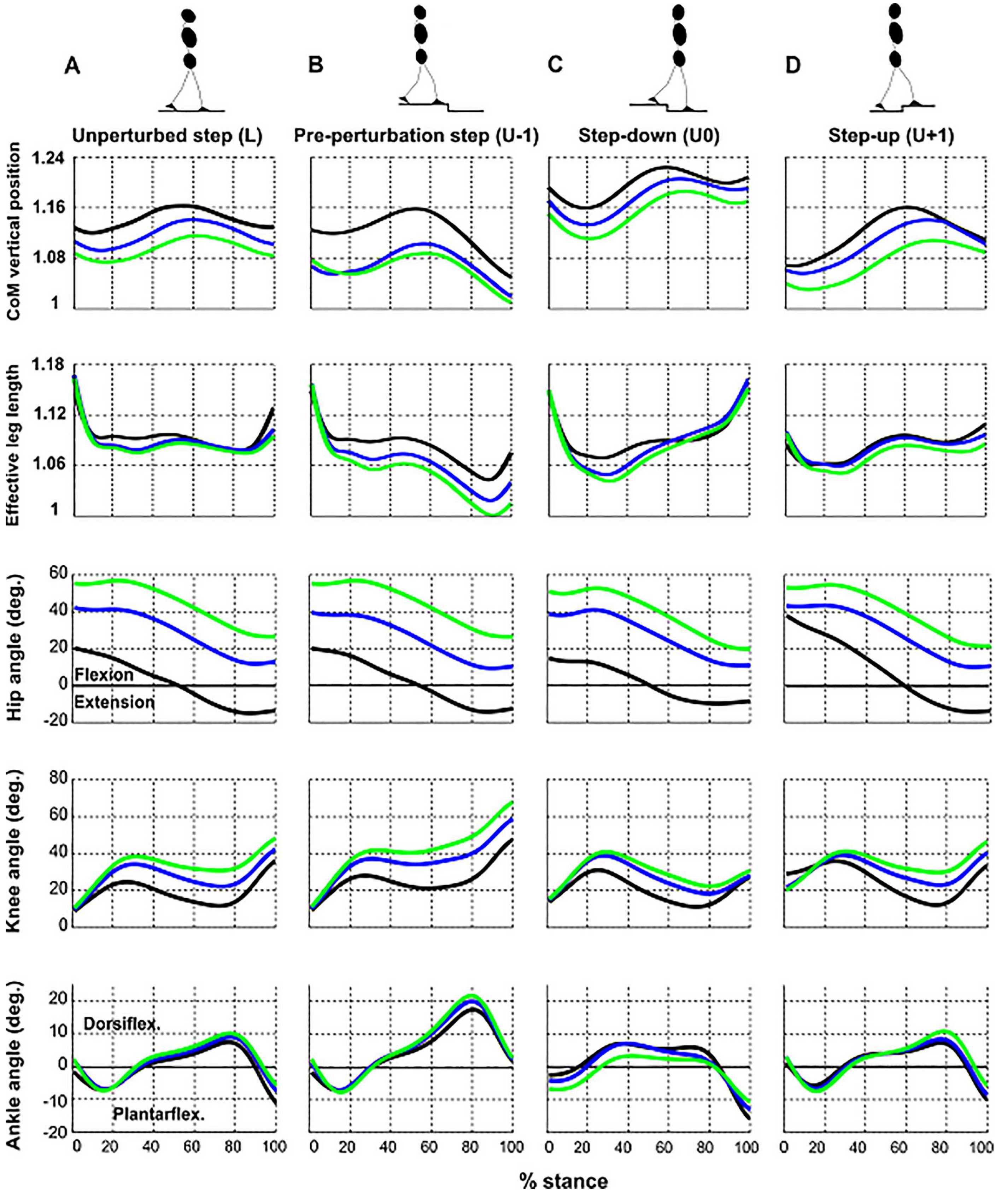
A
B
C
D
Unperturbed step (L)
Pre-perturbation step (U-1)
Step-down (U0)
Step-up (U+1)
CoM vertical position
1.24
1.16
1.08
1
Effective leg length
1.18
1.12
1.06
1
Hip angle (deg.)
60
40
20
0
-20
Flexion
Extension
Knee angle (deg.)
80
60
40
20
0
Ankle angle (deg.)
20
10
0
-10
-20
Dorsiflex.
Plantarflex.
0
20
40
60
80
100
% stance

Fig 4. Normalized CoM, normalized effective leg length and lower limb joint angle trajectories. Shown are ensemble-averaged normalized vertical position of center of mass (CoM), normalized effective leg length, hip, knee, and ankle angles pertaining to (A) unperturbed step (L), (B) pre-perturbation step (U-1), (C) step-down (U0) and (D) step-up (U+1) in the sagittal plane during the stance phase for RE (black), TF1 (blue) and TF2 (green) (N = 12). RE, regular erect trunk; TF1, ~30˚ trunk flexion; TF2, ~50˚ trunk flexion.

https://doi.org/10.1371/journal.pone.0190135.g004

the trunk in human locomotion is of clinical interest. In this study, we investigated the adaptive kinematic behavior of able-bodied walking while negotiating uneven ground with altered trunk orientations. In line with our hypotheses, we observed step-specific effects of posture on the kinematic behavior of able-bodied gait in most of the parameters of interest (Table 1). As compared with regular upright walking, trunk-flexed gaits across uneven ground exhibited: a) more crouched legs, characterized by sustained knee flexion during stance (Fig 4, Table 1), b) a greater TD-TO kinematic discrepancy in the effective leg (i.e. shorter legs at toe-off) (Fig 4, Table 1) and c) a marginally flatter leg angle at TD (Fig 5B, Table 1). Participants rotated their trunk backwards during step-down regardless of the trunk orientation (Fig 2C). A more pronounced trunk backwards rotation in trunk-flexed walking contributed to the observed elevated center of mass (CoM) trajectories during the step-down (Fig 4C) which may have facilitated drop negotiation. Finally, at the end of the step-up, participants restored the kinematic parameters to the level step values (Fig 4, Table 1), suggesting stability and robustness of the gait in able-bodied participants.

Kinematic adaptations during the pre-perturbation step (U-1)

Our results partly supported our expectation of the step-specific effect of the trunk posture on the kinematic behavior of able-bodied walking in the pre-perturbation step. Compared to the unperturbed step, the participants demonstrated kinematic adjustments only in the effective leg length and knee angle at TO (Figs 3B, 3F and 4A, Table 1). In preparation to step-down, individuals increased their knee flexion, and the magnitude of the flexion was proportionally increased with an increase of the trunk flexion, which led to a shorter effective leg length at TO (Fig 4B, Table 1). In addition, the ankle angle tended to be more dorsiflexed (main effect) (Fig 5E). These kinematic adjustments in the lower limb resulted in a lower CoM position relative to the corresponding level steps (Figs 4B and 5C) in preparation to step down. This finding is consistent with a study by Muller et. al [9], who reported that at the end of the step before a visible drop during regular upright walking, individuals modulate their knee and ankle flexion which in turn leads to a lower vertical position of the CoM. Plus, the vertical position of the CoM lowered proportionally with an increase of the trunk flexion (Fig 5A).

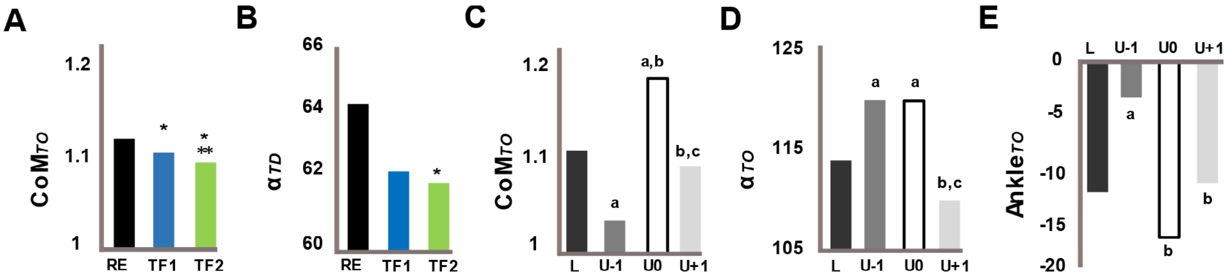

Fig 5. Main effects of posture and step. Shown are the main effects of posture on (A) CoM at TO and (B) leg angle at TD, and the main effect of step on (C) CoM, (D) leg angle and (E) ankle position at TO (N = 12). Significant differences from RE and TF1 are indicated with '*' and '**', respectively for the posture effect ($p<0.05$). Significant differences from 'L', 'U-1', and 'U0' are indicated with 'a', 'b', and 'c', respectively for the step effect ($p<0.05$). RE (black), regular erect trunk; TF1 (blue), ~30˚ trunk flexion; TF2 (green), ~50˚ trunk flexion; L, unperturbed level step (dark grey); U-1, pre-perturbation step (grey); U0, step-down (white); U+1, step-up (light grey).

https://doi.org/10.1371/journal.pone.0190135.g005

Comparing the effective leg length between TO and TD in the pre-perturbation step to that of the unperturbed step, we observed a much shorter effective leg during the pre-perturbation step due to an increase of the trunk flexion (Fig 4B). In agreement with our previous study [5], where we reported a kinematic asymmetry in leg function, characterized by a longer effective length at TD than at TO when transforming posture from upright to almost horizontal orientation, here we found such discrepancy in the effective leg length with a pronounced difference in the preparatory step. The observed kinematic adjustments in the approach step seemed to be driven by the visual perception of the perturbation which may have allowed adaptive motor control strategies.

Kinematic adaptations during step-down (U0)

Comprising approximately 50% of the total body mass [45], a deviation in the trunk orientation can have a significant effect on the position of the CoM and thus on human locomotion [5, 7, 14, 27]. Trunk kinematic adjustments during accommodating uneven ground can be influenced by the height of the drop and the availability of the visual guidance. In downward step on a camouflaged surface, the trunk backward rotation becomes larger than stepping into a visible drop and tends to increase proportionally with the drop height [9]. In both upright trunk gait with straight legs [9] and trunk-flexed gaits associated with crouched legs during traversing uneven ground, the trunk appears to reduce its angle in a compensatory fashion to diminish variations in the CoM position. The utilization of this mechanism with a more pronounced adaptation during trunk-flexed gaits resembles the small birds' locomotion in exploiting their legs (i.e. a zig-zag-like configuration) to negotiate large terrain perturbations [47]. The backward rotation of the trunk as found in our young, healthy participants (Fig 2C) not only contributes to the significantly higher vertical position of the CoM relative to the pre-perturbation step across trunk-flexed gaits, but may counteract a potential increase in angular momentum during a step-down (Figs 3H and 4C, Table 1). This opens up new perspectives on the role of the trunk in locomotion, notably for specific populations e.g. elderly with a forward inclined trunk orientation [18, 48] or patients who display atypical trunk postures [49]. Thus, backward trunk rotation when dealing with step-down may reflect an adaptive strategy to enhance gait stability. To the best of our knowledge, no studies are available whether elderly or patients with an altered trunk posture already employ this strategy for negotiating downward steps in unassisted locomotion, e.g. when stepping down from a curb or walking down inclines.

In the present study, participants landed on a lowered level with almost no significant changes in the effective leg length (Figs 3A and 4C, Table 1). A more extended ankle compensated the more flexed knee; however, these kinematic adaptations in the step-down were not significantly different from their counterparts in unperturbed steps. In addition, an increase of the trunk flexion did not lead to significant changes in knee and ankle joints across gait postures (Figs 3E, 3G and 4C, Table 1). The only change occurred at the hip: the more flexed the trunk, the more flexed the hip at TD (Figs 3C and 4C, Table 1). While no step-dependent effects of posture on the leg angle at TD were observed, walking with 50° of trunk flexion (TF2) was associated with a flatter leg angle across steps (Fig 5B), possibly to compensate for the loss in the horizontal distance between the CoM and the CoP induced by a trunk flexion. Moreover, the standard deviation of plantarflexion was much higher for the step-down (U0) compared with the other steps, indicating that some participants used toe-landing at TD of step-down (Table 1).

The results partially confirmed our expectation for step-specific effects of posture at TO in the step-down. The leg configuration at TO was characterized by significant knee and ankle extension in order to elongate the leg and to facilitate the restoration of the CoM height during the following step-up (U+1) across gait postures (Figs 3B and 4C). The main effect of step at TO revealed a significant increase of leg angle (Fig 5D) and ankle plantar flexion (Fig 5E). The potential loss in CoM height due to an increased leg angle was overcompensated by the simultaneous elongation of the effective leg. In comparison to the preceding step and unperturbed level step, the discrepancy in effective leg length between TD and TO in the step U0 was minimized, as participants were attempting to launch themselves onto the elevated ground (Fig 4C).

Kinematic adaptations during step-up (U+1)

In agreement with our expectation that step-specific effects of posture would occur and likely differ between TD and TO instants in the step U+1, individuals exhibited significantly different kinematic adaptations at TD from those of other steps (Figs 3 and 4D, Table 1). They landed on the elevated step (post-perturbation step) with a shortened effective leg at TD as compared to the corresponding unperturbed steps across gait postures (Figs 3A and 4D, Table 1). This observation was reflected in significant increases in the knee flexion across gait postures and a significant increased hip flexion during RE gait (Figs 3C and 4D, Table 1). A shortened effective leg length led to a lowered vertical position of the CoM across gait postures relative to the corresponding unperturbed steps; however, the vertical position of the CoM did not exhibit a significant change with an increase of the trunk flexion (Figs 3H and 4D, Table 1). The former finding can be attributed to a considerable flexion across lower limb joints (Table 1) and trunk (Fig 2C) (i.e. crouched posture) during RE gait, walking with a regular erect trunk, leading to a significant decrease in the CoM height while stepping up immediately after a visible step-down in ground. Therefore, the second expectation that kinematic adaptations would become more pronounced with an increase of the trunk flexion was weakly supported, as individuals attempted to accommodate the immediate recovery step from the perturbation during trunk-flexed gaits with a kinematic behavior that was not remarkably different from the upright walking. These findings suggest that kinematic adjustments in the global leg and CoM displacement in the step U+1 tended to be rather step-dependent than posture-dependent.

Remarkably, for each gait posture, the kinematic parameters returned to the mean values of the unperturbed corresponding steps at TO (Figs 3 and 4D, Table 1). This may have been facilitated by moderation of the CoM trajectory during step down (relative height of CoM increased significantly during step-down, diminishing absolute changes of CoM height), a strategy that has been suggested to be effective in improving the dynamic stability [50, 51]. The step-specific effects of posture on walking kinematic parameters indicate that modulation of the leg posture was necessary to achieve this. Considering that there were no significant changes in kinematic parameters comparing step-up and the level steps at TO for each gait posture (Table 1), we assume that the recovery of the gait was achieved at the end of the step-up, suggesting stability and robustness of the gait. This may have been facilitated by the sequence of step-down directly followed by step-up and the presence of the visual perception of the perturbation. We however do not know whether a comparable immediate recovery would be achieved when stepping down on a permanently lowered level. Moreover, having observed the kinematic strategy of backward trunk rotation during stepping down while adopting various trunk orientations alongside other step-specific global kinematic adjustments in able-bodied gait motivates examining the role of trunk movements in balance-compromised cohorts to see to what extent their control of trunk–accounting for nearly 50% of total body mass–might be different from that of able walkers.

Conclusion

In summary, the results of the present study indicate that negotiating changes in ground level requires step-specific compensatory kinematic adaptations in lower limbs to maintain dynamic stability regardless of the trunk orientation. These adaptations occur not only at the end of the step-down, but also at TO of the pre-perturbation step and at TD of the step-up. Backward rotation of the trunk during step-down was not only a preventive strategy employed by able-bodied participants possibly to control forward horizontal and angular momentum of the body, but also to moderate changes in the CoM trajectory in trunk-flexed gaits. The young healthy participants recovered to steady gait in the step immediately following a downward step in ground even in the presence of trunk flexion. Trunk-flexed gait is associated with impaired postural control [18]. The incorporation of exercises with a greater focus on voluntary backward rotation of the trunk for negotiating step-down into fall-prevention intervention programs may be useful to enhance gait stability in patients and elderly who exhibit trunk-flexed postures during walking. Further perturbation experiments on humans with and without normal trunk posture in comparable conditions will be required to shed further light on the interaction between the trunk posture and locomotion.

Acknowledgments

Authors thank Johanna Vielemeyer for her valuable contribution in collecting experimental data.

Author Contributions

Conceptualization: Soran Aminiaghdam, Reinhard Blickhan, Roy Muller.

Data curation: Soran Aminiaghdam, Reinhard Blickhan, Roy Muller.

Formal analysis: Soran Aminiaghdam, Christian Rode.

Investigation: Soran Aminiaghdam, Reinhard Blickhan, Roy Muller.

Methodology: Soran Aminiaghdam, Reinhard Blickhan, Roy Muller, Christian Rode.

Project administration: Soran Aminiaghdam, Reinhard Blickhan, Roy Muller.

Resources: Soran Aminiaghdam, Reinhard Blickhan, Roy Muller.

Software: Soran Aminiaghdam.

Supervision: Soran Aminiaghdam, Reinhard Blickhan, Roy Muller, Christian Rode.

Validation: Soran Aminiaghdam, Reinhard Blickhan, Christian Rode.

Visualization: Soran Aminiaghdam, Christian Rode.

Writing – original draft: Soran Aminiaghdam.

Writing – review & editing: Soran Aminiaghdam, Christian Rode.

References

1. Blickhan R, Ernst M, Koch M, Muller R. Coping with disturbances. Hum Mov Sci. 2013; 32(5):971–83. Epub 2013/07/09. https://doi.org/10.1016/j.humov.2013.02.009 S0167-9457(13)00029-8 [pii]. PMID: 23830489.
2. Dietz V, Quintern J, Sillem M. Stumbling reactions in man: significance of proprioceptive and pre-programmed mechanisms. J Physiol. 1987; 386:149–63. Epub 1987/05/01. PMID: 3681704; PubMed Central PMCID: PMC1192455.

3. Hirschfeld H, Forssberg H. Phase-dependent modulations of anticipatory postural activity during human locomotion. J Neurophysiol. 1991; 66(1):12–9. Epub 1991/07/01. https://doi.org/10.1152/jn.1991.66.1.12 PMID: 1919662.

4. Birn-Jeffery AV, Daley MA. Birds achieve high robustness in uneven terrain through active control of landing conditions. J Exp Biol. 2012; 215(Pt 12):2117–27. Epub 2012/05/25. https://doi.org/10.1242/jeb.065557 215/12/2117 [pii]. PMID: 22623200.

5. Aminiaghdam S, Rode C, Muller R, Blickhan R. Increasing trunk flexion transforms human leg function into that of birds despite different leg morphology. J Exp Biol. 2017; 220(Pt 3):478–86. Epub 2016/11/27. https://doi.org/10.1242/jeb.148312148312 [pii]. PMID: 27888201.

6. Grasso R, Zago M, Lacquaniti F. Interactions between posture and locomotion: Motor patterns in humans walking with bent posture versus erect posture. J Neurophysiol. 2000; 83(1):288–300. PubMed PMID: ISI:000084777800026. https://doi.org/10.1152/jn.2000.83.1.288 PMID: 10634872

7. Saha D, Gard S, Fatone S. The effect of trunk flexion on able-bodied gait. Gait Posture. 2008; 27 (4):653–60. Epub 2007/10/09. doi: S0966-6362(07)00214-7 [pii] https://doi.org/10.1016/j.gaitpost.2007.08.009 PMID: 17920272.

8. Muller R, Ernst M, Blickhan R. Leg adjustments during running across visible and camouflaged incidental changes in ground level. J Exp Biol. 2012; 215(Pt 17):3072–9. Epub 2012/08/10. https://doi.org/10.1242/jeb.072314 215/17/3072 [pii]. PMID: 22875771.

9. Muller R, Tschiesche K, Blickhan R. Kinetic and kinematic adjustments during perturbed walking across visible and camouflaged drops in ground level. J Biomech. 2014; 47(10):2286–91. Epub 2014/05/23. https://doi.org/10.1016/j.jbiomech.2014.04.041 S0021-9290(14)00262-0 [pii]. PMID: 24845695.

10. Massion J, Popov K, Fabre J-C, Rage P, Gurfinkel V. Is the erect posture in microgravity based on the control of trunk orientation or center of mass position? Experimental Brain Research. 1997; 114 (2):384–9. PMID: 9166928

11. Mouchnino L, Aurenty R, Massion J, Pedotti A. Is the trunk a reference frame for calculating leg position? Neuroreport. 1993; 4(2):125–7. PMID: 8453047

12. Maus HM, Lipfert SW, Gross M, Rummel J, Seyfarth A. Upright human gait did not provide a major mechanical challenge for our ancestors. Nat Commun. 2010; 1:70. Epub 2010/09/16. https://doi.org/10.1038/ncomms1073 ncomms1073 [pii]. PMID: 20842191.

13. Muller R, Rode C, Aminiaghdam S, Vielemeyer J, Blickhan R. Relevance of force direction patterns for postural stability in human walking. Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences. 2017;In review.

14. Gillet C, Duboy J, Barbier F, Armand S, Jeddi R, Lepoutre FX, et al. Contribution of accelerated body masses to able-bodied gait. Am J Phys Med Rehabil. 2003; 82(2):101–9. Epub 2003/01/25. https://doi.org/10.1097/01.PHM.0000046629.78324.28 00002060-200302000-00004 [pii]. PMID: 12544755.

15. Blickhan R, Andrada E, Muller R, Rode C, Ogihara N. Positioning the hip with respect to the COM: Consequences for leg operation. J Theor Biol. 2015; 382:187–97. Epub 2015/07/06. https://doi.org/10.1016/j.jtbi.2015.06.036 S0022-5193(15)00315-X [pii]. PMID: 26142948.

16. Leroux A, Fung J, Barbeau H. Postural adaptation to walking on inclined surfaces: I. Normal strategies. Gait Posture. 2002; 15(1):64–74. Epub 2002/01/26. doi: S0966636201001813 [pii]. PMID: 11809582.

17. Muller R, Ertelt T, Blickhan R. Low back pain affects trunk as well as lower limb movements during walking and running. J Biomech. 2015; 48(6):1009–14. Epub 2015/02/24. https://doi.org/10.1016/j.jbiomech.2015.01.042 S0021-9290(15)00058-5 [pii]. PMID: 25700607.

18. de Groot MH, van der Jagt-Willems HC, van Campen JP, Lems WF, Beijnen JH, Lamoth CJ. A flexed posture in elderly patients is associated with impairments in postural control during walking. Gait Posture. 2014; 39(2):767–72. Epub 2013/11/26. https://doi.org/10.1016/j.gaitpost.2013.10.015 S0966-6362(13)00649-8 [pii]. PMID: 24268470.

19. Ganz DA, Bao Y, Shekelle PG, Rubenstein LZ. Will my patient fall? Jama. 2007; 297(1):77–86. https://doi.org/10.1001/jama.297.1.77 PMID: 17200478

20. Andrada E, Rode C, Sutedja Y, Nyakatura JA, Blickhan R. Trunk orientation causes asymmetries in leg function in small bird terrestrial locomotion. Proc Biol Sci. 2014; 281(1797). Epub 2014/11/08. https://doi.org/10.1098/rspb.2014.1405 20141405 [pii] rspb.2014.1405 [pii]. PMID: 25377449; PubMed Central PMCID: PMC4240980.

21. Hohne A, Stark C, Bruggemann GP, Arampatzis A. Effects of reduced plantar cutaneous afferent feedback on locomotor adjustments in dynamic stability during perturbed walking. J Biomech. 2011; 44 (12):2194–200. Epub 2011/07/06. https://doi.org/10.1016/j.jbiomech.2011.06.012 S0021-9290(11) 00457-X [pii]. PMID: 21726865.

22. Marigold DS, Patla AE. Adapting locomotion to different surface compliances: neuromuscular responses and changes in movement dynamics. J Neurophysiol. 2005; 94(3):1733–50. Epub 2005/05/13. doi: 00019.2005 [pii] https://doi.org/10.1152/jn.00019.2005 PMID: 15888535.

23. Tang PF, Woollacott MH, Chong RK. Control of reactive balance adjustments in perturbed human walking: roles of proximal and distal postural muscle activity. Exp Brain Res. 1998; 119(2):141–52. Epub 1998/04/16. PMID: 9535563.

24. Shinya M, Fujii S, Oda S. Corrective postural responses evoked by completely unexpected loss of ground support during human walking. Gait Posture. 2009; 29(3):483–7. Epub 2009/01/09. https://doi.org/10.1016/j.gaitpost.2008.11.009 S0966-6362(08)00378-0 [pii]. PMID: 19128973.

25. van der Linden MH, Hendricks HT, Bloem BR, Duysens J. Hitting a support surface at unexpected height during walking induces loading transients. Gait Posture. 2009; 29(2):255–60. Epub 2008/10/28. https://doi.org/10.1016/j.gaitpost.2008.08.017 S0966-6362(08)00263-4 [pii]. PMID: 18952434.

26. van Dieen JH, Spanjaard M, Konemann R, Bron L, Pijnappels M. Balance control in stepping down expected and unexpected level changes. J Biomech. 2007; 40(16):3641–9. Epub 2007/07/24. doi: S0021-9290(07)00272-2 [pii] = https://doi.org/10.1016/j.jbiomech.2007.06.009 PMID: 17644100.

27. Leteneur S, Gillet C, Sadeghi H, Allard P, Barbier F. Effect of trunk inclination on lower limb joint and lumbar moments in able men during the stance phase of gait. Clin Biomech. 2009; 24(2):190–5. https://doi.org/10.1016/j.clinbiomech.2008.10.005 PubMed PMID: ISI:000263701200011. PMID: 19091448

28. Leteneur S, Simoneau E, Gillet C, Dessery Y, Barbier F. Trunk's Natural Inclination Influences Stance Limb Kinetics, but Not Body Kinematics, during Gait Initiation in Able Men. PLoS One. 2013; 8(1). doi: ARTN e55256 https://doi.org/10.1371/journal.pone.0055256 PubMed PMID: ISI:000315563800137. PMID: 23383128

29. McGibbon CA, Krebs DE. Age-related changes in lower trunk coordination and energy transfer during gait. J Neurophysiol. 2001; 85(5):1923–31. PubMed PMID: ISI:000168675100013. https://doi.org/10.1152/jn.2001.85.5.1923 PMID: 11353009

30. Magarian EO, Dietz AJ, Freeman DS, Carlson JD. Effect of prazosin and beta-blocker monotherapy on serum lipids: a cross-over, placebo-controlled study. J Clin Pharmacol. 1987; 27(10):756–61. Epub 1987/10/01. PMID: 2892862.

31. Kluger D, Major MJ, Fatone S, Gard SA. The effect of trunk flexion on lower-limb kinetics of able-bodied gait. Hum Mov Sci. 2014; 33:395–403. Epub 2014/01/16. https://doi.org/10.1016/j.humov.2013.12.006 S0167-9457(13)00180-2 [pii]. PMID: 24423389.

32. Ferris DP, Liang K, Farley CT. Runners adjust leg stiffness for their first step on a new running surface. J Biomech. 1999; 32(8):787–94. Epub 1999/08/05. doi: S0021-9290(99)00078-0 [pii]. PMID: 10433420.

33. Grimmer S, Ernst M, Gunther M, Blickhan R. Running on uneven ground: leg adjustment to vertical steps and self-stability. J Exp Biol. 2008; 211(Pt 18):2989–3000. Epub 2008/09/09. https://doi.org/10.1242/jeb.014357 211/18/2989 [pii]. PMID: 18775936.

34. Muller R, Blickhan R. Running on uneven ground: leg adjustments to altered ground level. Hum Mov Sci. 2010; 29(4):578–89. Epub 2010/07/02. https://doi.org/10.1016/j.humov.2010.04.007 S0167-9457(10)00063-1 [pii]. PMID: 20591519.

35. Muller R, Grimmer S, Blickhan R. Running on uneven ground: leg adjustments by muscle pre-activation control. Hum Mov Sci. 2010; 29(2):299–310. Epub 2010/03/23. https://doi.org/10.1016/j.humov.2010.01.003 S0167-9457(10)00007-2 [pii]. PMID: 20304516.

36. Muller R, Siebert T, Blickhan R. Muscle preactivation control: simulation of ankle joint adjustments at touchdown during running on uneven ground. J Appl Biomech. 2012; 28(6):718–25. Epub 2012/07/21. doi: 2010–0181 [pii]. PMID: 22814314.

37. Aminiaghdam S, Rode C. Effects of altered sagittal trunk orientation on kinetic pattern in able-bodied walking on uneven ground. Biol Open 2017. https://doi.org/10.1242/bio.025239.

38. Farcy JP, Schwab FJ. Management of flatback and related kyphotic decompensation syndromes. Spine (Phila Pa 1976). 1997; 22(20):2452–7. Epub 1997/11/14. PMID: 9355229.

39. Lin CJ, Guo LY, Su FC, Chou YL, Cherng RJ. Common abnormal kinetic patterns of the knee in gait in spastic diplegia of cerebral palsy. Gait Posture. 2000; 11(3):224–32. Epub 2000/05/10. doi: S0966636200000497 [pii]. PMID: 10802435.

40. Malone A, Kiernan D, French H, Saunders V, O'Brien T. Do children with cerebral palsy change their gait when walking over uneven ground? Gait Posture. 2015; 41(2):716–21. Epub 2015/03/01. https://doi.org/10.1016/j.gaitpost.2015.02.001 S0966-6362(15)00035-1 [pii]. PMID: 25724259.

41. Potter BK, Lenke LG, Kuklo TR. Prevention and management of iatrogenic flatback deformity. J Bone Joint Surg Am. 2004; 86-A(8):1793–808. Epub 2004/08/05. doi: 86/8/1793 [pii]. PMID: 15292431.

42. Sarwahi V, Boachie-Adjei O, Backus SI, Taira G. Characterization of gait function in patients with post-surgical sagittal (flatback) deformity: a prospective study of 21 patients. Spine (Phila Pa 1976). 2002; 27 (21):2328–37. Epub 2002/11/20. https://doi.org/10.1097/01.BRS.0000030304.83145.01 PMID: 12438980.

43. Coren S, Porac C. The validity and reliability of self-report items for the measurement of lateral preference. British Journal of Psychology. 1978; 69(2):207–11.

44. Sadeghi H, Allard P, Prince F, Labelle H. Symmetry and limb dominance in able-bodied gait: a review. Gait Posture. 2000; 12(1):34–45. Epub 2000/09/21. doi: S0966636200000709 [pii]. PMID: 10996295.

45. de Leva P. Adjustments to Zatsiorsky-Seluyanov's segment inertia parameters. J Biomech. 1996; 29 (9):1223–30. Epub 1996/09/01. doi: 0021929095001786 [pii]. PMID: 8872282.

46. Gard SA, Miff SC, Kuo AD. Comparison of kinematic and kinetic methods for computing the vertical motion of the body center of mass during walking. Hum Mov Sci. 2004; 22(6):597–610. Epub 2004/04/06. https://doi.org/10.1016/j.humov.2003.11.002 S016794570300085X [pii]. PMID: 15063043.

47. Blum Y, Birn-Jeffery A, Daley MA, Seyfarth A. Does a crouched leg posture enhance running stability and robustness? J Theor Biol. 2011; 281(1):97–106. https://doi.org/10.1016/j.jtbi.2011.04.029 PMID: 21569779

48. Halliday SE, Winter DA, Frank JS, Patla AE, Prince F. The initiation of gait in young, elderly, and Parkinson's disease subjects. Gait & Posture. 1998; 8(1):8–14.

49. Hirose D, Ishida K, Nagano Y, Takahashi T, Yamamoto H. Posture of the trunk in the sagittal plane is associated with gait in community-dwelling elderly population. Clin Biomech. 2004; 19(1):57–63.

50. Byl K, Tedrake R. Metastable walking machines. The International Journal of Robotics Research. 2009; 28(8):1040–64.

51. Wisse M, Schwab AL, van der Linde RQ, van der Helm FC. How to keep from falling forward: elementary swing leg action for passive dynamic walkers. IEEE Transactions on Robotics. 2005; 21(3):393–401.

Chapter 5

5 General conclusion

5.1 Summary

In this work, I explored the relationship between changes in posture and biomechanics of locomotion during human walking on uneven ground as compared to walking on level ground. We gained more insight into the role of trunk orientation in human locomotion, having used both mostly empirical and partially model-based approaches. By examining human leg function during walking under changes in the trunk kinematics — up to the maximal sagittal flexion — and comparing it to that of small-bodied birds, in line with our hypothesis, we found that mimicking birds' posture causes a comparable behavior in leg function, despite the different morphology of the segmented legs. In addition, comparison of two simplified models, namely spring and damper in series and parallel spring and damper, for the first time, revealed that the former model performs superior in the prediction of the axial leg forces during stance phase of walking than the latter model. This superiority held true during walking with various degrees of trunk orientations (Fig. 5-1G).

As hypothesized, trunk could be utilized to accommodate changes in ground level by exhibiting a backward rotation during step down. Human walkers rotated their trunk backwards during step-down (2- to 3-fold backwards rotation compared with level steps regardless of trunk posture) are likely to control the kinetic energy they gain during stepping down (Fig. 5-1A). In contrast with our expectation, increasing trunk flexion did not lead to a greater variation in gait kinetic parameters while traversing uneven ground. Interestingly, the pre-adaptations were found essential in the preceding step to the drop when walking with a regular upright trunk.

With increased trunk flexion, between-step changes in the GRF kinetic parameters tended to decrease relative to upright walking on level ground.

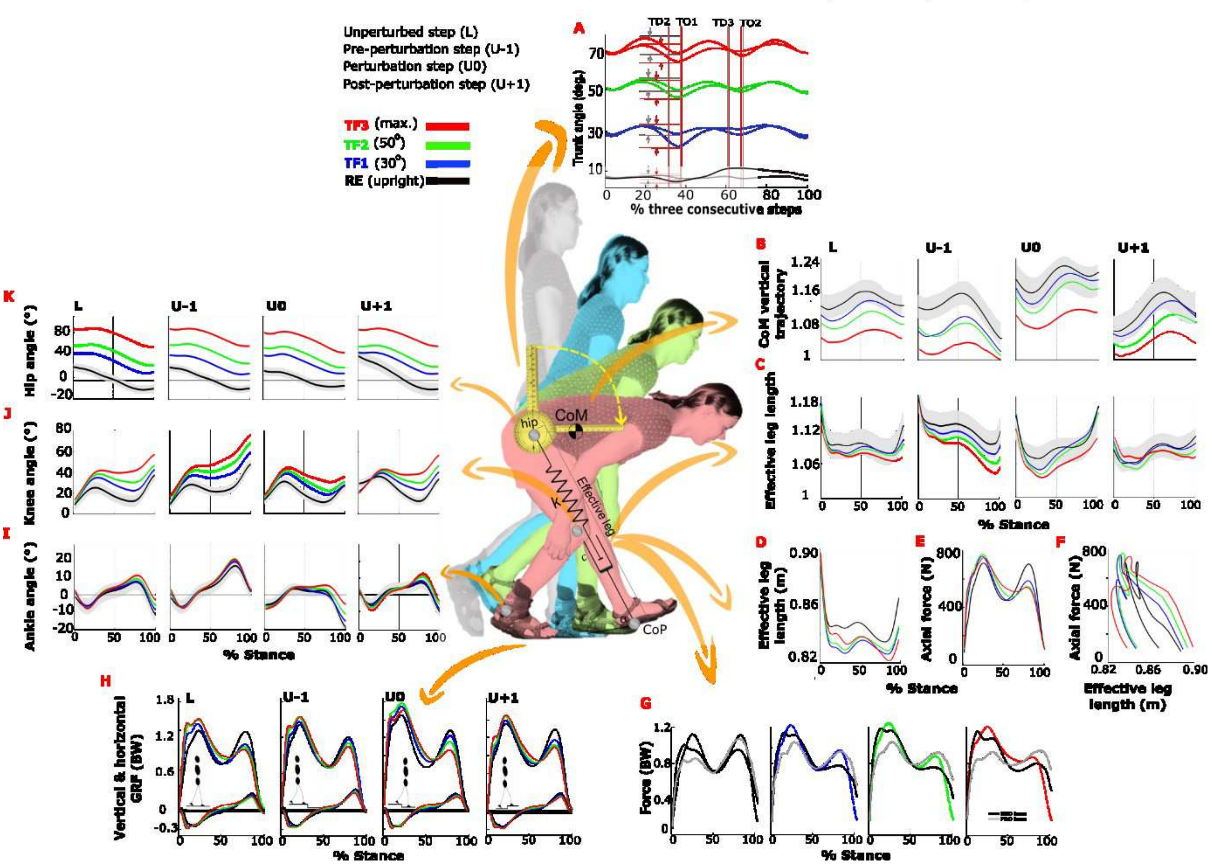

Fig. 5-1. Schematic diagram of human locomotion with various trunk orientations as well as relevant kinematic, kinetic, axial leg function and model versus experimental axial forces figures. (A) The ensemble-averaged trunk kinematics in the sagittal plane across three level (blurred lines) and three uneven steps (solid lines) with different walking postures. The vertical grey and red lines represent TD and TO instants pertaining to the three consecutive steps during level and uneven walking, respectively. The horizontal grey and red lines highlight the maximum of the trunk angle in the step ‘U-1’ and the minimum of the trunk angle in the step ‘U0’ for each walking postures, respectively. (B) Ensemble-averaged normalized vertical position of the CoM, (C) ensemble-averaged normalized effective leg length, ensemble-averaged (D) leg length, (E) axial leg force and (F) axial loop (axial force versus leg length). (G) Model forces versus experimental axial force for different walking conditions involving normalized ensemble-averaged leg axial force (dashed lines), fit from SSD model (series-spring-damper, solid black curve) and fit from PSD model (parallel spring-damper, solid grey curve). SSD model produces better predictions of leg axial forces in across all gait conditions. (H) GRFs for different walking conditions. Shown are ensemble-averaged horizontal and vertical GRFs (normalized to participant body weight (BW)) during unperturbed level step and perturbed steps in uneven ground. The eensemble-averaged (I) ankle, (J) knee and (K) hip angles in the sagittal plane across the stance phase of different steps with various walking postures. The grey shaded area represents s.d. of RE gait. The contact time is normalized to 100%. TD, touchdown; TO, toe-off; CoM, center of mass; Ground reaction forces, GRFs; k, stiffness parameter of serial spring; c, damping parameter of serial spring; α, leg orientation; CoP, center of pressure.

We argue that the trunk plays a compensatory role with a more pronounced movement strategy (i.e., a greater backward rotation) in trunk-flexed walking during stepping-down. This facilitates accommodating changes in ground level by a backward movement regardless of its initial orientation (Fig. 5-1A) in an attempt to maintain the vertical position of the CoM (Fig. 5-1B) and to regulate the relationship between the CoM and the base of support. Able-bodied individuals were found to recover nearly all kinematic parameters comprised of the vertical position of the CoM (Fig. 5-1B), effective leg length (Fig. 5-1C) and angle as well as hip (Fig. 5-1I), knee (Fig. 5-1J) and ankle (Fig. 5-1K) joint angles at the end of the step-up. Although the transformation of the body posture from the orthograde to the virtually pronograde during walking may lead to a substantial muscular demand and mechanical load, however, assuming such zig-zag-like crouched posture while traversing uneven ground was found not to require significant changes in the GRF parameters. Furthermore, the restoration of the movement strategy to the undisturbed path within a range observed during upright walking at the end of the set-up following a step-down implies that the stability of the periodic movement does not seem to be hampered by bending the trunk. This may resemble the ability of small birds in adjusting their crouched legs to cope with irregular terrains (Blum et al. 2011). Based on such kinetic and kinematic observations, we believe that, although walking with bent trunk might be strenuous, but a robustly stable gait in able walkers suggests that the control of such gait may not be difficult.

5.2 The paradigm of a bent posture

While walking upright with extended legs is a hallmark feature of human locomotion, the adaptability of our locomotor system allows walking with various degrees of trunk orientation (Grasso et al. 2000; Saha et al. 2008; Gallagher et al. 2011; Kluger et al. 2014). Unavoidable gait postures, e.g. in some occupational settings (as in low-seam coal mines), often do not permit upright walking instead require laborers to stoopwalk in order to accomplish their daily tasks (Gallagher et al. 2011). Moreover, altered trunk posture might be the consequence of degenerative aging process. Flexed posture – characterized by an increased thoracic kyphosis – associated with a more variable and less structured gait pattern, and a more irregular trunk acceleration pattern has been documented in older adults (de Groot et al. 2014). At a functional level in the sport context, incorporation of the sagittal plane trunk inclination during running is suggested as an effective strategy to reduce loading at the knee (Teng 2013).

Control of posture and locomotion are believed to share some common principles of spatial organization as their functions are interdependent at different levels of the central nervous system (Massion 1992; Lacquaniti et al. 1997). A smooth execution of locomotion requires not only a dynamic equilibrium, but also a continuous adaption to potential threats, such as postural changes and uneven ground. To this end, the coordinated interactions between different body segments are paramount (Dietz et al. 1987; Hirschfeld and Forssberg 1991). Disturbances, conceived as an induced deviation of a desired condition, may be natural either as part of an everyday experience or artificial as imposed by experiment. Advancement in our understanding of a system properties can be achieved through the study of adaptions and responses of that system to disturbances (Blickhan et al. 2013).

Experimentally induced trunk-flexed postures during walking are associated with biomechanical changes in dynamics of lower limbs. A forwardly bent trunk during locomotion results in a posterior shift in the hip position with respect to the CoM, leading to more crouched lower limbs. Such compensatory kinematic adjustments contribute to maintaining the CoM trajectory within the base of support. An increased sagittal trunk flexion, as associated with more crouched lower limbs, creates an increased phase lag between hip and ankle joints as compared with upright walking. This, in turn, results in a phase lag in the vertical position, velocity, and acceleration of the CoM (Saha et al. 2008). However, the trunk-flexed gaits (e.g. up to 50° trunk flexion) cause no changes in the shape of the time-normalized waveforms of the elevation angles of the thigh, shank, and foot segments throughout the gait cycle (Grasso et al. 2000).

Given the vertical GRF is corresponding to the vertical acceleration of the CoM, changes in the dynamics of the CoM derived from the deviation of trunk from upright is associated with the systematic changes in the GRF pattern (Grasso et al. 2000; Saha et al. 2008). Under such walking conditions, the amplitude of the first and the second peaks tends to become higher and lower, respectively, in a way displaying the patterns intermediate between the typical GRF waveforms of walking and running.

In terms of lower-limb kinetics, supporting the anteriorly flexed heavy trunk up to 50° necessitates a significant increased hip extensions and an increased knee joint extensor moments earlier in the stance phase (Kluger et al. 2014). With such energetic demands, assuming an increased muscular activity that may contribute to a rapid muscular fatigue is convincible.

The measurement of the electromyographic (EMG) activity of the gluteus maximus, biceps femoris, rectus femoris, vastus lateralis, lateral gastrocnemius, and tibialis anterior during trunk-flexed gaits demonstrates that EMG activity of all above mentioned muscles increases relative to a regular walking with an upright trunk (Grasso et al. 2000).

The spatio-temporal parameters of the gait are also influenced by changes in the trunk kinematics. Our findings reveal that except for a normalized step length, other gait parameters vary with an increase of the sagittal trunk flexion; an upward trend in the velocity and cadence, and a downward trend in the stance time and swing time. However, increasing the trunk orientation from ~50° to a maximum angle in the sagittal plane led to no differences in the spatio-temporal gait parameters. An unchanged step length may be attributed to the restrictions of the experiment in terms of foot strikes in a left–right–left sequence on the three force-platforms embedded at the equal distances in the walkway.

Since an active ankle push-off is responsible for initiating the leg swing in humans (Lipfert et al., 2014), a bent trunk during locomotion may interfere with a proper push-off as judged from the lower vertical GRF second peak and the unloading rate compared with an upright gait. This results in a right-skewed profile of the vertical GRFs (Fig. 5-1H) as characterized by greater weight acceptance loads associated with higher loading rates, smaller push-off forces associated with lower unloading rates and lower vertical impulses. Under such circumstances, for a swift transition from stance to swing, the support of the body weight and the maintenance of balance is made possible at a higher cadence, which in turn provokes a higher speed when trunk flexion increases.

5.3 Leg function: human versus avian

The morphological discrepancies and disproportions can affect the modes of locomotion. Despite some morphological differences such as femur orientation and an tarsometatarsal shape as well as moving posture (digitigrade in birds vs. plantigrade in human), both humans and avian use bipedalism. A comparative biomechanical analysis of their locomotion advances our understanding of terrestrial locomotion.

In part of this work, we aimed to explore the biomechanical aspects of human walking while mimicking pronograde posture in birds. Human walkers were instructed to reorient their trunk to 30°, 50° and maximum flexion in the sagittal plane while walking on both level and uneven ground. Build upon our knowledge obtained from the previous study (Andrada et al. 2014) where the influence of the pronograde posture on leg function in small birds was scrutinized, we were interested in examining the effects of such trunk geometry in human locomotion (Fig. 5-1). To do so, we investigated the leg function – characterized by effective leg length (connecting hip to CoP) and axial leg force (projected GRF onto effective leg vector) – under different walking postures. The leg function is linked to the trunk orientation. In humans with an erect trunk orientation, the leg can operate in a more elastic and flexible fashion owing to the location of the hip below the CoM. In the human runners, a slightly behind and apparently inferior position of the hip relative to the CoM results in a high elastic storage and allows a less asymmetric operation of the legs (Blickhan et al. 2015). When this close to a vertical arrangement varies by e.g. a forward shift of the trunk orientation, the functional task of stability during locomotion induces some constraints on the leg function.

An increased sagittal trunk flexion led to increasingly greater kinetic and kinematic intra-limb asymmetries during level walking (Figs.5-1D and E). The effective leg length which behaved independent of walking postures by remaining unchanged at TD tended to become increasingly shorter at toe-off by bending the trunk more anteriorly (Figs.5-1C and D). Meanwhile, maintaining a sufficient step length during trunk-flexed gaits required a flatter leg angle at TD to offset a posterior shift of the pelvis. Walking with increasing trunk flexion is performed by a sustained knee flexion throughout the stance phase coupled with an increased hip and ankle flexion, leading to a decreased angular range of motion across lower limb joints. In addition, in the trunk-flexed gaits, TO occurred swifter at a steeper angle with more flexed lower limb joints than in upright walking in order to maintain stability during each step. The kinematic analysis of bird's locomotion also revealed a comparable asymmetric leg function (Andrada et al. 2014).

Proceeding to a maximum trunk flexion transformed the symmetric, M-shaped vertical GRF pattern to a right-skewed one, characterized by a higher first peak of the vertical GRF than the second one (Fig. 5-1H). Moreover, the braking phase tended to be shorter than the propulsion phase. Under such circumstances, walking with a constant locomotion velocity requires the greater braking forces than the propulsive forces (i.e., zero impulse in horizontal direction). Interestingly, the similar kinetic behavior, interpreted as a kinetic asymmetry, has been found in the locomotion of the small birds. A functional task of balancing a heavy trunk during locomotion, particularly in a more horizontal posture can substantially affect the stiffness and damping properties of the leg. The more anteriorly shifted the trunk, the greater the leg damping since counteracting the acceleration of the CoM may necessitate the leg to dissipate energy. In a simulation model by Andrada et al. (2014), the damper was found to cause an asymmetric profile of the GRFs by exerting greater forces at TD and attenuated forces late in the stance phase. This led to an earlier TO. Therefore, a reduced braking time and subsequently the greater forces at early stance phase induced by an augmented leg damping in the leg right-skews the vertical GRF profile. Given these similarities in the leg function between birds and humans (when maintaining a bent trunk) we assert that the maintenance of a bent posture, at least in these two species, constrains the basic properties of the leg function independent of the specific leg morphology.

5.4 Stability during an expected twofold perturbation

As mentioned before, the study of the reactive and the proactive responses of biological or technical systems to both or either internal and external perturbations helps to advance our understanding of how the normal locomotor synergy is adapted to the properties of the environment. Our locomotor system is capable of adapting the motor behavior to the disturbing environmental conditions in order to minimize the error likelihood however at the cost of higher efforts, for example, by means of more rapid corrective movements, an increased muscular contraction or altered movement patterns (van Dieën et al. 2003; Emken et al. 2007; Franklin et al. 2007; Izawa et al. 2008).

The postural synergy integrated by the CNS is task- and perturbation-specific. The maintenance of the stability — as the most important concern during locomotion — constraints the planning and modulation of the motor pattern for achieving the target motor goal (Winter et al. 1990). For example, the modulation of e.g. the step length for a proper placement of the foot in response to changes in environment requires a prompt synergy of our locomotor system to ensure the dynamic stability. Therefore, perturbations might elicit context-specific adaptations as they vary in terms of quality and quantity. On the other hand, the quality and the quantity of the adaptations are contingent upon the adaptability of a system. In this work, we examined the mechanical behavior of human locomotor system in response to the destabilizing agents (i.e., altered postures and uneven ground) that could induce a deviation from a desired steady state during locomotion. In both experimental and simulation locomotion-focused studies, one of the conventional methods to explore the stability and robustness is to study the behavior of a system in confrontation with changes in ground levels. The goal of such perturbation experiment is to determine, in first place, whether the system is capable of disturbance avoidance, and in the second place, what adaptive or/and compensatory mechanisms may emerge for accomplishment of the task.

When envisioning the spatial properties of the ground during locomotion, the visual perception of the environment may allow pre-adaptations in our locomotor systems to deal with external perturbations (Muller et al. 2014). In fact, incoming visual information from the environment is key to the selection of the appropriate responses and eventually a tailored motor response programming. The quality of all these involved stages in the information-processing can be influenced by the external and the internal conditions. The study of human walking across uneven ground with a regular upright trunk (Muller et al. 2014) has demonstrated the step-specific kinematic and kinetic adjustments to the variable-height changes in ground level. In a preceding step to the hole, the kinematic adjustments are not merely limited to the lower limbs, but also involve the trunk. Muller et al. (2014) further showed that obscuring the perturbation, which restricts the visually guided preadaptations, leads to the reduced kinematic adjustments prior to stepping down into the hole. In the visible perturbed steps (i.e., the drop), the individuals land without making considerable kinematic changes at TD; however, the GRF first peak systematically increases with the drop height. During step into a camouflaged drop, the kinematic and the kinetic adjustments were found to be augmented. For instance, a decrease and an increase in trunk angle at TD and TO, respectively, and an increase and a decrease in the GRF first and second peaks, respectively are greater than those of walking across visible changes in ground level (Muller et al. 2014). This indicates context-specific adaptations in the kinematic and the kinetic aspects of human locomotor system.

To further identify the ability of locomotor apparatus, and to elicit the functional role of the trunk, we tested the human bipedal locomotion with various trunk orientations – up to maximal sagittal trunk flexion – while traversing a hole in the ground. Specifically, we explored the interaction effects between step and posture on a multiple number of kinematic and kinetic parameters of human walking. The step-specific effects of posture were more pronounced on the kinematic parameters than the kinetic ones. This implies that the maintenance of dynamic balance in able-bodied individuals when their trunk orientation deviates from upright during uneven walking requires a greater modulation of the leg kinematics. These kinematic adjustments led to the lower variations in gait kinetics as we observed the reduced between-step adjustments in the GRF parameters during trunk-flexed gaits.

In our study, the control of the trunk movement during the negotiation of a visible drop in ground was found imperative in able-bodied walking. Since two-thirds of the total body mass is located at two-thirds of the body height from the ground (Winter etal.,1990), alteration of the trunk orientation can have a substantial impact on the dynamics of the CoM. During normal walking, the CoM lies posterior to the heel at the beginning of the single support, shifts anteriorly with the forward momentum of the body and moves toward outside of the base of support during the push-off (Winter etal.,1990). Walking, therefore, is described as a "continuous process of recovery from a loss of balance" (Murray et al. 1969), and the only way to prevent falling is a proper positioning of the swinging foot lateral to and ahead of a forward-moving CoM. Here, we challenged this functional task in able-bodied walkers not only by reorienting the trunk posture, but also by presenting an expected step-down to human walkers to see how these types of perturbations can interfere with a prime functional goal of human locomotion, namely stability. To maintain the stability of gait during negotiating a step-down, as in stepping from a curb, an increased forward momentum of the body during the descent, must be controlled. In our study, the step-specific and more precisely the TD- and TO-specific kinematic adjustments, leading to the consistent between-step GRF parameters during trunk-flexed gaits in uneven ground demonstrated the capacity of the able-bodied walkers to deal with such an expected destabilizers factors. In fact, the stability of a periodic movement found not to be hampered by increasing the trunk flexion so that the deviation of the kinematic trajectories was small and within a range observed during locomotion with an upright trunk. Although the young, able walkers in this laboratory experiment successfully executed the tasks by returning to the undisturbed path within a following step-up; however, it is unknown how individuals with poor gait and balance capacities such as post-stroke, Parkinson and likely older adults accommodate changes in ground level and to which extent the recovery from the perturbation would be strenuous for them.

As a consequence, the study of the able-bodied gait in the presence of an expected twofold perturbation allowed us to shed some light on the mechanics of the human locomotor system and mechanisms underlying the gait stability. Our findings highlighted the functional role of the trunk as a measure to accommodate uneven ground. The trunk tended to rotate backward, regardless of maintaining various degrees of sagittal trunk flexion, as the body approached the drop. We argue that this may be a compensatory mechanism ahead of stepping down that contributes to the gait stability by reducing the kinetic energy that the body gains during descent (van Dieën et al. 2008; van Dieen and Pijnappels 2009). When it comes to control, the able-bodied walkers are found capable of regulating the whole-body angular momentum actively specific to the task requirements (Silverman et al. 2012). The results of a study by Silverman et al. (2012) showed that during able gait the individuals modulate the angular momentun on sloped surfaces different than level walking. They asserted that walking on an irregular surface, such as a sloped terrain, is associated with a larger range of angular momentum in incline walking than level walking. This requires a strict control of the whole-body angular momentum to help prevent a slip or fall. In addition, directing the GRFs to a point above the CoM of the whole-body (virtual pivot point, VPP) is known to stabilize both upright human gait (Maus et al. 2010) and pronograde avian gait (Andrada et al. 2014) such as a physical pendulum. Both increasing trunk flexion and stepping downwards could potentially alter the relative position of the VPP with respect to the CoM as they increase forward rotation of the system. For instance, a forward shift of the CoM due to trunk bending in the sagittal plane induces larger hip extension torques and less flexion torques which in turn leads to an intra-limb asymmetry of the GRF patterns, i.e. higher forces early in stance phase and lower forces as approaching the toe-off. There, the control of total angular momentum requires smaller and larger lever arms of the GRFs with respect to the CoM, respectively. Furthermore, this is associated with an intersection point of the GRFs which emerges posteriorly and more superiorly to the CoM of the whole-body as compared to upright walking. Having observed the existence of VPP in walking with various trunk orientations, but varying in terms of relative position to the whole-body CoM, this strategy can therefore contribute to the control of the angular momentum during motor tasks (Müller et al. 2017).

Knowing the short and long-term consequences of fall, coupled with devoting significant efforts to identifying the risk factors and developing screening and prevention modalities, our findings may be of clinical importance for clinician to place more emphasis on the functional performance of the trunk during locomotion not only for the evaluation of dysfunctional gait, but also in the design, development and monitoring of the progression of the rehabilitation programs. At mechanical level, our findings suggest that proceeding to a maximum trunk flexion (i.e., zig-zag-like configuration), the upper body seems to be transformed into an active component of the human locomotor system by adjusting its angle during the step-down. Such a compensatory mechanism as achieved by the global kinematic adjustments, with the aim of reducing the variation in the CoM height, manifested to facilitate the negotiation of changes in ground level. These results highlight how able-bodied walkers modulate the whole-body posture relative to an expected twofold perturbation, and provide a baseline for making comparison with individuals with compromised balance derived from postural impairments or spinal deformities.

5.5 Limitation and perspectives for the future studies

This thesis has focused on the adjustment of posture as a measure for accommodating uneven ground to elucidate the role of trunk in human walking. To this end, we developed an empirical experiment to explore the walking pattern of the young, able-bodied participants under an expected twofold perturbation. To simulate uneven ground in outdoor setting, we used a custom-build walkway which allowed us to lower a height-adjustable force-platform by 10-cm as a drop. Such experimental designs always involve inherent limits in terms of the reliability and quantity of the data that can be collected. Here, due to the experiment setup, our measurement volume was restricted to three consecutive steps and the participants were permitted to perform the practice trials prior to the data collection in order to be familiar with the task and the setup. Therefore, our evaluations were made only across limited contacts and the motor behavior of participants during the experiment was likely influenced by learning experience. The locomotion in the real world may elicit different posture and gait control strategies than in the laboratory setting. Another limitation concerns the visibility of the perturbation. It has been well documented that the availability of visual stimuli can substantially affect the quality and the quantity of adaptations to the environmental perturbations (Muller et al. 2014). Furthermore, due to the organizational reasons and the complexity of executing the strenuous styles of walking with a high number of repetitions (64 successful trials per subject), our experiment in terms of setup, namely first level walking and secondly uneven walking, and the postural task, i.e. an incremental increase of trunk angle, was implemented in a fixed and unrandomized fashion. The order effect was thus not avoided. In addition, to eliminate the effect of the leg dominance (Sadeghi et al. 2000) on the biomechanical adjustments particularly during uneven walking, participants were instructed to regulate their consecutive steps in a left-right-left sequence. Build upon the limitations listed above, the future studies may simply address or modify these criteria to gain more insight into the interaction between posture and locomotion.

Given the specificity of the neuromechanical responses to the nature of perturbations and the locomotion tasks, further research is needed to differentiate the biomechanical behavior of human gait (both walking and running) while encountering surfaces with various properties. For instance, walking across obscured perturbations, adopting other walking postures, introducing gait to various drop or obstacle heights and the presence of unexpected changes in ground level all may elicit the mechanical responses that are significantly different from those we observed in our work.

Moreover, additional techniques such as the inverse dynamic for the calculation of the energetics of lower limb joints, and the electromyography (EMG) for the measurement of the muscular activity as supplementary procedures to the kinematic and the kinetic aspects of the gait can provide more analytical depth about the effects of the alteration in posture on lower limb dynamics. Using wearable technologies e.g. a tri-axial accelerometer to measure an overall and directional trunk acceleration amplitudes as well as the trunk acceleration ratio during walking on even and uneven ground may assist us in improving our understanding of the role of trunk in the mobility of patients — who exhibit trunk-flexed postures — in interaction with changes in ground level.

As referred to before, the present work may serve as a basis for the clinical studies on the pathological populations who exhibit an altered trunk orientation and might be therefore at a higher risk of fall during locomotion. For example, the extension of current insight to the clinical biomechanics with a special emphasis on the role of trunk kinematics on dynamics of walking in older adults might be of research interest. This may involve investigating the adaptive capacities of walking while negotiating various typical terrain perturbations faced by older adults during every day locomotion such as an obstacle, a drop or stepping down from and stepping up onto a curb. By comparing the proactive and the reactive motor responses of the elderly to changes in ground levels with that of the young, healthy counterparts, we may be able to characterize the degrees by which the control strategies and the adaptive mechanisms may have been influenced by age. Understanding, for instance, the quality of trunk contribution to gait dynamics can lead to a better identification of mechanisms underlying fall, as elderlies are known to exhibit some degrees of inclined trunk orientation which may in turn reduce their ability to respond to perturbations during walking. Therefore, further understanding of the key aspects of the gait in elderlies can guide the advancement of the fall prevention strategies and the applied clinical interventions.

Bibliography

Alexander, R. M. (2003). Principles of animal locomotion, Princeton University Press.

Alexander, R. M. (2004). "Bipedal animals, and their differences from humans." J Anat **204**: 321-330.

Allen, V., K. T. Bates, Z. Li and J. R. Hutchinson (2013). "Linking the evolution of body shape and locomotor biomechanics in bird-line archosaurs." Nature **497**: 104-107.

Andrada, E., J. A. Nyakatura, F. Bergmann and R. Blickhan (2013). "Adjustments of global and local hindlimb properties during terrestrial locomotion of the common quail (Coturnix coturnix)." Journal of Experimental Biology **216**: 3906-3916.

Andrada, E., C. Rode, Y. Sutedja, J. A. Nyakatura and R. Blickhan (2014). "Trunk orientation causes asymmetries in leg function in small bird terrestrial locomotion." Proc Biol Sci **281**.

Asay, J. L., A. Mündermann and T. P. Andriacchi (2009). "Adaptive patterns of movement during stair climbing in patients with knee osteoarthritis." Journal of Orthopaedic Research **27**: 325-329.

Balzini, L., L. Vannucchi, F. Benvenuti, M. Benucci, M. Monni, A. Cappozzo and S. J. Stanhope (2003). "Clinical characteristics of flexed posture in elderly women." Journal of the American Geriatrics Society **51**: 1419-1426.

Bartholomew, G. A. and H. H. Caswell (1951). "Locomotion in kangaroo rats and its adaptive significance." Journal of Mammalogy **32**: 155-169.

Berg, W. P., H. M. Alessio, E. M. Mills and C. Tong (1997). "Circumstances and consequences of falls in independent community-dwelling older adults." Age and ageing **26**: 261-268.

Biewener, A. A. (1989). "Scaling body support in mammals: limb posture and muscle mechanics." Science **245**: 45-48.

Blackburn, J. T. and D. A. Padua (2008). "Influence of trunk flexion on hip and knee joint kinematics during a controlled drop landing." Clinical Biomechanics **23**: 313-319.

Blackburn, J. T. and D. A. Padua (2009). "Sagittal-plane trunk position, landing forces, and quadriceps electromyographic activity." Journal of Athletic Training **44**: 174-179.

Blickhan, R., E. Andrada, R. Muller, C. Rode and N. Ogihara (2015). "Positioning the hip with respect to the COM: Consequences for leg operation." Journal of Theoretical Biology **382**: 187-197.

Blickhan, R., M. Ernst, M. Koch and R. Muller (2013). "Coping with disturbances." Hum Mov Sci **32**: 971-983.

Blickhan, R., M. Ernst, M. Koch and R. Müller (2013). "Coping with disturbances." Human movement science **32**: 971-983.

Blum, Y., A. Birn-Jeffery, M. A. Daley and A. Seyfarth (2011). "Does a crouched leg posture enhance running stability and robustness?" Journal of Theoretical Biology **281**: 97-106.

Borghese, N. A., L. Bianchi and F. Lacquaniti (1996). "Kinematic determinants of human locomotion." The Journal of physiology **494**: 863-879.

Bramble, D. M. and D. E. Lieberman (2004). "Endurance running and the evolution of Homo." Nature **432**: 345-352.

Cavagna, G. A., N. C. Heglund and C. R. Taylor (1977). "Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure." American Journal of Physiology-Regulatory, Integrative and Comparative Physiology **233**: R243-R261.

Cavagna, G. A., H. Thys and A. Zamboni (1976). "The sources of external work in level walking and running." The Journal of physiology **262**: 639-657.

D'Août, K., P. Aerts, D. De Clercq, K. De Meester and L. Van Elsacker (2002). "Segment and joint angles of hind limb during bipedal and quadrupedal walking of the bonobo (Pan paniscus)." American journal of physical anthropology **119**: 37-51.

Daley, M. A. and J. R. Usherwood (2010). "Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain." Biology letters **6**: 418-421.

Davidson, P. R. and D. M. Wolpert (2005). "Widespread access to predictive models in the motor system: a short review." Journal of Neural Engineering **2**: S313.

de Groot, M. H., H. C. van der Jagt-Willems, J. P. van Campen, W. F. Lems, J. H. Beijnen and C. J. Lamoth (2014). "A flexed posture in elderly patients is associated with impairments in postural control during walking." Gait Posture **39**: 767-772.

Dean, C. (1990). An introduction to human evolutionary anatomy, Academic Press.

Dietz, V. (2003). "Spinal cord pattern generators for locomotion." Clinical Neurophysiology **114**: 1379-1389.

Dietz, V., J. Quintern and M. Sillem (1987). "Stumbling reactions in man: significance of proprioceptive and pre-programmed mechanisms." J Physiol **386**: 149-163.

Dominici, N., Y. P. Ivanenko, G. Cappellini, A. d'Avella, V. Mondì, M. Cicchese, A. Fabiano, T. Silei, A. Di Paolo and C. Giannini (2011). "Locomotor primitives in newborn babies and their development." Science **334**: 997-999.

Donelan, J. M. and R. Kram (2001). "Mechanical and metabolic determinants of the preferred step width in human walking." Proceedings of the Royal Society of London B: Biological Sciences **268**: 1985-1992.

Emken, J. L., R. Benitez, A. Sideris, J. E. Bobrow and D. J. Reinkensmeyer (2007). "Motor adaptation as a greedy optimization of error and effort." Journal of Neurophysiology **97**: 3997-4006.

Farcy, J. P. and F. J. Schwab (1997). "Management of flatback and related kyphotic decompensation syndromes." Spine (Phila Pa 1976) **22**: 2452-2457.

Forssberg, H. (1985). "Ontogeny of human locomotor control I. Infant stepping, supported locomotion and transition to independent locomotion." Experimental Brain Research **57**: 480-493.

Franklin, D. W., G. Liaw, T. E. Milner, R. Osu, E. Burdet and M. Kawato (2007). "Endpoint stiffness of the arm is directionally tuned to instability in the environment." Journal of Neuroscience **27**: 7705-7716.

Galik, K., B. Senut, M. Pickford, D. Gommery, J. Treil, A. J. Kuperavage and R. B. Eckhardt (2004). "External and internal morphology of the BAR 1002'00 Orrorin tugenensis femur." Science **305**: 1450-1453.

Gallagher, S., J. Pollard and W. L. Porter (2011). "Locomotion in restricted space: kinematic and electromyographic analysis of stoopwalking and crawling." Gait Posture **33**: 71-76.

Ganz, D. A., Y. Bao, P. G. Shekelle and L. Z. Rubenstein (2007). "Will my patient fall?" Jama **297**: 77-86.

Garcia-Rill, E. (1986). "The basal ganglia and the locomotor regions." Brain Research Reviews **11**: 47-63.

Garwicz, M., M. Christensson and E. Psouni (2009). "A unifying model for timing of walking onset in humans and other mammals." Proceedings of the National Academy of Sciences **106**: 21889-21893.

Gatesy, S. M., Biewener, A., A. (1991). "Bipedal locomotion: effects of speed, size and limb posture in birds and humans." J Zool **224**: 127-147.

Geyer, H., A. Seyfarth and R. Blickhan (2003). "Positive force feedback in bouncing gaits?" Proceedings of the Royal Society of London B: Biological Sciences **270**: 2173-2183.

Geyer, H., A. Seyfarth and R. Blickhan (2006). "Compliant leg behaviour explains basic dynamics of walking and running." Proceedings of the Royal Society B-Biological Sciences **273**: 2861-2867.

Goh, J., A. Thambyah and K. Bose (1998). "Effects of varying backpack loads on peak forces in the lumbosacral spine during walking." Clinical Biomechanics **13**: S26-S31.

Grasso, R., A. Peppe, F. Stratta, D. Angelini, M. Zago, P. Stanzione and F. Lacquaniti (1999). "Basal ganglia and gait control: apomorphine administration and internal pallidum stimulation in Parkinson's disease." Experimental Brain Research **126**: 139-148.

Grasso, R., M. Zago and F. Lacquaniti (2000). "Interactions between posture and locomotion: Motor patterns in humans walking with bent posture versus erect posture." Journal of Neurophysiology **83**: 288-300.

Haile-Selassie, Y. (2001). "Late Miocene hominids from the middle Awash, Ethiopia." Nature **412**: 178-181.

Hancock, J. A., N. J. Stevens and A. R. Biknevicius (2007). "Whole-body mechanics and kinematics of terrestrial locomotion in the Elegant-crested Tinamou Eudromia elegans." Ibis **149**: 605-614.

Hasday, C. A., T. L. Passoff and J. Perry (1983). "Gait abnormalities arising from latrogenic loss of lumbar lordosis secondary to Harrington instrumentation in lumbar fractures." Spine **8**: 501-511.

Hirasaki, E., N. Ogihara, Y. Hamada, H. Kumakura and M. Nakatsukasa (2004). "Do highly trained monkeys walk like humans? A kinematic study of bipedal locomotion in bipedally trained Japanese macaques." Journal of Human Evolution **46**: 739-750.

Hirasaki, E., N. Ogihara, Y. Hamada, H. Kumakura and M. Nakatsukasa (2004). "Do highly trained monkeys walk like humans? A kinematic study of bipedal locomotion in bipedally trained Japanese macaques." J Hum Evol **46**: 739-750.

Hirschfeld, H. and H. Forssberg (1991). "Phase-dependent modulations of anticipatory postural activity during human locomotion." Journal of Neurophysiology **66**: 12-19.

Höhne, A., C. Stark, G.-P. Brüggemann and A. Arampatzis (2011). "Effects of reduced plantar cutaneous afferent feedback on locomotor adjustments in dynamic stability during perturbed walking." Journal of biomechanics **44**: 2194-2200.

Irschick, D. J. and B. C. Jayne (1999). "Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards." Journal of Experimental Biology **202**: 1047-1065.

Ivanenko, Y. P., N. Dominici and F. Lacquaniti (2007). "Development of independent walking in toddlers." Exercise and sport sciences reviews **35**: 67-73.

Ivanenko, Y. P., W. G. Wright, V. S. Gurfinkel, F. Horak and P. Cordo (2006). "Interaction of involuntary post-contraction activity with locomotor movements." Experimental Brain Research **169**: 255-260.

Ivanenko, Y. P., W. G. Wright, R. St George and V. S. Gurfinkel (2013). "Trunk orientation, stability, and quadrupedalism." Frontiers in neurology **4**.

Izawa, J., T. Rane, O. Donchin and R. Shadmehr (2008). "Motor adaptation as a process of reoptimization." Journal of Neuroscience **28**: 2883-2891.

Kimura, T. (1996). "Centre of gravity of the body during the ontogeny of chimpanzee bipedal walking." Folia Primatologica **66**: 126-136.

Kluger, D., M. J. Major, S. Fatone and S. A. Gard (2014). "The effect of trunk flexion on lower-limb kinetics of able-bodied gait." Hum Mov Sci **33**: 395-403.

Kluzik, J., F. B. Horak and R. J. Peterka (2005). "Differences in preferred reference frames for postural orientation shown by after-effects of stance on an inclined surface." Experimental Brain Research **162**: 474-489.

Kuo, A. D. (2007). "The six determinants of gait and the inverted pendulum analogy: A dynamic walking perspective." Human movement science **26**: 617-656.

La Grone, M. (1988). "Loss of lumbar lordosis. A complication of spinal fusion for scoliosis." The Orthopedic clinics of North America **19**: 383-393.

Lacquaniti, F., Y. P. Ivanenko and M. Zago (2012). "Development of human locomotion." Current opinion in neurobiology **22**: 822-828.

Lacquaniti, F., C. Maioli, N. A. Borghese and L. Bianchi (1997). "Posture and movement: coordination and control." Arch Ital Biol **135**: 353-367.

Lee, D. V., M. R. Isaacs, T. E. Higgins, A. A. Biewener and C. P. McGowan (2014). Scaling of the Spring in the Leg during Bouncing Gaits of Mammals, The Society for Integrative and Comparative Biology.

Leteneur, S., C. Gillet, H. Sadeghi, P. Allard and F. Barbier (2009). "Effect of trunk inclination on lower limb joint and lumbar moments in able men during the stance phase of gait." Clinical Biomechanics **24**: 190-195.

Leteneur, S., E. Simoneau, C. Gillet, Y. Dessery and F. Barbier (2013). "Trunk's Natural Inclination Influences Stance Limb Kinetics, but Not Body Kinematics, during Gait Initiation in Able Men." PLoS One **8**.

Lovejoy, C. O. (2005). "The natural history of human gait and posture: Part 1. Spine and pelvis." Gait & Posture **21**: 95-112.

Marigold, D. S. and A. E. Patla (2002). "Strategies for dynamic stability during locomotion on a slippery surface: effects of prior experience and knowledge." Journal of Neurophysiology **88**: 339-353.

Massion, J. (1992). "Movement, posture and equilibrium: interaction and coordination." Prog Neurobiol **38**: 35-56.

Maus, H. M., S. W. Lipfert, M. Gross, J. Rummel and A. Seyfarth (2010). "Upright human gait did not provide a major mechanical challenge for our ancestors." Nat Commun **1**: 70.

McMahon, T. A., G. Valiant and E. C. Frederick (1987). "Groucho running." J Appl Physiol (1985) **62**: 2326-2337.

Merker, A., J. Rummel and A. Seyfarth (2011). "Stable walking with asymmetric legs." Bioinspir Biomim **6**: 045004.

Mori, S. (1987). "Integration of posture and locomotion in acute decerebrate cats and in awake, freely moving cats." Progress in neurobiology **28**: 161-195.

Muller, R., A. V. Birn-Jeffery and Y. Blum (2016). "Human and avian running on uneven ground: a model-based comparison." J R Soc Interface **13**.

Müller, R., C. Rode, S. Aminiaghdam, J. Vielemeyer and R. Blickhan (2017). Force direction patterns promote whole body stability even in hip-flexed walking, but not upper body stability in human upright walking. Proc. R. Soc. A, The Royal Society.

Muller, R., K. Tschiesche and R. Blickhan (2014). "Kinetic and kinematic adjustments during perturbed walking across visible and camouflaged drops in ground level." J Biomech **47**: 2286-2291.

Murray, M. P., R. C. Kory and B. H. Clarkson (1969). "Walking patterns in healthy old men." Journal of gerontology **24**: 169-178.

Napier, J. R. and P. H. Napier (1967). "A handbook of living primates."

Oberländer, K. D., G.-P. Brüggemann, J. Höher and K. Karamanidis (2012). "Reduced knee joint moment in ACL deficient patients at a cost of dynamic stability during landing." Journal of biomechanics **45**: 1387-1392.

Perry, J. and J. R. Davids (1992). "Gait analysis: normal and pathological function." Journal of Pediatric Orthopaedics **12**: 815.

Pontzer, H., D. A. Raichlen and M. D. Sockol (2009). "The metabolic cost of walking in humans, chimpanzees, and early hominins." J Hum Evol **56**: 43-54.

Potter, B. K., L. G. Lenke and T. R. Kuklo (2004). "Prevention and management of iatrogenic flatback deformity." JBJS **86**: 1793-1808.

Qiao, M. and D. L. Jindrich (2014). Compensations during unsteady locomotion, Oxford University Press.

Radford, T. (2013). "Human evolution: Us and them." Nature **503**: 34-35.

Roberts, T. J. and E. Azizi (2011). "Flexible mechanisms: the diverse roles of biological springs in vertebrate movement." Journal of Experimental Biology **214**: 353-361.

Rose, J. and J. Gamble (1994). Human walking. 2nd ed. Baltimore, Williams & Wilkins.

.

Rubenson, J., D. B. Heliams, D. G. Lloyd and P. A. Fournier (2004). "Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase." Proceedings of the Royal Society B: Biological Sciences **271**: 1091.

Sadeghi, H., P. Allard, F. Prince and H. Labelle (2000). "Symmetry and limb dominance in able-bodied gait: a review." Gait Posture **12**: 34-45.

Saha, D., S. Gard and S. Fatone (2008). "The effect of trunk flexion on able-bodied gait." Gait Posture **27**: 653-660.

Saibene, F. and A. E. Minetti (2003). "Biomechanical and physiological aspects of legged locomotion in humans." European journal of applied physiology **88**: 297-316.

Selionov, V. A., Y. P. Ivanenko, I. A. Solopova and V. S. Gurfinkel (2009). "Tonic central and sensory stimuli facilitate involuntary air-stepping in humans." Journal of Neurophysiology **101**: 2847-2858.

Shen, Z. H. and J. E. Seipel (2012). "A fundamental mechanism of legged locomotion with hip torque and leg damping." Bioinspir Biomim **7**: 046010.

Sherrington, C. (1906). "Yale University Mrs. Hepsa Ely Silliman memorial lectures. The integrative action of the nervous system."

Shimokochi, Y., S. Yong Lee, S. J. Shultz and R. J. Schmitz (2009). "The relationships among sagittal-plane lower extremity moments: implications for landing strategy in anterior cruciate ligament injury prevention." Journal of Athletic Training **44**: 33-38.

Shinya, M., S. Fujii and S. Oda (2009). "Corrective postural responses evoked by completely unexpected loss of ground support during human walking." Gait & Posture **29**: 483-487.

Silverman, A. K., J. M. Wilken, E. H. Sinitski and R. R. Neptune (2012). "Whole-body angular momentum in incline and decline walking." Journal of biomechanics **45**: 965-971.

Sinaki, M., R. H. Brey, C. A. Hughes, D. R. Larson and K. R. Kaufman (2005). "Balance disorder and increased risk of falls in osteoporosis and kyphosis: significance of kyphotic posture and muscle strength." Osteoporos Int **16**: 1004-1010.

Snyder, R. C. (1952). "Quadrupedal and bipedal locomotion of lizards." Copeia **1952**: 64-70.

Sockol, M. D., D. A. Raichlen and H. Pontzer (2007). "Chimpanzee locomotor energetics and the origin of human bipedalism." Proc Natl Acad Sci U S A **104**: 12265-12269.

Storer, R. W. (1971). "Classification of birds." Avian biology **1**: 1-18.

Teng, H.-L. (2013). Influence of sagittal plane trunk posture on lower extremity biomechanics during running, University of Southern California.

Teng, H.-L. and C. M. Powers (2015). "Influence of trunk posture on lower extremity energetics during running." Med Sci Sports Exerc **47**: 625-630.

Thorstensson, A., J. Nilsson, H. Carlson and M. R. ZOMLEFER (1984). "Trunk movements in human locomotion." Acta Physiologica **121**: 9-22.

Tobias, P. (1992). "The upright head in hominid evolution." The Head–Neck Sensory Motor System: 5-16.

van Dieën, J. H., I. Kingma and J. Van der Bug (2003). "Evidence for a role of antagonistic cocontraction in controlling trunk stiffness during lifting." Journal of biomechanics **36**: 1829-1836.

van Dieen, J. H. and M. Pijnappels (2009). "Effects of conflicting constraints and age on strategy choice in stepping down during gait." Gait Posture **29**: 343-345.

van Dieen, J. H., M. Spanjaard, R. Konemann, L. Bron and M. Pijnappels (2007). "Balance control in stepping down expected and unexpected level changes." J Biomech **40**: 3641-3649.

van Dieën, J. H., M. Spanjaard, R. Könemann, L. Bron and M. Pijnappels (2008). "Mechanics of toe and heel landing in stepping down in ongoing gait." Journal of biomechanics **41**: 2417-2421.

Vereecke, E., K. D'Août, D. De Clercq, L. Van Elsacker and P. Aerts (2003). "Dynamic plantar pressure distribution during terrestrial locomotion of bonobos (Pan paniscus)." American journal of physical anthropology **120**: 373-383.

Voloshina, A. S., A. D. Kuo, M. A. Daley and D. P. Ferris (2013). "Biomechanics and energetics of walking on uneven terrain." Journal of Experimental Biology **216**: 3963-3970.

Wang, T.-M., H.-P. Huang, J.-D. Li, S.-W. Hong, W.-C. Lo and T.-W. Lu (2015). "Leg and joint stiffness in children with spastic diplegic cerebral palsy during level walking." PLoS One **10**: e0143967.

Ward, C. V. (2002). "Interpreting the posture and locomotion of Australopithecus afarensis: Where do we stand?" American journal of physical anthropology **119**: 185-215.

Wasylenko, M., S. R. Skinner, J. Perry and D. J. Antonelli (1983). "An analysis of posture and gait following spinal fusion with Harrington instrumentation." Spine **8**: 840-845.

Winter, D. A. (1991). Biomechanics and motor control of human gait: normal, elderly and pathological.

Winter, D. A. (1995). "Human balance and posture control during standing and walking." Gait & Posture **3**: 193-214.

Winter, D. A. (2009). Biomechanics and motor control of human movement, John Wiley & Sons.

Winter, D. A., A. E. Patla and J. S. Frank (1990). "Assessment of balance control in humans." Med prog technol **16**: 31-51.

Wright, W. (2011). "Tonic postural lean after-effects influenced by support surface stability and dynamics." Human movement science **30**: 238-248.

Wright, W. G., Y. P. Ivanenko and V. S. Gurfinkel (2012). "Foot anatomy specialization for postural sensation and control." Journal of Neurophysiology **107**: 1513-1521.

Wunderlich, R. and J. Schaum (2007). "Kinematics of bipedalism in Propithecus verreauxi." Journal of Zoology **272**: 165-175.

Zollikofer, C. P., M. S. P. de León, D. E. Lieberman, F. Guy, D. Pilbeam, A. Likius, H. T. Mackaye, P. Vignaud and M. Brunet (2005). "Virtual cranial reconstruction of Sahelanthropus tchadensis." Nature **434**: 755-759.

Curriculum vitae

Name: Soran Aminiaghdam
Citizenship: Iranian
Date of birth: 16 September 1982
Place of birth: Mahabad, Iran
Marital status: Married

Education

- 10.2014 onward, PhD student, the Department of Motion Science at the Institute of Sport Science, Faculty of Social and Behavioral Sciences within Friedrich-Schiller University of Jena, Jena, Germany
- 03.2014-.07.2014, Diploma in Football, International Coaching Course, Leipzig University, Leipzig, Germany
- 07.2008-03.2014, faculty member at Islamic Azad University – Saghez branch, Saghez, Iran
- 09.2005-05.2007, M.Sc. in Physical Education and Sports Science with emphasis on Sports Traumatology, Razi University, Kermanshah, Iran. Thesis subject: Lower Extremity Malalignments and History of Knee Injuries
- 02.2002-07.2005, B.Sc. in Physical Education and Sports Science, The University of Guilan, Rasht, Iran
- 09.1999-07.2000, Pre-university degree (qualification for university entrance), Mahabad, Iran
- 1999, high school degree in Physics and Mathematics (Diploma), Mahabad, Iran

Publications in peer reviewed journals

- Aminiaghdam S., Rode C., Müller, R., Blickhan. R. (2017). Increasing trunk flexion transforms human leg function into that of birds despite different leg morphology. *Journal of Experimental Biology.* 220 (3): 478-486 (DOI http://dx.doi.org/10.1242/jeb.148312).

- Aminiaghdam S., Rode C. (2017). Effects of altered sagittal trunk orientation on kinetic pattern in able-bodied walking on uneven ground. *Biology Open*. 6, 1000-1007 (DOI https://doi.org/10.1242/bio.025239).

- Aminiaghdam S., Blickhan. R., Müller, R., Rode C. (2017). Posture alteration as a measure to accommodate uneven ground in able-bodied gait. *PLoS ONE*. 12(12): e0190135 (https://doi.org/10.1371/journal.pone.0190135).

- Müller, R., Aminiaghdam S., Vielemeyer, J., Blickhan. R., Rode C. (2017). Force direction patterns promote whole body stability even in hip-flexed walking, but not upper body stability in human upright walking. *Journal of The Royal Society Interface*. Nov; 473(2207): 20170404. (https://doi.org/10.1098/rspa.2017.0404)

- Aminiaghdam S., Blickhan. R. (2017). Effects of an expected twofold perturbation on spatial-temporal parameters of able-bodied gait: trunk flexion and uneven ground surface. *Journal of Gait & Posture*. [submitted]

Publications in conference proceedings

- Aminiaghdam, S., Rode, C., Blickhan, R. Interaction effects of posture and uneven ground on able-bodied walking kinetics. *35th International Conference on Biomechanics in Sports (ISBS)*, 14th-18th June 2017, German Sport University Cologne, Cologne, Germany. [oral]

Conference abstracts

- Aminiaghdam, S., Muller, R., Blickhan, R. Pronograde Locomotion Induces an Asymmetric Leg Function During Stance Phase in Able Men. *22nd Congress of the European Society of Biomechanics (ESB),* 10th-13th July 2016, Lyon, France. [oral]

- Aminiaghdam, S., Muller, R., Blickhan, R. Kinetic Adjustments as a Function of the Trunk Orientation in Able Men during Stance Phase of Walking. *22nd Congress of the European Society of Biomechanics (ESB),* 10th-13th July 2016, Lyon, France. [oral]

- Aminiaghdam, S., Blickhan, R., Muller, R. and Vielemeyer J. The Influence of Trunk Orientation on Lower Limb Kinematics and Leg Function. *21th annual congress of the European College of Sport Science (ECSS),* 6th-9th July 2016, Vienna, Austria. [oral]

Jena,

Erklärung

Hiermit erkläre ich, dass mir die geltende Promotionsordnung der Fakultät bekannt ist und dass ich die Dissertation selbst angefertigt habe, insbesondere die Hilfe eines Promotionsberaters nicht in Anspruch genommen, und alle von mir benutzten Hilfsmittel und Quellen in meiner Arbeit angegeben habe. Bei der Auswahl und Auswertung des Materials haben mich keine Personen unterstützt.

Die Kapitel 2–4 meiner Arbeit entsprechen den Anforderungen an Veröffentlichungen in internationalen wissenschaftlichen Zeitschriften. Bereits wissenschaftlich publiziert sind Kapitel 2 und 3, eingereicht und unter Begutachtung ist Kapitel 4. Für die publizierten und zur Publikation eingereichten Teile meiner Arbeit habe ich von meinen Mitautoren Dr. Christian Rode, Dr. Roy Müller und Prof. Dr. Reinhard Blickhan konzeptionelle Unterstützung bei der Erstellung der Manuskripte erhalten. Ich habe die Experimente und die statistischen Analysen durchgeführt. Dr. Christian Rode und ich haben die Manuskripte verfasst und die Gutachterkommentare bearbeitet. Weitere Personen haben mich bei der Erstellung der Manuskripte nicht unterstützt. Weiterhin erkläre ich, dass Dritte weder unmittelbar noch mittelbar geldwerte Leistungen von mir für Arbeiten erhalten haben, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen. Die Dissertation wurde noch nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung eingereicht und keine gleiche, in wesentlichen Teilen ähnliche oder andere Abhandlung liegt bei einer anderen Hochschule als Dissertation vor.

Ich versichere, nach bestem Wissen die reine Wahrheit gesagt und nichts verschwiegen zu haben.

Jena, 21.09.2017

Soran Aminiaghdam