"Biomechanical and muscular adjustments realized after a perturbation of unexpected timing evoked during running"

Scohier, Mikaël

Abstract
The present work focuses on the motor control after a sudden ankle dorsiflexion mechanically evoked during the swing phase of running. We investigated the running pattern adjustments and the muscular responses, reflex or not, realized after the perturbation. Results show that the running pattern adjustments are appropriate and modulated within the swing phase. The step length and duration are maintained as constant as possible to continue running at the speed imposed by the treadmill without stumbling or falling. The only strong modification is a decreased impact observed after the perturbations evoked in late swing, when the ankle is still in a more dorsiflexed position at foot touch-down. In human subjects, the stretch of a muscle evokes a series of electromyographic reflex bursts in this muscle called 'stretch reflex' responses. The sudden ankle dorsiflexion induces a stretch of the plantarflexors muscles. Our results show that the early component of the reflex response is sup...

Document type: Thèse (Dissertation)

Référence bibliographique
Scohier, Mikaël. Biomechanical and muscular adjustments realized after a perturbation of unexpected timing evoked during running. Prom. : Schepens, Bénédicte ; De Jaeger, Dominique
Biomechanical and muscular adjustments
realized after a perturbation of unexpected
timing evoked during running

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Thèse présentée en vue de l’obtention du grade de
docteur en sciences de la motricité

September 2014
Acknowledgements

This thesis is the result of a long-term process which started in September 2006. During this long adventure, I had the pleasure to meet people who helped me somehow. I could not present this work without mentioning some important persons who have largely contributed to this work.

First, I would like to thank all members of my jury: Gilles Cathy, Dominique De Jaeger, Christine Detrembleur, Jacques Duysens, Norman Heglund, Marc Francaux and Bénédicte Schepens. First, I thank Marc Francaux to have accepted to be the president of my jury. Then, I thank Christine Detrembleur for her precious comments during the meetings of the coordinating committee. I would also like to adress a special thank to Norman Heglund for his helpful comments and writing assistance. I thank all members, including Gilles Cathy and Jacques Duysens, for having accepted to read this thesis in depth. Your comments were precious and I hope I have correctly integrated all your advices to improve the document. Last but not least, I would like to thank and to express my sincere gratitude to my supervisors, Professors Bénédicte Schepens and Dominique De Jaeger, for their support and their guidance during all these years. Our collaboration was an enriching experiment from the scientific perspective as well as the human one. And even these last four years, despite our charged agenda, you always found any time to give me frequent and precious advices. Thank you for all Bénédicte and Dominique.
My acknowledgements are also dedicated to all my colleagues from the “Faculté des sciences de la motricité” and more specifically from the laboratory of the “Physiologie et biomécanique de la locomotion”. Thanks to all of you for our enriching exchanges. I address a special thank to Bruno Fievet for his technical assistance during the conception of the exoskeleton and to Guillaume Bastien for his precious help in program writing.

I would like also to thank my colleagues and the students from the “Haute Ecole Louvain en Hainaut”. You give me the opportunity to improve my knowledge through your questions and discussions.

All my gratitude goes also to my family, to my family-in-law and to all my friends. You offer me an adequate environment. Thanks to my parents for their permanent support. I know you had to make sacrifices in order to give us the possibility to do studies. I am proud to have so good parents. Thanks to my ‘little’ brother François for his writing assistance.

Finally, I am grateful to my wife. I think it is not always easy to accept that at times, I spend more time with my computer than with my family. I like so much every time spent with you and our two children Thibault and Clara. An huge thank to you Géraldine and to you Thibault and Clara. You are my first motivation.
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<tr>
<td>CNS</td>
<td>Central Nervous System</td>
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<tr>
<td>CV</td>
<td>Coefficient of Variation (%)</td>
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<td>Electromyography</td>
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<tr>
<td>$F_x$</td>
<td>Lateral component of the ground reaction force (N)</td>
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<td>$F_y$</td>
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<td>$F_{y,brake}$</td>
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<td>GRF</td>
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<td>$L_{pert}$</td>
<td>Left perturbed step</td>
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<td>LG</td>
<td>Lateral Gastrocnemius muscle</td>
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<tr>
<td>LLR</td>
<td>Long-Latency Response</td>
</tr>
<tr>
<td>MG</td>
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<tr>
<td>MLR</td>
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<tr>
<td>RF</td>
<td>Rectus Femoris muscle</td>
</tr>
<tr>
<td>SA</td>
<td>Symmetry Angle (%)</td>
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<tr>
<td><strong>SLR</strong></td>
<td>Short-Latency Response</td>
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<tr>
<td><strong>SM</strong></td>
<td>SemiMembranosus muscle</td>
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<td><strong>T</strong></td>
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<tr>
<td><strong>t1</strong></td>
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<tr>
<td><strong>t3</strong></td>
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<tr>
<td><strong>t4</strong></td>
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<td><strong>t5</strong></td>
<td>80-100% of the left step duration</td>
</tr>
<tr>
<td><strong>TA</strong></td>
<td>Tibialis Anterior muscle</td>
</tr>
<tr>
<td><strong>TD</strong></td>
<td>Touch-Down</td>
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<td><strong>TO</strong></td>
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Introduction

Running is characterized by a great accessibility and the simplicity of its practice. That is one of the most popular activities. According to a recent survey conducted by Kantar Media® and Uniteam Active®, 5.9 million of French people over 15 years old practiced jogging or running in 2013 and 75% of them run 2 to 4 times a week.

i.1 Running characteristics

Running is a means of gait allowing rapid displacements, generally faster than walking, and is defined by a series of successive cycles. Each cycle begins when one foot comes in contact with the ground and ends when the same foot contacts the ground again (Fig. i-1). The first contact is referred to as touch-down and marks the beginning of the stance phase. It is considered as a critical period (Christensen et al. 2001, van der Linden et al. 2007) and a lot of lower limb muscles are active in anticipation of and just after touch-down (Novacheck 1998). The contact of the foot with the ground is categorized as rear-foot strike when the heel lands first, mid-foot strike when the heel and ball of the foot land simultaneously and fore-foot strike when the ball of the foot lands before the heel comes down (Fig. i-2).
Figure i-1. Typical vertical ground reaction force during an entire cycle for a runner with a rear-foot strike. The black boxes represent the two periods in which neither foot is in contact with the ground.

Figure i-2. The first contact of the foot with the ground is categorized as rear-foot (left), mid-foot (middle) and fore-foot strike (right).

Except sprinters, most of the runners adopt a rear-foot strike (Hasegawa et al. 2007) inducing a high impact of the vertical ground
reaction force, an abrupt collision force of approximately 1.5 to 3 times body weight within the first 50 ms after touch-down (Fig. i-1). After impact, the vertical ground reaction force slightly decreases and then increases to peak at mid-stance. Thereafter, it continuously decreases until the end of the stance phase, when the foot is no longer in contact with the ground. The first half of the stance is for absorption (braking phase) and the second half for propulsion (push-off phase). The toe-off marks the beginning of the swing phase of the gait cycle. Two periods in which neither foot is in contact with the ground occur at the beginning and at the end of the swing phase (Fig. i-1). Running can be distinguished from walking by the presence of these two periods and by the absence of double support (i.e. both feet simultaneously in contact with the ground) during the stance phase of the gait cycle (Ounpuu 1990, Novacheck 1995).

i.2 Motor control during gait

In running, the gravitational potential and kinetic energy of the centre of gravity of the body are in phase (Cavagna et al. 1964) while they are almost completely out of phase in walking (Cavagna and Margaria 1966). Because in running there is no transfer from kinetic to potential energy and inversely, another mechanism is required to save energy: the bouncing mechanism (Fig. i-3). Humans and other animals bounce when the feet are on the ground using springs to store and return elastic energy (Cavagna et al. 1988, Blickhan 1989, McMahon and Cheng 1990), decreasing the quantity of chemical energy to be supplied by muscles. Running and bouncing can be
modeled by a simple spring-mass model that predicts the running step frequency and the vertical displacement of the center of mass.

**Figure i-3 (from Farley et al. 1993).** The spring-mass model. The model consists of a mass mounted on a spring joining the foot to the centre of mass. The figure shows the model for a runner at the beginning (left), at the middle (centre) and at the end (right) of the stance phase. $L_0$ = initial length of the leg spring, $\Delta L$ = maximum compression of the leg spring, $\Delta y$ = downward vertical displacement of the mass during the stance phase, $\theta$ = half of the angle swept by the leg spring during the stance phase.

Behind this simple mechanism, running is considered as a complex behavior which implies the adjustment of a great number of parameters depending on the situation. In order to predict ground reaction force and knee joint loading, McLean et al. (2003) had to implement in their model detailed kinematics of the lower extremity together with muscle stimulation patterns. The adjustment of these parameters also implies the ability to process a lot of information in a short time. The major part of the information could be processed directly around the spinal cord. Previous studies suggest the existence of a rhythmic central pattern generator in the spinal cord for animal and human locomotion (Dimitrijevic et al. 1998, Gerasimenko et al. 2010, e.g. Grillner et al. 2008). Nevertheless, running in daily life
requires the ability to adapt gait in response to environmental conditions. Indeed any type of functional control of locomotion must include sensory feedback (e.g. Grillner et al. 2008).

This ability to adapt to situations in which gait stability is challenged has already been largely studied in human walking by means of balance perturbations. For any given perturbation such as slipping (Marigold and Patla 2002), tripping (Eng et al. 1994), obstacle avoidance (Schillings et al. 2000, Weerdesteyn et al. 2004), loss of ground support (Shinya et al. 2009), medio-lateral translations of the surface (Hak et al. 2012) or unexpected compliant surface (Marigold and Patla 2005), fast and appropriate adjustments have been observed. These studies pointed out that reflex responses, i.e. automatic or involuntary responses to a stimulus, could contribute to the accommodation of some perturbations.

One of the most common reflex responses is the ‘stretch reflex’ which corresponds to a reflex activity observed in a muscle previously stretched (Fig. i-4). Several bursts of reflex activity are successively observed and often referred to as the short-, the medium- and the long-latency reflex responses. In human soleus muscle, the stretch reflex has already been mechanically evoked by a sudden ankle dorsiflexion at rest (Allum et al. 1982, Toft et al. 1991, Ogiso et al. 2002), during walking (Sinkjaer et al. 1996, Andersen and Sinkjaer, 1999, Grey et al. 2002) or even in cycling (Grey et al. 2002).
Figure 1-4 (from Pearson and Gordon 2000). Illustration of the stretch reflex. Stretch reflexes are mediated by monosynaptic pathways. Ia afferent fibers from muscle spindle make excitatory connections on two sets of motor neurons: alpha motor neurons that innervate the same (homonymous) muscle from which they arise and motor neurons that innervate synergist muscles. They also act through inhibitory interneurons to inhibit the motor neurons that innervate antagonist muscles. When a muscle is stretched the Ia afferents increase their firing rate. This leads to contraction of the same muscle and its synergists and relaxation of the antagonist. The reflex therefore tends to counteract the stretch, enhancing the spring-like properties of the muscles.

These studies show that the reflex responses are modulated from one task to another (task-dependency) and within a specific task (phase-dependency). For example during walking, it has been observed that the triceps surae stretch reflex is higher in the stance phase than in the swing phase (Sinkjaer et al. 1996, Andersen and Sinkjaer 1999, Zehr and Stein 1999). From these observations, it seems that a greater soleus stretch reflex is evoked when the triceps surae plays an important role in maintaining balance. The short-latency response
could contribute to secure the stability around the ankle in case of external perturbations by stiffening the ankle joint (Sinkjaer et al. 1996, Cronin et al. 2011). The medium- and long-latency responses could contribute to provide an increased control for the postural demands when balance must be controlled (Grey et al. 2002). However to our knowledge, a triceps surae stretch reflex has never been mechanically evoked during running and its modulation and functional role must be clarified in this activity.

### i.3 Purposes of the thesis

The public interest for running has aroused a comparable interest in running research. Beyond all studies investigating injuries, training and performance in running which is not the purpose of this thesis, numerous studies have investigated the effect of various expected ‘perturbations’ on the running biomechanics and the musculoskeletal system: for example the type of surface (Tessuti et al. 2012, Wang et al. 2012, Pinnington and Dawson 2001, Lejeune et al. 1998), the camber of a road (Unfried et al. 2013), the type of shoes (Logan et al. 2010, Willy and Davis 2014), the slope (Gottschall and Kram 2005, Telhan et al. 2010) and the speed (Breine et al. 2014). The biomechanical and muscular adaptations after these expected ‘perturbations’ are described but little is known about how humans recover from a sudden perturbation during running.

Our purpose is to understand the motor control of running through two main questions: “What are the modifications observed after a sudden perturbation during running?” and “Could a stretch
reflex be evoked during running?” Moreover in stretch reflex studies, little attention is given to the recovery strategy from the perturbation evoked to induce a stretch reflex. The present work gives an overview of the recovery strategy, reflex or not, after a perturbation of unexpected timing during running. In order to do that, we studied the adjustments after a perturbation delivered at the level of the ankle joint with a powered exoskeleton. We have restricted our investigations to perturbations evoked during the swing phase of running for safety reasons. We have limited the power of the exoskeleton, and as a consequence, we could not evoke a clear perturbation during the stance phase of running due to the large plantarflexion torque at the ankle joint at this time.

In the Chapter 1, we focus on the biomechanical adjustments observed after the ankle dorsiflexion perturbation. Biomechanical adjustments after an unexpected perturbation have already been studied during walking (e.g. Schillings et al. 2000, Marigold and Patla 2002, Shinya et al. 2009) and in a lesser extent during running (Grimmer et al. 2008, Müller et al. 2010). The recovery responses are fast and seem to be adapted to each specific situation. The main purpose of the Chapter 1 is to identify the modifications of the running pattern realized to adapt to an ankle perturbation evoked during the swing phase of running (441 perturbations, 7 subjects). Two questions arise from this purpose: “Is the strategy different if the perturbation is evoked early or late in the swing phase?” and “Are the adjustments realized only just after the perturbation or also during several steps after it?” In order to respond to these questions, the swing phase was divided in five timing groups and seven steps after
the perturbation were investigated. The Chapter 1 is presented as it was published in *Gait & Posture* (Scohier et al. 2012).

In the **Chapter 2**, we describe the running pattern, its variability and its asymmetry during running without and with the exoskeleton. We point out three main questions: “Is the ‘natural’ running pattern of our subjects similar to the one of similar population and speed in the literature?”, “Does the exoskeleton modify the characteristics of running?” and “Are the biomechanical adjustments induced by the ankle perturbations substantial in relation to the running variability with exoskeleton?” We re-analyze the data presented in the Chapter 1, together with data taken when subjects were running first without and then with the exoskeleton before the first perturbation.

After a detailed analysis of the biomechanical adjustments, we investigate the muscular adjustments observed after the perturbation. The **Chapter 3** is focused on the reflex responses of the triceps surae muscles. “Is a stretch reflex response elicited after the ankle dorsiflexion of unexpected timing evoked during swing?” “Is this response task- and time-dependent?” We analyze the early and late reflex responses for the soleus, the medial gastrocnemius and the lateral gastrocnemius. In order to evaluate the task-dependency, the reflex responses observed during the swing phase of running were compared to those observed at rest in a supine position. In order to evaluate the phase-dependency, the responses to perturbations were analyzed for each timing group separately (from early to late swing). The Chapter 3 is presented as it will be published in *Motor Control* (Scohier et al. 2014, in press).
During running, the foot touch-down is considered as a major event for the control of locomotion (Christensen et al. 2001, van der Linden et al. 2007), so we expect some muscular adjustments around touch-down. The purpose of Chapter 4 is to have an overview of the muscular responses realized to control the locomotion and to answer the two following questions: “What is the global muscular strategy adopted after the perturbation?” “Is this strategy different if the perturbation is evoked in early or late swing phase?” Here, we analyze the electromyographic activity just prior to the foot touch-down and during the following stance phase in order to evaluate the muscular adjustments when the triceps surae muscles are naturally active.

In Chapters 1 to 4, we analyzed the effect of moderate perturbations on the running pattern and on the ipsilateral lower leg muscles activity as a function of the time of perturbation. In Chapter 5, we apply larger ankle dorsiflexions in early swing phase and we measure the electromyographic activity of ipsi- and contralateral leg muscles. Indeed during the early right swing phase of running, the left foot is in contact with the ground and the contralateral triceps surae is active; a crossed reflex response could be elicited. The Chapter 5 is a pilot study intended to answer questions such as “What is the effect of a larger perturbation evoked in early swing phase?” “Could a perturbation evoked in early swing phase induce a reflex response in the contralateral leg?”
References


Chapter 1: Adjustments after an ankle dorsiflexion perturbation during human running

**Published as:**
DOI: 10.1016/j.gaitpost.2011.07.019

**Keywords:**
human running, perturbation, exoskeleton, ground reaction forces
Abstract

In this study we investigated the effect of a mechanical perturbation of unexpected timing during human running. With the use of a powered exoskeleton, we evoked a dorsiflexion of the right ankle during its swing phase while subjects ran on a treadmill. The perturbation resulted in an increase of the right ankle dorsiflexion of at least 5 degrees. The first two as well as the next five steps after the perturbation were analyzed to observe the possible immediate and late biomechanical adjustments.

In all cases subjects continued to run after the perturbation. The immediate adjustments were the greatest and the most frequent when the delay between the right ankle perturbation and the subsequent right foot touch-down was the shortest. For example, the vertical impact peak force was strongly modified on the first step after the perturbations and this adjustment was correlated to a right ankle angle still clearly modified at touch-down. Some late adjustments were observed in the subsequent steps predominantly occurring during left steps. Subjects maintained the step length and the step period as constant as possible by adjusting other step parameters in order to avoid stumbling and continue running at the speed imposed by the treadmill.

To our knowledge, our experiments are the first to investigate perturbations of unexpected timing during human running. The results show that humans have a time-dependent, adapted strategy to maintain their running pattern.
1.1 Introduction

Running is one of the most popular recreational activities. This could explain why the biomechanics of normal running are so well documented (Novacheck 1998, Schepens et al. 1998). Although in the real world humans must negotiate various perturbations during running, little is known about the way they do it.

In walking, the effects of unexpected perturbations such as slipping (Marigold and Patla 2002), tripping (Eng et al. 1994), obstacle avoidance (Schillings et al. 2000, Weerdesteyn et al. 2004), loss of ground support (Shinya et al. 2009) or unexpected compliant surface (Marigold and Patla 2005) have been investigated. For any given perturbation, rapid and appropriate adjustments have been observed allowing the subjects to avoid falling and continue walking. Perturbations such as a mechanically evoked ankle dorsiflexion have also received a lot of interest during walking (Yang et al. 1991, Sinkjaer et al. 1996). The amplitude of the plantar-flexor muscles reflex responses was investigated but little attention was paid to the walking pattern adjustments realized by the subject after that perturbation.

In running, Grimmer and colleagues (Grimmer et al. 2008, Müller et al. 2010) measured the biomechanical adjustments made by subjects running over an uneven track which incorporated a clearly visible force plate of adjustable height. The runners maintained their running pattern by adjusting their leg contact angle and ankle joint stiffness to the height of the vertical step.
In animals, the strategies used to negotiate an unexpected perturbation during running have been discussed over the last 10 years (Jindrich and Full 2002, Daley et al. 2006, Daley et al. 2007, Daley and Biewener 2006). Jindrich and Full (2002) showed that a running cockroach pushed to one side, recovered within two strides and continued running on its original path. Daley and colleagues (Daley et al. 2006, Daley et al. 2007, Daley and Biewener 2006) investigated the reactions of guinea fowl to an unexpected drop in terrain height during running. The drop of 8.5 cm (approximately 40% of the leg length) was dissimulated by a thin paper. In all experimental trials, the guinea fowls recovered and continued running at about the same preferred speed as before; in only one trial, an animal stumbled, but without falling.


In this study, we investigated the adjustments made to the running pattern after an ankle perturbation of unexpected timing, by measuring the angular position of the ankle and the ground reaction forces. We used an innovative powered ankle-foot exoskeleton to mechanically evoke ankle dorsiflexion at random timing inside the
swing phase. We observed whether the adjustments were modulated as a function of the perturbation timing. The two steps following the perturbation were analyzed for the immediate adjustments made by the subject, and the subsequent five steps were analyzed for the late adjustments.

1.2 Methods

1.2.1 Subjects

Seven healthy young men (age=26.2±2.2 years, body mass=75.6±9.1kg, height=1.81±0.03m) participated in this study. All subjects were free of lower leg injuries at the time of the experiment. Subjects were informed of the experimental conditions and provided their written consent to participate. Experiments were performed according to the Declaration of Helsinki and approved by the local ethics committee.

1.2.2 Materials

All subjects ran on an instrumented treadmill at a speed of 2.8 m.s\(^{-1}\) while wearing regular running shoes and equipped with a powered exoskeleton on their right leg (Fig. 1-1A&B).

This new device, inspired by that of Andersen and Sinkjær (1995), was designed to deliver a well-defined perturbation to the right ankle joint while the subject is running on the treadmill. It consists of two carbon fiber shells, custom-made for each subject,
placed around the foot and the lower leg. The shells are linked by a joint pivoting at the centre of rotation of the ankle and allowing only dorsi-plantar movements. An optical encoder in the pivot (1 kHz sampling rate, Avago Technologies®, HEDS-9200) measured the angular position of the ankle (deg). A clutch and actuator (SEW®, connected to a servomotor (Parker Compumotor® AT6250) by Bowden cables, could flex the ankle at speeds up to 600 deg.s⁻¹ with a maximal torque of 300 N.m. The clutch and actuator could be activated at any predetermined moment during running. The whole device weights less than 1 kg. As a part of the device was worn inside the right shoe, an insole was placed in the left shoe to compensate for the thickness of the right foot shell.

A strain-gauge sensor under each corner of the treadmill (1 kHz sampling) measured the three orthogonal components of the ground reaction force (GRF) (Heglund 1981): vertical \( F_z \), fore-aft \( F_y \) and lateral \( F_x \), in N.

1.2.3 Experimental protocol

Each session started with the habituation of the subject to the treadmill. Two one-minute runs were first recorded, then the subject was equipped with the exoskeleton and after habituation we again recorded 2 one-minute runs without perturbation. Thereafter perturbations consisting of dorsiflexion of the right ankle were evoked at any time during running.

The perturbations analyzed in this paper were provoked during the swing phase preceding the right foot touch-down (right TD, Fig.
The timing of the perturbation was predetermined using a delay relative to the left foot touch-down (left TD), determined from the $F_z$. The same perturbation timing was used for 3-7 successive perturbations, and then randomly modified. There were randomly 15-30 steps between two successive perturbations, to avoid subject anticipation and cumulative effects of the perturbations. The number of perturbations analyzed by subject was variable (from 27 to 122).

1.2.4 Data processing

The angular position of the right ankle and the GRFs were recorded on a personal computer and analyzed with Labview® v8.6.

A 10-steps sequence beginning with a left TD was used to analyze the effect of the perturbation (Fig. 1-1C). We defined a step as the period between one TD and the next one. The right ankle was always perturbed during a swing phase, specifically during a left step ($L_{pert}$). The seven steps following $L_{pert}$ ($R_{pert}, L_{+1}, R_{+1}, ...$) were used to analyze the perturbation effects. The two preceding steps were used as control ($L_{ctrl}, R_{ctrl}$); $L_{ctrl}$ was the reference for $L_{pert}$, $L_{+1}, L_{+2}, L_{+3}$; $R_{ctrl}$ was the reference for $R_{pert}$, $R_{+1}, R_{+2}$ and $R_{+3}$.

The exact onset of the perturbation was visually determined as the time at which the ankle position and velocity curves of the perturbed step were differentiated from those of the corresponding control step. Each perturbation was assigned to a timing group corresponding to one fifth of the step duration: 0-20% (t1), 20-40% (t2), 40-60% (t3), 60-80% (t4) or 80-100% (t5) (Fig. 1-1C). In total 441 perturbations were analyzed with the following repartition: n=74,
57, 80, 101 and 129 for respectively t1, t2, t3, t4 and t5. The perturbation was in addition characterized by its rise time (ms), amplitude (deg), average speed (deg.s\(^{-1}\)) and hold time (ms) (see Fig. 1-2A).
The ground reaction force signals ($F_y$ and $F_z$) were Butterworth first-order low-pass filtered at a cutoff of 40 Hz; the data were passed through the filter in both directions to avoid any phase lag. $F_x$ was not studied.

\textbf{Figure 1-1.} (A): Powered exoskeleton designed to deliver a perturbation to the right ankle joint during running. Two carbon fiber shells around the foot and the lower leg are linked by a hinged joint pivoting at the center of rotation of the ankle. (B): Subject with exoskeleton running on the treadmill. (C): Typical trace of the vertical ground reaction force ($F_z$, N) of one subject; only the first four steps of the sequence, including the control steps ($L_{\text{ctrl}}$ and $R_{\text{ctrl}}$) and the perturbed steps ($L_{\text{pert}}$ and $R_{\text{pert}}$), are shown. TD=touch-down of a foot. TO=toe-off of a foot. L or R for Left or Right, ctrl or pert subscripts for control or perturbed steps. The vertical interrupted line indicates the first TD following the perturbation (right TD). The vertical dotted lines indicate TD or TO. The white boxes represent the swing phases while the grey boxes represent the contact phases. Perturbations were applied to the right ankle during its swing phase, more precisely during the contact phase of the left foot or the flight phase preceding the right TD, \textit{i.e.} during $L_{\text{pert}}$ as defined at the bottom of the Fig. 1-1C. The perturbations were classified into five timing groups as shown: t1, t2, t3, t4 and t5, see Methods for details. The parameters $t_c$, $t_f$, $F_{z,\text{max}}$, $F_{z,i}$ and $t_{z,i}$ are described in the text.
Contact and flight phases were visually determined from $F_z$ traces to obtain the contact ($t_c$, ms), flight ($t_f$, ms) and total ($T$, ms) durations of each step (see Fig. 1-1C). The maximal amplitude of the negative fore-aft ($F_{y,\text{brake}}$, N), of the positive fore-aft ($F_{y,\text{push}}$, N) and of the vertical ($F_{z,\text{max}}$, N) GRFs was measured. The step length ($L_{\text{step}}$, mm) was calculated as $T$ multiplied by the averaged treadmill speed during $T$. During heel-toe running, which is the most used running technique by our subjects, a distinct vertical impact peak can be detected in the first 50 ms of a step. The amplitude ($F_{z,i}$, N) and the time ($t_{z,i}$, ms) of this impact peak were measured when present. The mean loading rate ($G_{z,i}$, N.ms$^{-1}$) was calculated as the ratio of $F_{z,i}$ divided by $t_{z,i}$.

1.2.5 Statistics

For each parameter, the value measured at any step after the perturbation was compared to its value in the corresponding control step. The difference was calculated and compared to zero with a one-sample Student’s $t$-test ($\alpha=0.05$).

1.3 Results

We did not observe any fall, and all the subjects continued to run normally, in spite of the ankle perturbations.
1.3.1 Effect of the perturbation on the right ankle angle

The perturbations were quite similar between timing groups (t1 to t5, Fig. 1-2A); the average right ankle dorsiflexion was characterized by a rise time of 43±9 ms, an absolute amplitude of 9.0±3.5 deg, an absolute speed of 206±66 deg.s\(^{-1}\) and an hold time ≈100-150 ms. An example is illustrated for a t2 perturbation in Fig. 1-2A. The mean delay between the perturbation and the \(R_{\text{pert}}\) TD is 327±28, 252±26, 181±24, 113±22 and 45±16 ms for respectively t1, t2, t3, t4 and t5. The relative amplitude of the perturbation decreased slightly from t1 to t5 but was not significantly different between timing groups (from 7.9 to 5.3 deg, Fig. 1-2B; grey bars).

The right ankle angle was measured at different moments after the perturbation (\(L_{\text{pert}}\) TO, \(R_{\text{pert}}\) TD, \(R_{\text{pert}}\) TO and \(L_{+1}\)TD) and was compared to the values obtained during the control stride (Fig. 1-2). For t1 and t2, we observed a dorsiflexion increase only at \(L_{\text{pert}}\) TO (2.4 and 5.2 deg, respectively). For t3, the increase was 6.3 deg at \(L_{\text{pert}}\) TO and still 2.4 deg at \(R_{\text{pert}}\) TD. For t4, the right ankle dorsiflexion increased by 2.2 deg at \(L_{\text{pert}}\) TO and by 5.6 deg at \(R_{\text{pert}}\) TD. For t5, in which the perturbations were evoked after \(L_{\text{pert}}\) TO, the dorsiflexion ankle angle was increased by 4.8 deg at \(R_{\text{pert}}\) TD. For t4 and t5, the right ankle dorsiflexion was still slightly increased at \(R_{\text{pert}}\) TO and \(L_{+1}\) TD compared to control steps. So, perturbations of late timing (t4 and t5) had a longer lasting effect on the right ankle angle than perturbations of early timing (t1 and t2).
A. Left step
- Control stride
- Perturbed stride

B. Perturbation onset

Δ Right ankle dorsiflexion (deg)

Time (ms)
-400 -300 -200 0 100 200 300 400
Figure 1-2. Effect of the perturbation on the right ankle angle. Panel A shows an example of the right ankle dorsiflexion for a t2 timing group perturbation. The control stride (dashed trace) and the perturbed stride (continuous trace) are superimposed and synchronized on the right TD (time 0, vertical interrupted line). The dashed arrow shows the perturbation onset. The rise time (1) is the duration from the beginning of the perturbation to a plateau. The hold time (2) corresponds to the duration during which the ankle joint was locked in its position (plateau). The absolute amplitude of the perturbation (3) corresponds to the ankle angular displacement measured during the rise time. The relative amplitude (4) was obtained by subtracting the ankle angular displacement of the control step $L_{ctrl}$ from the absolute amplitude of the perturbation. The absolute speed was calculated as (3)/(1). Panel B shows for each timing group t1 to t5 the relative right ankle dorsiflexion at specific times after the perturbation: at the end of the rise time (grey bar) and at the following toe-offs and touch-downs ($L_{pert}$ TO, $R_{pert}$ TD, $R_{pert}$ TO and $L_{+1}$ TD; black bars) as indicated. The values are expressed as the difference between the right ankle position at these specific times and its position at the corresponding time of the control step. Bars represent mean±s.d. For t1 to t5 the arrow shows the mean value of the perturbation onset. Note the time scale is the same in Panels A & B. * indicates a significant difference from 0 ($P < 0.05$).
1.3.2 Immediate effect of the perturbation on the running pattern ($R_{pert}$ and $L_{+1}$, Table 1-1)

There seemed to be a time-dependent effect of the perturbation on the following first two steps ($R_{pert}$ and $L_{+1}$): the shorter the delay between the perturbation and the right TD (groups t4 and t5), the greater the number and the size of significant modifications.

In group t1, none of the measured parameters was significantly modified during $R_{pert}$. During $L_{+1}$, few small significant modifications were observed.

In group t2, $t_c$, $T$ and $L$ significantly increased and $F_{z,max}$ decreased during $R_{pert}$. During $L_{+1}$, $L$ and $F_{y,push}$ decreased and $F_{z,i}$ increased.

In group t3, $T$ and $L$ significantly increased and $F_{z,max}$ decreased during $R_{pert}$, as was observed for t2. During $L_{+1}$, $t_{z,i}$, $t_c$ and $F_{z,i}$ increased.

In group t4, beside a small increase of $t_c$, we observed larger modifications (more than 10%, see bold in Table 1-1) in the vertical impact peak during $R_{pert}$: on an average the peak occurred 5 ms later with a decreased amplitude of 97 N resulting in a reduction of its loading rate by 7 N.ms$^{-1}$ (Fig. 1-3). During $L_{+1}$, there were many significant modifications but none were greater than 10%: $t_{z,i}$, $t_c$ and $T$ increased and $t_f$ decreased. The forces applied by the subject against the ground were also modified; in the fore-aft direction, $F_{y,brake}$ increased and $F_{y,push}$ decreased; in the vertical direction, $F_{z,i}$ increased and $G_{z,i}$ slightly decreased.
In group t5, the same strong modification (more than 10%) of the vertical impact peak was observed during $R_{\text{pert}}$ step: $t_{z,i}$ increased, $F_{z,i}$ and $G_{z,i}$ decreased (Fig. 1-3). There were many other smaller modifications: $T$ decreased with a decrease $t_f$ and an increase $t_c$. $F_{y,\text{brake}}$ decreased, $F_{y,\text{push}}$ increased. During $L_{+1}$, there were also many small but significant modifications: $t_{z,i}$, $t_c$, $T$ and $L$ increased and $t_f$ decreased. As in the t4 group, $F_{y,\text{brake}}$ increased and $F_{y,\text{push}}$ decreased. In addition, $G_{z,i}$ and $F_{z,\text{max}}$ decreased.

Figure 1-3. Effects of the perturbation for each timing group on the following right foot impact parameters: $t_{z,i}$ (ms, Panel A), $F_{z,i}$ (N, Panel B) and $G_{z,i}$ (N. ms$^{-1}$, Panel C). The results are expressed as the difference between the parameter value in the perturbed step and its value in the corresponding control step. * indicates a significant difference from 0 ($P < 0.05$).
Table 1-1. Significant adjustments observed during the first seven steps following the perturbation.

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<td></td>
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<td>-6.9±32.6</td>
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</tbody>
</table>

The values are expressed as the difference between the mentioned step and the corresponding control step (R_{ctrl} or L_{ctrl}). The Table shows the mean±standard deviation of the differences only if they are significantly different from 0 (P < 0.05). The parameters are defined in the Methods. Modifications greater than 10% are in bold; the % increase was calculated as 100 x (experimental value – control value)/control value. Note that two subjects were excluded from the vertical impact peak analysis (t_{zi}, F_{zi} and G_{zi}) because they did not run with a distinct heel strike.
1.3.3 Late effect of the perturbation on the running pattern (R_{+1} to R_{+3}, Table 1-1)

The modifications observed later (after the first two steps) were small and disperse. They occurred more often on the left steps than on the right steps. The most affected parameter was t_c, which was always increased during the left steps L_{+2} and L_{+3} in groups t3, t4 and t5. On the other hand, T and L were two stable parameters. Indeed, T was modified only during R_{+3} for t3, and L during R_{+3} for t3 and during L_{+2} for t4. The significant modifications of the vertical impact peak were small and infrequent.

1.4 Discussion

An important result coming from our experiments is that in all cases subjects continued to run normally after the perturbation. They were able to rapidly adjust their running pattern to maintain their stable progression on the treadmill. This ability has already been observed in animal running after an unexpected perturbation (Jindrich and Full 2002, Daley et al. 2006, Daley et al. 2007, Daley and Biewener 2006) and was called dynamic stability (Daley 2008, Alexander 2007).

Our perturbation was evoked on the right ankle during its swing phase. We observed immediate and late adjustments, respectively occurring during the first two steps following the perturbation (R_{pert} and L_{+1}), and during the next five steps (R_{+1} to R_{+3}).
1.4.1 Immediate adjustments

In order to maintain their running pattern, the subjects realized many small but significant adjustments to their first two post-perturbation steps. (1) The step length and the step period were quite stable. When both were modified, they varied in the same direction, which is functionally important to continue running at the speed imposed by the treadmill and consequently to avoid falling. An increase in the step period was associated with a delayed vertical impact peak, and a longer contact time not compensated by a reduced flight time. (2) The strongest modifications of the vertical component of the GRFs concerned the impact of the foot, specifically for the perturbations of late timing (t4 and t5). (3) Finally, modifications of the fore-aft component of the GRFs were observed principally when the perturbations were evoked just before the foot contact (t4 and t5). During \( R_{\text{pert}} \), the subjects exerted a smaller maximal braking force and pushed off with a greater maximal force. By contrast, during the next step \((L+1)\) subjects exerted a greater maximal braking force and pushed off with a smaller maximal force. Thus subjects seemed to adjust the fore-aft component of the GRF to deal with the perturbation. This component, although considered essential to the understanding of the biomechanics of normal running (Cavanagh and Lafortune 1980, Munro et al. 1987), has been much less studied than the vertical component in experiments on perturbed locomotion, and would seem to deserve more attention in the future.

The adjustments observed in the first two steps following the perturbation seem to be time-dependent. The longer the delay between
the perturbation and the next TD, the less frequently the adjustments were observed in the first two steps. This is shown most clearly in the first step \( R_{\text{pert}} \): no biomechanical modification was observed in \( R_{\text{pert}} \) when the delay was on average 327 ms (t1). The modifications were limited when the delay was on average 252 and 181 ms (respectively t2 and t3). When the delay was shorter (on average 113 and 45 ms for respectively t4 and t5), many significant biomechanical modifications were observed. In human walking, Weerdesteyn et al. (2004) reported that the first reactions to avoid an obstacle occurred at short latencies; the differentiated acceleration curve of the foot deviated from the control by 122 ms on average after the appearance of an obstacle. In our study, in groups t1, t2 and partially t3, the delay seemed to be long enough for the system to realize the needed adjustments before the next touch-down.

When the perturbation was evoked just before the right step touch-down (t4 and t5), we observed an increased ankle dorsiflexion at \( R_{\text{pert}} \) TD associated with a strongly delayed and reduced vertical impact peak force, along with a decreased loading rate. To further investigate the relationship between ankle position at TD and vertical impact, we tested the correlations between the two. As expected, a greater dorsiflexion at TD was correlated with a delayed vertical impact peak (Fig. 1-4A) whose amplitude (Fig. 1-4B) and loading rate (Fig. 1-4C) were reduced. All three curve fit slopes were significantly different from 0 \( (P < 0.05) \) with low \( r^2 \) (respectively 0.22, 0.10 and 0.23). Together, these results indicated that the ankle position at TD was one of the factors likely to explain the observed modifications to the vertical impact.
Figure 1-4. Variation of the vertical force impact peak time \( t_{z,i} \) (ms, Panel A), amplitude \( F_{z,i} \) (N, Panel B) and mean loading rate \( G_{z,i} \) (N.ms\(^{-1}\), Panel C) as a function of the variation in the right ankle dorsiflexion at touch-down (right TD). Data from all traces showing a distinct heel-strike are plotted from all timing groups (t1-t5, \( n = 307 \)). The least-squares linear curve fits presented on each plot are significantly different from 0 \( (P < 0.05) \). The coefficient of determination \( (r^2) \) is indicated at the top of each figure. The results are expressed as the difference between the parameter value in the perturbed step and its value in the corresponding control step. *indicates a significant difference from 0 \( (P < 0.05) \).
The effect of ankle position at TD on the vertical impact peak has been observed previously. Using a modeling approach to normal human running, Gerritsen and colleagues (1995) showed that at TD an increased angle between the shoe sole and the ground (corresponding to an increased ankle dorsiflexion if the lower leg position is not modified) decreased the amplitude as well as the loading rate of the vertical impact peak. In an experimental study comparing bare-foot and shod running, De Wit et al. (2000) observed in the shod condition a greater ankle dorsiflexion at TD associated with a delayed vertical impact peak and a decrease of the loading rate. Other factors at TD, not measured in our study, such as the leg angle (Gerritsen et al. 1995), the knee angle (De Wit et al. 2000, Nigg et al. 1988), the vertical speed of the heel (Gerritsen et al. 1995) or of the shank segment (Bus 2003), could also influence the vertical impact. In fact, the overall geometry at TD could induce a succession of passive regulations (Grimmer et al. 2008, Full and Koditschek 1999) like those observed on the vertical impact. In such a passive regulation system, it may be sufficient, as suggested by Daley (2008), to check the foot placement or the leg stiffness only at critical moments (TD or TO, for example) in order to prepare for the next step. In our study, however, the modified ankle position resulted from a perturbation and therefore we cannot exclude the possibility that some of the observed adjustments were induced by an active regulation of the leg muscle activity. It would be interesting to study the electromyographic responses to see whether a modification of the leg muscles activation could also partially explain the modifications of the impact of the foot against the ground. In walking Shinya et al. (2009) have observed an
ankle muscular reflex co-contraction after an unexpected perturbation (drop) and suggested that this response could contribute to the absorption of the impact on the ground by stiffening the ankle joint.

1.4.2 Late adjustments

There were still a few small but significant modifications during the steps following $L_{+1}$ ($R_{+1}$ to $R_{+3}$). These late adjustments probably contributed to maintain the step length and the step period as constant as possible. The stability of these two parameters allowed the subject to continue running at the speed imposed by the treadmill without stumbling or falling. Another interesting observation was that the late adjustments predominantly occurred on the left steps, which could have been perceived by the subjects as being more ‘secure’ since the perturbation could only occur on the right ankle, the only one equipped with the exoskeleton.

In conclusion, this innovative study using a powered ankle-foot exoskeleton shows that humans are able to maintain their running pattern after a mechanically evoked ankle dorsiflexion. This perturbation, whatever its timing during the swing phase, modified the right ankle position and induced some time-dependent modifications of the running pattern. It is still not clear whether these modifications resulted from a passively modified ankle and leg geometry at touch-down, or were at least partly the result of an active regulation. To sort this out, the leg muscles’ electromyographic responses to such
perturbations could be investigated together with the biomechanical running pattern adjustments.

Conflict of interest statement

None of the authors have financial or other conflicts of interest in regard to this research.

References


Chapter 2: Step variability and asymmetry while running with an exoskeleton

Abstract

The purpose of this chapter was to investigate the effect of the exoskeleton on the pattern, the variability and the asymmetry of running and to compare the modifications induced by the perturbations presented in Chapter 1 to the variability of the running pattern. In order to achieve that, we measured the value of all parameters defined in Chapter 1, their coefficient of variation and their symmetry angle while subjects ran on the treadmill first without and then with the exoskeleton.

The data observed during running without the exoskeleton are in agreement with those of the literature. With the exoskeleton, we observed a decrease of the stride, step and flight durations, of the step length and of the maximal amplitude of the vertical ground reaction force. However, the effect of the exoskeleton on the variability and asymmetry of running was weak. The step duration and the step length were the most symmetric and stable parameters without and with the exoskeleton. Finally, the comparison of the results presented in Chapter 1 with the variability of each parameter showed that the vertical impact peak adjustments observed after perturbations in late swing were the most relevant adaptations.

Our findings suggest that the exoskeleton does not induce strong modifications of the running pattern.
2.1 Introduction

The previous chapter highlighted that subjects realized many small adjustments after the ankle dorsiflexion perturbation principally when evoked in late swing (t4-t5). We suggested that all these small corrections were required to maintain dynamic stability via a step length and a step period kept as constant as possible. The biggest modifications concerned the impact of the foot, especially on the right step after the perturbations of late timing. As described in Chapter 1, we used a powered exoskeleton attached to the right leg of our subjects to evoke a sudden ankle dorsiflexion during running on treadmill. The device is inspired by the one of Andersen and Sinkjaer (1995). Although the exoskeleton only weights 0.9kg, it could affect the characteristics of running; i.e. variability and asymmetry of the ‘natural’ running pattern. Variability is often quantified by measures such as standard deviation and coefficient of variation while asymmetry in running is defined as the difference between the left and right sides (Robinson et al. 1987, Zifchock et al. 2008).

The first goal of this Chapter was to describe the running pattern, its variability and its asymmetry when running without the exoskeleton (‘natural’ running pattern). We expected observing running pattern values in agreement with those presented in the literature (e.g. De Wit et al. 2000, Nakayama et al. 2010). About variability, we hypothesized that the step length and the step duration are the most stable parameters due to the constant running speed imposed by the treadmill. Finally, we should observe a relatively symmetrical natural running pattern as shown in other studies.
(Karamanidis et al. 2003, Zifchock et al. 2006, Bredeweg et al. 2013). The second goal was to investigate the effect of the exoskeleton on the pattern, its variability and its asymmetry by comparing running without and with exoskeleton. With a similar exoskeleton, Andersen and Sinkjaer (1995) showed that the step duration was unchanged and that the walking pattern was only slightly modified. Consequently, we did not expect to observe strong modifications of the running pattern with the exoskeleton. The third goal was to compare the modifications induced by the ankle perturbations to the variability of the running pattern in order to support the results previously presented (see Chapter 1).

2.2 Methods

Each session started with the habituation of the subject to the treadmill. After habituation, two 1-min runs were recorded while the subject ran on the treadmill without the exoskeleton. During these two runs, we collected at least 25 strides to describe the natural running pattern. Thereafter the subject was equipped with the exoskeleton and, after habituation, two other 1-min runs were recorded while the subject ran on the treadmill with the exoskeleton but without perturbation. For each subject, the same number of steps were collected for each condition.

The parameters used to describe the running pattern are detailed in Chapter 1: the amplitude ($F_{zi}$), time ($t_{zi}$) and loading rate ($G_{zi}$) of the vertical impact peak; the contact ($t_{c}$), flight ($t_{f}$) and total ($T$) durations of the step; the step length ($L$); the maximal amplitude of
the negative fore-aft (\(F_{y,\text{brake}}\)), of the positive fore-aft (\(F_{y,\text{push}}\)) and of the vertical (\(F_{z,\text{max}}\)) ground reaction forces. The values of these parameters were measured for both left and right sides. In addition, we calculated the stride duration \((T_{\text{stride}})\) as the sum of left step \((T_{\text{left}})\) and right step \((T_{\text{right}})\) durations.

To quantify the variability of the running pattern, we used the coefficient of variation, calculated as:

\[
CV = \left| \frac{\text{standard deviation}}{\text{mean value}} \right| \times 100\%
\]

where \(CV\) is expressed in %.

To quantify the level of asymmetry, we used the symmetry angle (SA) proposed by Zifchock et al. (2008). We calculated the SA (\%) as:

\[
SA = \left| 45^\circ - \arctan \left( \frac{X_{\text{left}}}{X_{\text{right}}} \right) \right| \times 100\%
\]

where \(X_{\text{left}}\) and \(X_{\text{right}}\) are the values of the parameter at the left and right sides. In order to avoid that negative SA values in some subjects (due to greater values at the left side) would be compensated by positive SA values in other subjects (due to greater values at the right side), we used absolute values. The SA is a measure related to the angle formed by the vector of \(X_{\text{left}}\) and \(X_{\text{right}}\) when plotted in a Cartesian coordinate system where values of the left side are plotted
on the $y$-axis and values of the right side on the $x$-axis (Fig. 2-1). The values of the parameters used in our study to describe the running pattern are always positive. Consequently, the vector of $X_{\text{left}}$ and $X_{\text{right}}$ is always in the first quadrant of the trigonometric circle. When $X_{\text{left}}$ is equal to $X_{\text{right}}$, both values form a vector of perfect symmetry with an angle of 45 deg with the $x$-axis; thus a SA value of 0% indicates a perfect symmetry (Fig. 2-1, A). When $X_{\text{left}}$ is greater or lesser than $X_{\text{right}}$, both values form a vector going away from the vector of perfect symmetry with an angle comprised between 45 to 90 deg or 0 to 45 deg with the $x$-axis, respectively (Fig. 2-1, B-C). A SA value of 100% would indicate that the values of the left and right sides are equal and opposite (Fig. 2-1, D). The SA values in our study will always be comprised between 0 and 50%.

For each parameter and each subject, the mean value and its CV, and the mean SA were calculated. These values were then averaged for all subjects to obtain a value in each condition: running without/with the exoskeleton.

For the first and second goals, the running pattern without and with the exoskeleton was described by the parameters previously mentioned, measured for the right and left sides. For each parameter and each side, the CV was calculated to describe the variability. Finally, the SA comparing the right and left sides was calculated for each parameter in order to evaluate the level of symmetry. The values and CV of each condition (without/with exoskeleton) and each side (left/right) were compared for each parameter using a two-way repeated-measures analysis of variance test. The Holm-Sidak post-hoc test was used to test all pairwise multiple comparison. In order to
investigate the effect of the exoskeleton on the symmetry, the analysis was completed by paired $t$-tests comparing the SA without the exoskeleton to the SA with the exoskeleton. All analysis were executed in SigmaPlot 11.0 for Windows and the statistical significance was set at $P < 0.05$. For the third goal, the modifications described in Chapter 1 were compared to the CV measured when running with the exoskeleton.

**Figure 2-1.** Graphic representation of the symmetry angle. The left side values are plotted on the $y$-axis and the right side values on the $x$-axis. An angle of 45 deg indicates a perfect symmetry. The Panels A-C represent three possible situations in our study with a value for the left side equal to (A), greater (B) or lesser (C) than the right side. The Panel D represents a situation not found in our study inducing a SA value of 100%.
2.3 Results and discussion

2.3.1 Natural running pattern

The values of each parameter of running without exoskeleton are presented in Table 2-1. The stride duration is equal to $758\pm50$ ms. At the right side, the contact, flight and total durations of the step are equal to $269\pm28$, $111\pm24$ and $380\pm26$ ms, respectively, and the step length is equal to $1.06\pm0.07$ m. The maximal amplitude of the negative fore-aft, of the positive fore-aft and of the vertical ground reaction forces are equal to $302\pm36$, $207\pm42$ and $182\pm207$ N. The vertical impact peak appears $35\pm5$ ms after the touch-down, its amplitude is equal to $1222\pm144$ N and its loading rate to $36\pm7$ N.ms$^{-1}$. There is no difference between the right and the left sides ($P > 0.05$).

The observed values are in agreement with the literature. Indeed Nakayama et al. (2010) have observed a stride duration of approximately 700 and 685 ms at respectively 2.44 and 2.93 m.s$^{-1}$. De Wit et al. (2000) have observed when running at 3.5 m.s$^{-1}$ a step length of 1.33 m, contact and flight durations of 251 and 129 ms and a vertical impact peak at 38 ms after touch-down. The smaller step length and the greater contact duration we observed could be related to the slower speed we used; indeed our speed is 0.7 m.s$^{-1}$ smaller compared to De Wit et al. (2000). The contact duration observed in our study is equal to 35% of the running cycle, and is quite similar to 39% measured by Novacheck (1998) with subjects running at 3.2 m.s$^{-1}$. 
Table 2-1. Value (mean±s.d.) for each parameter for the left and right steps during running on treadmill without ('natural' running) and with the exoskeleton.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>no exosk.</th>
<th>exosk.</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>left</td>
<td>right</td>
<td>left</td>
</tr>
<tr>
<td>$t_{\text{c}}$ (ms)</td>
<td>268±29</td>
<td>269±28</td>
<td>273±31</td>
</tr>
<tr>
<td>$t_{\text{f}}$ (ms)</td>
<td>109±22</td>
<td>111±24</td>
<td>89±25</td>
</tr>
<tr>
<td>$T$ (ms)</td>
<td>378±24</td>
<td>380±26</td>
<td>362±23</td>
</tr>
<tr>
<td>$T_{\text{stride}}$ (ms)</td>
<td>758±50</td>
<td>718±47</td>
<td>718±47</td>
</tr>
<tr>
<td>$L$ (m)</td>
<td>1.05±0.07</td>
<td>1.06±0.07</td>
<td>1.01±0.07</td>
</tr>
<tr>
<td>$F_{\text{y,brake}}$ (N)</td>
<td>285±33</td>
<td>302±36</td>
<td>265±33</td>
</tr>
<tr>
<td>$F_{\text{y,push}}$ (N)</td>
<td>216±21</td>
<td>207±42</td>
<td>220±26</td>
</tr>
<tr>
<td>$F_{z,i}$ (N)</td>
<td>1214±100</td>
<td>1222±144</td>
<td>1146±91</td>
</tr>
<tr>
<td>$F_{z,\text{max}}$ (N)</td>
<td>1831±217</td>
<td>1826±207</td>
<td>1753±258</td>
</tr>
<tr>
<td>$G_{z,i}$ (N.ms$^{-1}$)</td>
<td>36.5±4.5</td>
<td>35.6±6.9</td>
<td>32.3±2.0</td>
</tr>
</tbody>
</table>

The parameters are defined in the Methods. At least 25 steps were used to calculate a mean value by subject. Then, the mean values of all subject were averaged (n = 7). Note that two subjects were excluded from the vertical impact peak analysis ($t_{z,i}$, $F_{z,i}$ and $G_{z,i}$) because they did not run with a distinct heel strike. The $P$ value columns are obtained with a two-way repeated-measures analysis of variance test except for $T_{\text{stride}}$ (paired $t$-test). $P$ values smaller than 0.05 are in **bold**. exosk. = exoskeleton; interact. = interaction (exoskeleton X side).
Table 2-2. Coefficient of variation (mean±s.d.) for each parameter for the left and right steps during running on treadmill without (‘natural’ running) and with the exoskeleton.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>no exosk.</th>
<th>exosk.</th>
<th>P value</th>
<th>side</th>
<th>interact.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>left</td>
<td>right</td>
<td></td>
<td>exosk.</td>
<td></td>
</tr>
<tr>
<td>( t_{zi} ) (ms)</td>
<td>7.9±0.5</td>
<td>9.0±2.9</td>
<td>7.5±1.5</td>
<td>7.3±2.3</td>
<td>0.113</td>
</tr>
<tr>
<td>( t_{c} ) (ms)</td>
<td>2.9±0.3</td>
<td>2.6±0.5</td>
<td>2.6±0.2</td>
<td>2.7±0.6</td>
<td>0.678</td>
</tr>
<tr>
<td>( t_{f} ) (ms)</td>
<td>8.5±2.1</td>
<td>7.5±2.3</td>
<td>9.5±3.6</td>
<td>9.0±2.8</td>
<td>0.237</td>
</tr>
<tr>
<td>( T ) (ms)</td>
<td>2.3±0.3</td>
<td>1.9±0.5</td>
<td>2.1±0.4</td>
<td>2.1±0.5</td>
<td>0.891</td>
</tr>
<tr>
<td>( T_{stride} ) (ms)</td>
<td>1.4±0.3</td>
<td>1.5±0.3</td>
<td></td>
<td>0.455</td>
<td>-</td>
</tr>
<tr>
<td>( L ) (m)</td>
<td>2.8±0.5</td>
<td>2.6±0.6</td>
<td>2.5±0.6</td>
<td>2.6±0.6</td>
<td>0.335</td>
</tr>
<tr>
<td>( F_{y,brake} ) (N)</td>
<td>11.2±2.6</td>
<td>10.5±3.3</td>
<td>10.7±1.2</td>
<td>9.8±2.8</td>
<td>0.595</td>
</tr>
<tr>
<td>( F_{y,push} ) (N)</td>
<td>15.3±5.8</td>
<td>15.4±5.4</td>
<td>11.8±1.9</td>
<td>14.5±6.1</td>
<td>0.143</td>
</tr>
<tr>
<td>( F_{z,i} ) (N)</td>
<td>7.1±1.0</td>
<td>7.4±1.6</td>
<td>7.0±1.7</td>
<td>9.6±2.9</td>
<td>0.232</td>
</tr>
<tr>
<td>( F_{z,max} ) (N)</td>
<td>2.8±0.6</td>
<td>2.9±0.7</td>
<td>2.7±0.5</td>
<td>3.6±1.0</td>
<td>0.363</td>
</tr>
<tr>
<td>( G_{z,i} ) (N.m.s(^{-1}))</td>
<td>10.7±1.5</td>
<td>11.7±2.2</td>
<td>10.0±1.0</td>
<td>11.4±1.9</td>
<td>0.326</td>
</tr>
</tbody>
</table>

For legend, see Table 2-1.
The values of the coefficients of variation are presented in the Table 2-2. The most variable parameter is the maximal amplitude of the positive fore-aft ground reaction force $F_{y,\text{push}}$ with a CV of about 15% and the most stable parameter is the stride duration $T_{\text{stride}}$ with a coefficient of variation less than 2%. The variability of the stride duration is in agreement with previous studies: from 1.0 to 2.0% in function of the speed and of the running experiment (Belli et al. 1995, Nakayama et al. 2010). The step duration variability is slightly greater than the stride duration variability, as also observed by Belli et al. (1995). To our knowledge, the variability of the other parameters presented here (Table 2-2) has not yet been studied; thus a comparison with the literature is not possible.

Table 2-3. Symmetry angle (mean±s.d.) while running on a treadmill at 2.78 m.s$^{-1}$ without and with the exoskeleton.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>no exosk.</th>
<th>exosk.</th>
<th>P value</th>
<th>SA (%) Bredeweg et al. 2013</th>
</tr>
</thead>
<tbody>
<tr>
<td>$t_{x,i}$</td>
<td>3.5±0.9</td>
<td>3.3±1.8</td>
<td>0.760</td>
<td>5.3±4.1</td>
</tr>
<tr>
<td>$t_{z,i}$</td>
<td>1.2±0.4</td>
<td>1.5±0.5</td>
<td>0.278</td>
<td>1.2±1.9</td>
</tr>
<tr>
<td>$t_{f}$</td>
<td>3.1±1.0</td>
<td>3.5±1.3</td>
<td>0.368</td>
<td>-</td>
</tr>
<tr>
<td>$T$</td>
<td>1.0±0.3</td>
<td>1.0±0.3</td>
<td>0.780</td>
<td>-</td>
</tr>
<tr>
<td>$L$</td>
<td>1.1±0.1</td>
<td>1.2±0.4</td>
<td>0.715</td>
<td>0.5±0.4</td>
</tr>
<tr>
<td>$F_{y,\text{brake}}$</td>
<td>5.1±1.4</td>
<td>6.0±1.3</td>
<td>0.061</td>
<td>-</td>
</tr>
<tr>
<td>$F_{y,\text{push}}$</td>
<td>6.3±2.2</td>
<td>8.1±4.6</td>
<td>0.252</td>
<td>-</td>
</tr>
<tr>
<td>$F_{z,i}$</td>
<td>2.4±0.5</td>
<td>4.2±1.5</td>
<td><strong>0.035</strong></td>
<td>2.6±2.4</td>
</tr>
<tr>
<td>$F_{z,\max}$</td>
<td>1.2±0.5</td>
<td>1.9±1.1</td>
<td>0.144</td>
<td>2.8±2.1</td>
</tr>
<tr>
<td>$G_{z,i}$</td>
<td>4.6±0.8</td>
<td>4.5±1.1</td>
<td>0.879</td>
<td>3.7±3.8</td>
</tr>
</tbody>
</table>

The parameters are defined in the Methods. exosk. = exoskeleton. The P value column indicates the results of a paired t-test comparing the SA without the exoskeleton to the SA with the exoskeleton. P values smaller than 0.05 are in **bold**. The values at the right are taken from the study of Bredeweg et al. 2013.
Concerning the asymmetry of the natural running pattern, the SA gives small values between 1.0±0.3% for $T$ and 6.3±2.2% for $F_{y,\text{push}}$ (Table 2-3). The asymmetry when running without the exoskeleton is close to the one observed for novice male runners at the same speed by Bredeweg et al. (2013); the maximum difference is of about 2% ($t_{z,i}$, cf. Table 2-3). The range in the SA values observed here between the different parameters (from 1.0 to 6.3%) is also observed in other studies (Karamanidis et al. 2003, Zifchock et al. 2006, Bredeweg et al. 2013). The SA values are small, meaning a symmetrical pattern. This is confirmed by the non-significant $P$ values for the side factor shown in Table 2-1. We also observed that the right side variability is equal to the left side variability (Table 2-2), except for $T$ (Holm-Sidak, $P = 0.017$).

The first goal of this Chapter was to describe the natural running pattern of our subjects and to quantify its variability and its asymmetry. The observed data are in agreement with those previously published. We have observed that the pattern is highly symmetrical and that the step duration ($T$) and length ($L$) are the most symmetric and stable parameters.

2.3.2 Running with the exoskeleton

The values of the parameters measured when running with the exoskeleton are presented in Table 2-1. Compared to running without the exoskeleton, we observed that the stride duration $T_{\text{stride}}$ is significantly decreased with the exoskeleton ($718\pm47$ vs $758\pm50$ ms, $P$
< 0.001). The step length $L$, the step duration $T$, the flight duration $t_f$ and the maximal amplitude of the vertical ground reaction force $F_{z,\text{max}}$ are also significantly decreased for both sides. The other parameters are not modified when running with the exoskeleton.

The results of the variability are presented in Table 2-2. Globally, the variability is not modified when running with the exoskeleton. The stride duration is the most stable parameter (CV = 1.5±0.3%), as it was during natural running (CV = 1.4±0.3%). The maximal amplitude of the positive fore-aft ground reaction force $F_{y,\text{push}}$ is still the most variable parameter (CV = 12-15%). The Holm-Sidak test shows an effect of the exoskeleton only on the variability of the right side for $t_{z,i}$ and $F_{z,i}$ ($P = 0.021$ and 0.034, respectively).

The SA indexes when running with the exoskeleton are between 1.0±0.3 for $T$ and 8.1±4.6% for $F_{y,\text{push}}$ (Table 2-3), close to the values of our subjects running without the exoskeleton and close to the values of Bredeweg et al. (2013). The paired $t$-tests comparing the SA between running without and with the exoskeleton show that the asymmetry is not modified by the exoskeleton, except for $F_{z,i}$ where the asymmetry is greater with the exoskeleton (4.2% compared to 2.4%, Table 2-3). This increase of asymmetry for $F_{z,i}$ results from a decreased value for the left side combined to an increased value for the right side (cf. interactions slightly above 0.050 in Table 2-1). Note also that the values of the left side are greater than those of the right side when running with the exoskeleton for $t_c$ and $L$ (Holm-Sidak, $P = 0.014$ and 0.008 respectively). Because the exoskeleton is worn at the
right leg, it means that subjects spend less time in contact with the ground with the exoskeleton than without.

The second goal of this Chapter was to investigate the effect of the exoskeleton on the running pattern, its variability and its asymmetry, by comparing running without and with exoskeleton. We have observed that the exoskeleton decreases the step duration $T$ and length $L$ (Table 2-1). Because the subjects must maintain the constant running speed imposed by the treadmill, the step duration and the step length evolve in the same way. The decreased step duration and the shorter step length could be induced by a decreased propulsion, expressed by a decrease of nearly 10% for $F_{y,\text{push}}$. Indeed, we might expect that a heavier load on the right lower leg (added mass for the exoskeleton = 0.9kg) is more difficult to propulse forward due to the greater inertial load. However in previous studies, Martin (1985) added 1kg and Divert et al. (2008) 0.2kg to the feet and they observed that adding extra mass to the feet increased the flight time, the stride duration and the stride length. Thus, the added mass is probably not the unique explanation and running with the exoskeleton could have induced a lack of comfort responsible for the decreased propulsion. As described previously, the effect of the exoskeleton on the variability and the asymmetry is weak. About variability, we only observe at the right side a decrease of variability for the time of the vertical impact peak and conversely an increase of variability for the amplitude of this peak. About asymmetry, our results show that the exoskeleton induces an asymmetry for the contact time, the step length (Table 2-1) and the amplitude of the vertical impact peak (Table 2-3).
2.3.3 Modifications of the running pattern after the perturbation in comparison with its variability

In the previous sections, we calculated the step variability when running without the exoskeleton and with the exoskeleton before the first perturbation. The variability of the control steps between perturbations \( R_{\text{ctrl}} \), i.e. the steps preceding each perturbation in Chapter 1) is presented in the upper part of the Table 2-4. The trends observed when running without and with the exoskeleton before the first perturbation (Table 2-2) are also observed in the control steps \( R_{\text{ctrl}} \) between perturbations (Table 2-4). The step duration (2.6±0.3%) and length (2.8±0.5%) are the most stable parameters.

In Chapter 1, we have shown that a sudden dorsiflexion of the ankle during the swing phase of running induced adjustments on the following steps and predominantly on the first step after the perturbation \( R_{\text{pert}} \), cf. Table 1-1). These adjustments were more frequent when the perturbation was evoked just before the touch-down of the right foot (t4 and t5, i.e. at the end of the swing phase). The Table 2-4 presents the adjustments of the right steps just after the perturbation \( R_{\text{pert}} \) steps) that are statistically significant; they are expressed in percent of the control steps. Note that the same results were presented in Table 1-1 in absolute difference. We observe that most adjustments are small even though statistically significant. The exception is the vertical impact peak \( (t_{z,i}, F_{z,i} \text{ and } G_{z,i}) \) when the perturbation was evoked in late swing (t4, t5).
Table 2-4. **Upper part**: Coefficient of variation (mean±s.d., in %) of the right control steps ($R_{ctrl}$). **Bottom part**: Significant adjustments (mean±s.d.) observed on the right step after the perturbation ($R_{pert}$).

<table>
<thead>
<tr>
<th></th>
<th>$t_{z,i}$</th>
<th>$t_c$</th>
<th>$t_f$</th>
<th>$T$</th>
<th>$L$</th>
<th>$F_y,\text{brake}$</th>
<th>$F_y,\text{push}$</th>
<th>$F_z,i$</th>
<th>$F_z,\text{max}$</th>
<th>$G_z,i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{ctrl}$ CV</td>
<td>12.0±1.4</td>
<td>3.5±0.6</td>
<td>3.9±0.4</td>
<td>2.6±0.3</td>
<td>2.8±0.5</td>
<td>10.1±1.7</td>
<td>13.4±3.9</td>
<td>8.9±1.0</td>
<td>4.2±0.8</td>
<td>15.8±1.7</td>
</tr>
<tr>
<td>$t1$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$t2$</td>
<td>-</td>
<td>1.5±4.0</td>
<td>-</td>
<td>1.1±2.6</td>
<td>0.9±3.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-1.4±5.1</td>
<td>-</td>
</tr>
<tr>
<td>$t3$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.0±3.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-1.3±4.8</td>
<td>-</td>
</tr>
<tr>
<td>$R_{pert}$ (% change)</td>
<td>14.4±16.0</td>
<td>1.0±3.9</td>
<td>-</td>
<td>0.8±3.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-6.7±12.6</td>
<td>-</td>
<td>-16.7±17.1</td>
</tr>
<tr>
<td>$t4$</td>
<td>11.0±15.8</td>
<td>1.4±3.3</td>
<td>-5.2±12.0</td>
<td>-0.8±2.9</td>
<td>-3.0±13.9</td>
<td>8.1±23.0</td>
<td>-11.4±10.6</td>
<td>-</td>
<td>-18.4±16.1</td>
<td></td>
</tr>
</tbody>
</table>

The CV are calculated from all control steps ($R_{ctrl}$) for each subject and then averaged for all subjects. Values are presented as mean±s.d. The $R_{pert}$ values are expressed as the % increase of the step after the perturbation relative to the corresponding control step ($R_{ctrl}$) calculated as 100 x (experimental value – control value)/control value. The $R_{pert}$ values are shown only if they are significantly different from 0 ($P < 0.05$). Modifications greater than 10% are in **bold**.
Indeed, the vertical impact peak adjustment is the only modification greater than 10% (see **bold** in Tables 1-1 and 2-4). In Chapter 1, we suggested that the vertical impact peak adjustments were the major modifications due to the perturbation. Here in Chapter 2, we calculated the variability of the running pattern. Interestingly we observe that the parameters modified by at least 10% (as defined in the Chapter 1) are also those whose modification was greater than their control variability ($R_{\text{ctrl CV}}$). This is the case for the vertical impact peak values after a perturbation evoked in late swing while the variability of $t_{z,i}$ and $G_{z,i}$ is high (Table 2-4).

The third goal of this Chapter was to compare the modifications induced by the ankle perturbations as observed in Chapter 1 with the variability of the running pattern, and specifically of the control steps ($R_{\text{ctrl CV}}$). This approach confirms that the vertical impact peak adjustments observed after the sudden ankle dorsiflexion in late swing appear to be the most relevant adaptations after the perturbation.

### 2.4 Conclusion

The natural pattern of our runners is highly symmetrical. The step duration and the step length which appeared quite stable after the perturbations, are the most symmetric and stable parameters. It seems that the system takes care of maintaining as constant as possible these two parameters during treadmill running and that it adjusts other parameters in order to achieve that.
The exoskeleton does not much modify symmetry and variability of the running pattern although the values of several parameters were modified (decrease of $T_{\text{stride}}$, $T_f$, $L$ and $F_{z,\text{max}}$). A decreased propulsion could be responsible for these modifications but the origin of this decreased propulsion is still unclear: mass or exoskeleton effect?

Finally, the comparison of the results presented in Chapter 1 with the variability of each parameter highlights that the vertical impact peak adjustments observed after the perturbations in late swing are the most relevant adaptations. We previously discussed that the modified impact could be a passive consequence of the modified lower limb geometry at touch-down or could be due to an active regulation. In the following chapters, we will investigate the effect of the perturbation on the leg muscles activity. The reflex responses will be analyzed in Chapter 3. In Chapter 4, the muscular adaptations around the foot touch-down will be studied.

References


Chapter 3: Triceps surae stretch reflex modulation after a mechanically evoked ankle dorsiflexion during the swing phase of human running

Published as:
DOI: 10.1123/mc.2013-0039
Abstract

The purpose of this study was to mechanically evoke a triceps surae stretch reflex during the swing phase of running, in order to study its within-the-step phase dependency. Seven participants ran on a treadmill at 2.8 m.s\(^{-1}\) wearing an exoskeleton capable of evoking a sudden ankle dorsiflexion. We measured the electromyographic activity of the soleus, medial and lateral gastrocnemii just after the perturbation to evaluate the triceps surae stretch reflex. Similar perturbations were also delivered at rest.

Our results showed that the stretch reflex was suppressed during the swing phase of running, except in late swing where a late reflex response was observed. At rest, all triceps surae muscles showed an early reflex response to stretch.

Our findings suggest that the triceps surae short/medium-latency stretch reflex cannot be evoked during swing phase and thus cannot contribute to the control of the locomotor pattern after a perturbation during this phase.
3.1 Introduction

When a muscle is stretched, a reflex activity follows. This response is called the stretch reflex (SR); several bursts of response activity are successively observed, often referred to as the short-, the medium- and the long-latency reflex responses. The SR can be induced in human soleus muscle by a mechanically evoked ankle dorsiflexion at rest (Allum et al. 1982, Toft et al. 1991, Ogiso et al. 2002) as well as during tasks like walking (Sinkjaer et al. 1996, Andersen and Sinkjaer 1999, Grey et al. 2002) or cycling (Grey et al. 2002). The functional role of the SR has been studied in relation to its excitability, which is modulated from one task to another (task-dependency), as well as within a specific task (phase-dependency). For example, Grey et al. (2002) observed that, for the same control-EMG activity level, the amplitude of the medium-latency component of the evoked soleus SR was greater when walking than when sitting or cycling. During walking, several authors observed that the SR response to a sudden ankle dorsiflexion was highest at mid-stance, relatively large in late swing and null during the transition from stance to swing (Sinkjaer et al. 1996, Andersen and Sinkjaer 1999). From these observations, it seems that a greater soleus SR is evoked when the triceps surae plays an important role in maintaining balance.

During running, the triceps surae SR excitability has not been studied through mechanical ankle dorsiflexion, even though some studies have suggested that the SR is naturally elicited in these muscles just after touch-down (Dietz et al. 1979, Ishikawa and komi 2007, Cronin et al. 2011). High frequency Achilles tendon vibration
was applied by Cronin et al. (2011) during running in order to
decrease the efficacy of the Ia afferent pathway from the muscle
spindles. As a result, they observed a reduced triceps surae activity at
the early contact phase and, simultaneously, an increased ankle yield
suggesting a possible contribution of the SR short-latency component
to ankle stability at touch-down during running. Other studies have
investigated the triceps surae H-reflex (HR) response modulation
during running (phase-dependency) and have compared it between
running and walking (task-dependency). They showed that HR
responses are larger in walking than in running (Capaday and Stein
1987) and that the HR is suppressed during the swing phase of
running while it is relatively large during the stance phase (Capaday
and Stein 1987, Simonsen and Dyhre-Poulsen 1999). These HR
results confirmed those obtained in walking for the SR and may
suggest a similar triceps surae SR behaviour during running.
However, Andersen and Sinkjaer (1999) showed that the amplitude of
the SR is smaller than that of the HR in late stance phase walking,
probably due to a decreased sensitivity of the muscle spindles at the
end of the push-off. Because HR bypasses the muscle spindles, one
cannot infer SR modulation from HR observed behaviour.

The goal of this study is to describe the modulation of the
triceps surae SR during the swing phase of running. We evoked
sudden ankle dorsiflexions and recorded EMG activity of the soleus,
medial and lateral gastrocnemii, and tibialis anterior. Our hypothesis
was that the triceps surae SR is suppressed during the first part of the
swing phase but is present at the end of this phase, when the triceps
surae could play a more important role in maintaining balance
(Sinkjaer et al. 1996, Grey et al. 2002). Task-dependency was also investigated by comparing the responses observed during running with those observed at rest.

3.2 Methods

The data presented here were collected during the same session as the results previously published in Scohier et al. (2012). The experimental set-up is identical and consequently the materials are only briefly described here.

3.2.1 Participants

Seven healthy young men free of leg injuries at the time of the experiment (age =26.2±2.2 years, body mass =75.6±9.1 kg, height =1.81±0.03 m) participated in this study. Participants were informed of the experimental conditions and provided their written consent to participate. Experiments were performed according to the Declaration of Helsinki and approved by the local ethics committee.

3.2.2 Experimental protocol and data collection

Subjects ran at a speed of 2.8 m.s$^{-1}$ on a motorised treadmill. They wore running shoes and were equipped on their right leg with an exoskeleton consisting in two carbon fiber shells placed around the foot and the lower leg and linked by a joint pivoting at the center of rotation of the ankle (Fig. 3-1A&B). Each exoskeleton was custom
made to fit the form of the lower leg and of the foot of each individual subject. The exoskeleton was strapped to the leg by means of non-elastic Velcro straps and to the foot by means of Velcro straps inside the shoe. Since part of the device was worn inside the right shoe, an insole was placed in the left shoe to compensate for the thickness of the right foot shell (Scohier et al. 2012). The exoskeleton allowed free dorsi-plantar movements during the entire cycle except when it delivered a predefined perturbation to the ankle joint. An optical encoder in the pivot of the exoskeleton measured the angular position of the ankle (1kHz sampling rate, Avago Technologies®). Strain-gauge sensors under each corner of the treadmill (1kHz sampling) measured the three orthogonal components of the ground reaction force (Heglund 1981).

Muscular activity was recorded using a BTS© Free-Emg system (1kHz sampling rate). A pair of surface EMG electrodes, separated by 2 cm, was positioned over the following right leg muscles: soleus (Sol), medial gastrocnemius (MG), lateral gastrocnemius (LG) and tibialis anterior (TA). Prior to placing the electrodes the skin was shaved and cleaned. The electrodes and cables were taped to the leg to minimize movement artifacts.

Each running session started with the habituation of the subject to the treadmill, first without and then with the exoskeleton. After habituation, perturbations were evoked at any time during the swing phase of the right leg, between the left and right touch-downs (TD, Fig. 3-1C). The timing of the perturbation was predetermined using a delay relative to the left foot touch-down. A similar perturbation timing was used for 3-7 successive perturbations, and then was
randomly modified. Afterwards, each perturbation was classified in a timing group (cf. *Data processing*). The perturbation applied to the right ankle consisted of a dorsiflexion of ~40 ms duration followed by a plateau of 100 ms before ankle release. There were randomly 15-30 steps between two successive perturbations to avoid subject anticipation and cumulative effects of the perturbations. Prior to the running protocol, similar perturbations were delivered at rest while the subjects were lying with the knee in extension and the ankle at ~90 degrees. Subjects were instructed not to “intervene”.

**3.2.3 Data processing**

The stance phases were visually determined from the vertical ground reaction force. The ankle perturbation was characterized by its amplitude (Fig. 3-2A&B) and speed. In running, the onset of the perturbation was visually determined as the time at which the ankle position and velocity curves differed from those of the preceding control cycle (Fig. 3-1C & Fig. 3-2B). Each perturbation was assigned to a timing group corresponding to one fifth of the duration between the left and the right TDs: 0-20% (t1), 20-40% (t2), 40-60% (t3), 60-80% (t4) or 80-100% (t5) (Fig. 3-1C). In total, 441 perturbations evoked during the right swing phase were analyzed. At rest, the onset of the perturbation was visually determined from the ankle position (Fig. 3-2A) and velocity curves. In total, 449 perturbations evoked at rest were analyzed.
Figure 3-1. (A) The wearable device designed to deliver a perturbation to the right ankle joint during running. The two carbon fiber shells which hold the foot and the lower leg can be seen. These shells are linked by a hinged joint pivoting at the centre of rotation of the ankle. (B) Subject wearing the exoskeleton and running on a treadmill equipped with strain-gauge sensors. (C) A typical trace of the angular position of the right ankle (top) and of the right soleus (Sol) EMG activity (bottom) shown as a function of time. Control and perturbed cycles are shown. TD = touch-down. Pert = perturbation. Sol_ref indicates the reference used to normalize the soleus EMG values. All perturbations were applied to the right ankle during the swing phase of the right leg. Depending on their timing, perturbations were classified into five groups: t1, t2, t3, t4 and t5 (cf. data processing for details).

The EMG signals were full-wave rectified and then bi-directionally low-pass filtered (40 Hz first-order Butterworth) to obtain a zero-phase shift envelope. The stretch reflex responses include three distinct components, the short-latency response (SLR), the medium-latency response (MLR) and the long-latency response (LLR) (e.g. Toft et al. 1991). During running, these peaks were not easily detectable; therefore we measured in both tasks the EMG activity from 40 to 90 ms after the perturbation (40-90) to evaluate the first two components, and from 90 to 140 ms after the perturbation (90-140) to evaluate the long-latency component. Control EMG activity was measured during the corresponding periods of the preceding cycle in running (control cycle, Fig. 3-1C and 3-2D) and during the 30 ms period after the perturbation onset at rest (0-30_ctrl, Fig. 3-2C).

To compare the effect of the perturbations during running (t1 to t5 timing groups) and at rest, EMG activity values were
normalized; they were expressed as percentage of a reference EMG measured during the control cycle of running. For each triceps surae muscle, the reference was its mean activity observed during the stance of the right leg (e.g. Sol_ref in Fig. 3-1C). For TA, the reference was its mean activity observed during the 100 ms preceding this right leg stance. For each running perturbation, the reference was measured during the preceding cycle (control cycle). At rest, for each subject, the reference was the average of all his references calculated for the running perturbations.

3.2.4 Statistics

The amplitude of the reflex responses was compared for each muscle (Sol, MG, LG, TA) and each analysis period (40-90, 90-140) using a two-way repeated-measures analysis of variance test with factors: group (rest, t1, t2, t3, t4, t5) X condition (control, perturbed). Differences between groups within the control condition and between conditions within each group were tested using the Holm-Sidak multiple-comparison test. Statistical significance was determined by obtaining a $P$ value of $< 0.05$. Only significant results are discussed.

3.3 Results

All the subjects performed the trials without stumbling or falling, and continued to run normally in spite of the perturbation.
3.3.1 Characteristics of the perturbation

At rest the amplitude of the evoked ankle dorsiflexion was 8.8±2.2 (mean±s.d.) deg and the speed was 166±54 deg.s⁻¹ (see typical trace in Fig. 3-2A).

Figure 3-2. Typical trace of the right ankle position in degrees (A-B) and soleus EMG activity in µV (C-D) as a function of time (ms) observed after the perturbation at rest (A&C) and during running (B&D, t4 perturbation; control trace=thin line, perturbed trace=thick line). The amplitude of the perturbation is shown in A and B. The second y-axis on the right in C and D indicates the EMG normalized value (%., cf. data processing for details). The periods during which the EMG responses were measured are highlighted by the boxes.
During running the perturbations were evoked at different times between the left and right TD; the delays between the perturbation and the following right TD were 327±28, 252±26, 181±24, 113±22 and 45±16 ms for respectively t1, t2, t3, t4 and t5. The amplitude of the perturbation during running was equal to 9.0±3.5 deg with a speed of 206±66 deg.s⁻¹ (see typical trace in Fig. 3-2B). The characteristics of the perturbation were quite similar between timing groups (see Scohier et al. 2012).

3.3.2 Background EMG activity

There was a significant effect of group on the control activity for each muscle and each analysis period. During running, the triceps surae control EMG activity increased when approaching the touchdown and reached its highest value in t5 (see black bars in Fig. 3-3). The activity measured at rest was not significantly different from the running control activity observed during the 40-90 period in t1-t3 and during the 90-140 period in t1-t2.

3.3.3 Characteristics of the stretch reflex at rest and during running

There was a significant main effect of condition only for LG in 40-90 and in 90-140: all groups together the perturbed values were greater than the control ones.
Figure 3-3. Normalized EMG activity (\%, cf. data processing for details) for soleus (A), medial gastrocnemius (B) and lateral gastrocnemius (C). The control values (black bars) and the values observed after the perturbation (empty bars) are shown for the 40-90 and 90-140 periods at rest (boxes) and for each of the 5 timing groups during running (t1 to t5). RSt = right stance. *indicates significant difference from the corresponding control value.

In 40-90, a group by condition interaction effect was observed for Sol and LG showing a different effect of the perturbation depending on the group. In the rest group, the EMG activity after the
perturbation was increased by +32.5% (Sol, see typical trace Fig. 3-2C) and +6.2% (LG). A significant increase was also observed for MG at rest (+6.0%). On the contrary, during running no increased EMG activity was observed after perturbation, except for LG in t5 (+5.3%). This is shown in Fig. 3-3, A-C (left side).

In 90-140, a group by condition interaction effect was observed for LG. No effect of the perturbation was observed in the rest group. On the contrary, during running there was an increased EMG activity when the perturbation was evoked late in the swing phase: +5.7% in t4 and +12.2% in t5. A significant increase was also observed for Sol in t5 (+10.6%) and for MG in t4 (+12.5%). This is shown in Fig. 3-3, A-C (right side).

3.4 Discussion

In this study, we evoked an ankle dorsiflexion of unexpected timing during the swing phase of running. Whatever the time of the perturbation, and despite the fact that the right ankle angle was modified (see Scohier et al. 2012 for details), all subjects were able to cope with the perturbation and maintain their stability.

3.4.1 Methodological considerations

The speed of the perturbation was always greater than 100 deg.s\(^{-1}\). This stretch speed is sufficient to evoke at rest a soleus SR while seated (Toft et al. 1991) or in the supine position (Shimba et al. 2010). When a muscle is stretched three successive reflex responses
have been described: short (SLR), medium (MLR) and long (LLR) latency responses. The group Ia afferent fibers contribute to the SLR via a monosynaptic excitation of spinal motoneurones (Matthews 1991, Friemert et al. 2010). The group II afferents could contribute to the MLR through an oligosynaptic spinal pathway (Grey et al. 2001, Friemert et al. 2010, Nardone et al. 1996) and a trans-cortical pathway probably contributes to the LLR (Petersen et al. 1998, Christensen et al. 2001, Mrachacz-Kersting et al. 2006). For the lower limb, the first response (SLR) appears with an onset latency of about 40 ms (Toft et al. 1991, Sinkjaer et al. 1996, Grey et al. 2002). The second response (MLR) appears with a peak latency of about 75-80 ms (Toft et al. 1991, Grey et al. 2002, Grey et al. 2001, Sinkjaer et al. 1999) and the third response (LLR) with a peak latency greater than 100 ms (Toft et al. 1991, Grey et al. 2002, Sinkjaer et al. 1999). The presence of these three components varied greatly in the literature. In our study, the successive peaks were not always easily distinguishable. Therefore we based our peak detection windows upon those from the literature. Specifically, we measured the EMG activity during the 40-90 period after the perturbation to observe the early reflex response (including SLR/MLR) and during the 90-140 period after the perturbation to observe the late reflex response (including LLR).

3.4.2 Early reflex response

When the subjects were at rest in the supine position, we observed that the triceps surae activity during the 40-90 period after the perturbation was increased (Fig. 3-2C and Fig. 3-3) and that the
TA activity was not modified. These results confirm those previously described at rest showing short- and medium-latency reflex responses in triceps surae observed after an evoked dorsiflexion (Toft et al. 1991, Ogiso et al. 2002, Grey et al. 2002). The 40-90 response observed at rest in the triceps surae was greater for soleus (+33%) than for the gastrocnemii (+6%), probably because the soleus receives greater spindle feedback than the gastrocnemii (Tucker and Türker 2004).

In contrast, during running almost no modification of the plantarflexors activity was observed after the perturbation, although in t1-t3 the background EMG activity was not different from that measured at rest and in t4-t5, it was higher. So, it seems that the triceps surae early reflex response is suppressed during the swing phase of running. This suppression has been shown for the triceps surae H-reflex during the swing phase of walking and running when its contraction would oppose the active dorsiflexion realized by the TA (Capaday and Stein 1987, Simonsen and Dyhre-Poulsen 1999, Edamura et al. 1991). In sitting, an active ankle dorsiflexion also induced a suppression of the soleus H-reflex (Crone et al. 1987). It was suggested that the suppression was due to presynaptic inhibition (e.g. Dietz et al. 1990). In our study, this mechanism probably also plays a role in the suppression of the triceps surae early reflex response mechanically evoked during the swing phase of running. The Ia afferents of TA could inhibit the triceps surae through the presynaptic inhibition during early and mid-swing. Indeed at the time the TA actively realizes the ankle dorsiflexion, the triceps surae is almost silent, and presynaptic inhibition has been shown for
motoneurones of muscles not involved in the contraction (Hultborn et al. 1987).

Supra-spinal pathways could also contribute to reduce the triceps surae stretch reflex, through direct inhibition of Ia afferents or through inhibitory interneurones. As suggested by Lavoie et al. (1997), in walking the major part of the triceps surae inhibition is probably centrally predetermined.

3.4.3 Late reflex response

In the present study, no late reflex response was observed in the triceps surae after the sudden ankle dorsiflexion evoked in supine position. This is in agreement with earlier studies in which the LLR was not seen in sitting subjects (Toft et al. 1991, Sinkjaer et al. 1999). We have also not observed a LLR when the perturbation was evoked in early-mid swing of running (t1-t3). In contrast, a LLR response was observed after perturbations evoked in late swing (in t4 for MG and LG, in t5 for Sol and LG; see Fig. 3-3). This late response has a latency long enough to be mediated by a trans-cortical pathway. Mrachacz-Kersting et al. (2006) observed in sitting subjects a specific facilitation of the LLR response only in the rectus femoris and not in the vastus medialis and vastus lateralis. They suggested that this response was controlled by supra-spinal centers. In our study, the observed LLR response in the triceps surae was only observed when it coincided approximately with the occurrence of the foot touch-down, which is a critical period for motor control during locomotion (Christensen et al. 2001, van der Linden et al. 2007). We hypothesize
that the triceps surae LLR response after a perturbation is facilitated at critical moments during running, probably by supra-spinal centers.

3.4.4 Limitations and future investigations

When a muscle is stretched three successive reflex responses have been described: short (SLR), medium (MLR) and long (LLR) latency responses. While it is difficult to discern the three peaks of the successive reflex responses during normal walking it is even more difficult during running because the background EMG levels are higher and more variable, thereby increasing the likelihood that small reflex responses are masked by background. The presence of these three components has been discussed previously because they are not always clearly visible. Recently, Finley et al. (2013) demonstrated that the acceleration of the perturbation modulated the triceps surae stretch reflex. They showed that the MLR peaked at moderate accelerations and was largely attenuated at high accelerations. In future stretch reflex investigations, it would be interesting to systematically evaluate the acceleration of the applied perturbations.

We used here a powered exoskeleton inspired by that of Andersen and Sinkjaer (1995) to evoke a sudden ankle dorsiflexion. Our device was not sufficiently powerful to produce the same ankle dorsiflexion during stance as during swing, because of the large plantarflexion torque at the ankle joint observed during stance. According to Schache et al. (2011), the plantarflexor torque reaches a peak value of 2.94±0.35 N.m.kg⁻¹ around mid-stance when running at 3.5 m.s⁻¹. For future investigations it would be interesting to develop a
sufficiently powerful device to permit pertubations during the stance phase. We would expect a spinal short/medium-latency SR in the triceps surae muscles to result from this evoked ankle dorsiflexion during the stance phase of running. Indeed during the stance phase, the triceps surae muscles are active and the TA muscle is almost silent. We would not expect the TA Ia afferents and supra-spinal influences to inhibit the soleus SR. Previous studies have shown that the soleus H-reflex and SR are present during the stance phase of walking (Sinkjaer et al. 1996, Capaday and Stein 1986).

The perturbations applied to the ankle were not measured directly on the ankle joint but by means of an optical encoder in the pivot of the exoskeleton. Thus it is possible that the measured amplitude and duration of a perturbation does not reflect the amplitude and duration of the movement of the ankle. Differences could result from either an incorrect measurement by the exoskeleton, or an imperfect coupling of exoskeleton movement into ankle movement. The aluminum frame of the exoskeleton containing the optical encoder was built specifically to be maximally rigid while lightweight (Fig. 3-1A), thus the measurements made by the optical encoder (temporal and spatial resolution of 1 ms and 0.1 deg) accurately reflect the movements of the exoskeleton. The coupling of the exoskeleton movements into the ankle is less certain. Each carbon fiber shell was customized to fit the anatomy of the leg and of the foot of each subject so that the optical encoder was precisely placed on the center of rotation of the ankle joint. Thus the only possible source of error is movements of the cast that result in movements of the soft tissue and not the ankle joint itself. In order to minimize this
possibility, the cast was strapped to the leg and to the foot by means of Velcro straps. As a result the angle measured by the optical encoder reasonably reflects the ankle displacement, and the similarity of the perturbation characteristics observed between timing groups suggests a high consistency of the ankle perturbation throughout the swing phase.

3.4.5 Conclusion

Our results suggest that the triceps surae short/medium-latency stretch reflex can not be evoked during the swing phase of running, and consequently it has no ‘functional’ role during this phase. However, a long-latency stretch reflex appeared in late swing and thus it could regulate, probably via a supra-spinal pathway, the locomotor pattern at the time of foot touch-down during running.

References


Chapter 4: Modulation of the lower leg muscle activity before the touch-down and during stance after an ankle dorsiflexion perturbation evoked during the swing phase of running

Abstract

In this chapter, we investigated the muscular responses triggered around touch-down that could counteract the sudden ankle dorsiflexion evoked during the swing phase of running. We measured the electromyographic activity of the soleus, medial and lateral gastrocnemii and tibialis anterior during the 100 ms prior to the touch-down and during the right foot contact (braking and push-off phases).

When the perturbation was evoked in the early swing phase, the ankle was already returned within control values at the time of the next touch-down. No modification of the ankle muscles activity was observed between the perturbation and the touch-down. So the ankle was back to its control position probably due to the passive elasticity of the ankle muscles. After perturbations evoked in mid-late swing, in contrast to early perturbations, the ankle position at touch-down was still dorsiflexed and we showed a systematic increase of the triceps surae activity during braking while the pre-stance activity was not modified. This extra-EMG activity of the triceps surae could contribute to the regulation of the locomotor pattern, the ankle being brought back to its normal position at the end of the contact phase.
4.1 Introduction

In the previous chapter, we showed that during running there was no early reflex response after an ankle dorsiflexion of unexpected timing evoked during swing. However, a late reflex response, probably mediated by supra-spinal pathways (e.g. Mrachacz-Kersting et al. 2006), was observed in the plantarflexors when the perturbations were evoked in late swing. For these perturbations, the late reflex response 90-140 includes the touch-down event and/or a part of the contact phase (Fig. 4-1). In human landing movements, the foot touch-down is considered as a critical period and when it is not as expected, fast functionally relevant adjustments are needed (McDonagh and Duncan 2002, Shinya et al. 2009, van der Linden et al. 2007, van der Linden et al. 2009). These studies highlight the likely existence of an internal model that compares the expected with the actual sensory feedback at touch-down. In previous chapters, we showed that the ankle position was still modified at touch-down only when the sudden ankle dorsiflexions were evoked in mid-late swing. For these mid-late perturbations, we hypothesized that the activity of the ankle muscles was adjusted after touch-down in order to regulate the locomotor pattern. This is why in this chapter we measured the electromyographic activity of the ankle muscles during the stance phase when the triceps surae muscles are naturally active. For the perturbations evoked in early swing, because the ankle was back to its control position at the time of foot touch-down while no reflex response was observed, the return of the ankle could be due to an active regulation triggered after the reflex windows and before the
touch-down (see Fig. 4-1). Consequently, we also measured the electromyographic activity of the ankle muscles just prior to the touch-down.

**Figure 4-1.** Representation of the analysis windows. The three specific phases analyzed in this chapter are presented by boxes: pre-stance, braking and push-off. The black circles correspond to the mean time of the perturbation for each group (t1-t5). The horizontal bars represent the windows 40-90 and 90-140 as described in Chapter 3. The EMG traces are typical traces of one subject during running without perturbation. Right TD = touch-down of the right foot; TA = tibialis anterior (dashed black line); MG = medial gastrocnemius (solid light grey line); LG = lateral gastrocnemius (solid dark grey line); Sol = soleus (solid black line).

### 4.2 Methods

The data were collected during the same session as those presented in previous chapters \((n = 441)\). The EMG analysis method was identical to that of Chapter 3, *i.e.* the normalized EMG activity
after the perturbation was compared to the normalized activity measured during the corresponding period of the control cycle (for details, see Chapter 3). In Chapter 3, we described the responses observed after the perturbations during two ‘reflex windows’ (40-90 and 90-140, see 40-140 in Fig. 4-1) in function of time. Here, we evaluated the right lower leg muscular adjustments after these same perturbations just before touch-down and during the right contact phase. We measured the EMG activity of the soleus (Sol), medial gastrocnemius (MG), lateral gastrocnemius (LG) and tibialis anterior (TA) after the perturbation in three specific phases: pre-stance, braking and push-off phases (Fig. 4-1). The pre-stance corresponds to the 100 ms prior to the right touch-down after the perturbation. The braking phase corresponds to the first half of the stance when the fore-aft ground reaction forces are negative and the push-off phase to the second half when they are positive. Note that the ‘reflex windows’ discussed in Chapter 3 are partially superimposed to pre-stance and/or the braking phase depending on the perturbation timing (Fig. 4-1). On average, for t3 the pre-stance includes 90-140 and the last milliseconds of 40-90; for t4 the pre-stance includes 40-90 and the first half of 90-140, the braking includes the second half of 90-140; for t5, the pre-stance includes the first five milliseconds of 40-90, the braking includes the rest of 40-90 and the whole 90-140.

The amplitude of the muscular responses was compared for each muscle (Sol, MG, LG, TA) and each period (pre-stance, braking and push-off) using a two-way repeated-measures analysis of variance test with factors: group (t1, t2, t3, t4, t5) X condition (control,
perturbed). The Holm-Sidak post-hoc test was used to test all pairwise multiple comparisons. Statistical significance was determined by obtaining a \( P \) value of < 0.05.

### 4.3 Results

The \( P \) values of the two-way repeated-measures analysis of variance test comparing the different timing groups (from t1 to t5) and the two experimental conditions (control and perturbed) are presented in Table 4-1 for each period and each muscle investigated. The results of the Holm-Sidak post-hoc test are graphically presented in Fig. 4-2.

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<th>Table 4-1. ( P ) values of the two-way repeated-measures ANOVA comparing the muscular responses (factors: group X condition).</th>
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\( P \) values lesser than 0.05 are in **bold**. group = t1, t2, t3, t4 and t5; condition = control and perturbed.
During pre-stance no EMG modification was observed after the perturbation neither in the triceps surae muscles (Sol, MG, LG) nor in the tibialis anterior whatever the timing of the perturbation (Table 4-1 & Fig. 4-2A).

The duration of the braking phase following the perturbation was not different from the control ones: 133±18 Vs 133±19 ms. During braking, there was a significant main effect of condition only for the soleus muscle whose activity was increased after the perturbation ($P = 0.016$, +9.7%, Table 4-1). This increase was systematically observed when the perturbation was evoked late in the swing phase, i.e. in t3, t4 and t5: +11.1, +12.9 and +11.1% (Holm-Sidak, $P = 0.037, 0.017$ and 0.036, Fig. 4-2B). A significant increase was also observed for the gastrocnemii when the perturbation was evoked in t4: +12.9% (Holm-Sidak, $P = 0.029$) and +15.7% (Holm-Sidak, $P = 0.005$), for respectively the medial and lateral gastrocnemii (Fig. 4-2B). Note that we also observe an increase of the tibialis anterior activity close to the significant level during the braking phase ($P = 0.056$, Table 4-1).

Similarly to the braking phase, the duration of the push-off phase was not modified after the perturbation: 126±19 Vs 124±19 ms.
Only a significant increase of the soleus activity was observed in t5 during the push-off phase: +5.9% (Holm-Sidak, \(P = 0.025\), Fig. 4-2C).

### 4.4 Discussion

First, it is important to note that the relative amplitude of the perturbations is comparable between timing groups (from 5.3 to 7.9 deg, see Fig. 1-2B). The results presented above show that the perturbation has no effect on the EMG activity observed during pre-stance. On the other hand, a modulation of the EMG activity seems to happen during the stance phase, and more specifically in the braking phase after the foot touch-down, when the perturbation is evoked in mid-late swing (t3-t5). For these mid-late perturbations, the ‘reflex windows’ are partially superimposed to pre-stance and/or to the braking phase (Fig. 4-1); consequently, the results of Chapter 4 are sometimes redundant to those presented in Chapter 3. The purpose of this discussion is to have an overview of the muscular strategies adopted to deal with the perturbation. First, we discuss the muscular adjustments observed after early perturbations (t1-t2) and then those observed after mid-late perturbations (t3-t5).

#### 4.4.1 Muscular strategy after a perturbation evoked during early swing (t1-t2)

In early swing, the perturbation is evoked on average 327±28 and 252±26 ms before the next touch-down. At the end of the perturbation, the ankle is in a more dorsiflexed position of about 8 deg compared to control values but at the time of the next touch-down, the
ankle is already returned within control values (Fig. 1-2). Because no reflex response was observed after the t1-t2 perturbations, the return of the ankle to control values could be due to an adjusted activity of the ankle muscles occurring after the reflex windows and before the next touch-down, *i.e.* during pre-stance. However, the results show that no modification of the lower leg muscles activity occurred during pre-stance. So the ankle is back to its control position without extra-EMG activity. As observed in Fig. 1-2, it seems that the return of the ankle to control values get started as soon as the external constraint is suppressed, *i.e.* at the end of the hold time when the ankle is ‘unlocked’. This return could be explained by the ‘equilibrium-point’ theory supporting the idea of a mass-spring model where the limb moves to a position defined by the relative tensions in the agonist and antagonist muscles (*e.g.* Schmidt and McGown 1980). The increased ankle dorsiflexion due to the perturbation induces an increased tension in the plantarflexors because they are being stretched and Conversely a decreased tension in the dorsiflexors because they are being shortened. When the external force is suddenly removed, *i.e.* when the ankle is ‘unlocked’, the mass-spring system tends to move the ankle back to the equilibrium-point defined by the tension in the ankle muscles.

After touch-down, the EMG activity during the braking and push-off phases is not modified. This was expected because the ankle position at touch-down and the biomechanical parameters measured during stance (see Chapter 1) are not altered after the early perturbations. So there is no reason why the lower leg muscles activity should be adjusted at this time.
4.4.2 Muscular strategy after a perturbation evoked during mid-late swing (t3-t5)

After perturbations evoked in mid-late swing, in contrast to early perturbations, the ankle position at touch-down is still dorsiflexed: +2.4, +5.6 and +4.8 deg, for respectively t3, t4 and t5 (Fig. 1-2). The perturbation is evoked on average 181±24, 113±22 and 45±16 ms before the next touch-down and this delay seems not long enough to bring back the ankle to its equilibrium-point at the time of the next touch-down. In Chapter 3, we showed that the perturbations evoked during late swing (t4-t5) induced some increases of the reflex responses (mainly in 90-140). These reflex windows always coincide at least partially with the occurrence of the pre-stance and/or braking phases (Fig. 4-1). Here, we show that the perturbations evoked in t3-t5 provoke a systematic increase of the triceps surae activity during braking while the pre-stance activity is not modified. Thus, the changes in the reflex responses seem to be due to an increased triceps surae activity triggered after the foot touch-down. This hypothesis is supported by the increase of soleus activity during the braking phase observed in t3 (Fig. 4-2B) while no reflex response was present after the t3 perturbations (Fig. 3-3 in Chapter 3). In this precise case, the response is clearly triggered after touch-down. A lot of studies have already shown that sensory feedback at foot touch-down was at the origin of fast adjustments (Grimmer et al. 2008, Marigold and Patla 2002, Marigold and Patla 2005, McDonagh and Duncan 2002, Shinya et al. 2009, van der Linden et al. 2007). Our results seem to confirm that the foot touch-down is a critical moment where the expected
sensory feedback is compared to the actual one (van der Linden et al. 2007).

This extra-EMG activity of the triceps surae observed during the contact phase could contribute to the regulation of the locomotor pattern. The foot trajectory is accurately controlled during locomotion (Ivanenko et al. 2002) and the increase of the soleus activity during braking after t3-t5 perturbations contributes to the ankle being brought back to its normal position at the end of the contact phase. In t4, the increase of dorsiflexion at touch-down is the greatest. The plantarflexion must be more important to bring back the ankle to its normal position and the contribution of the unique soleus could be insufficient. This is probably the reason why the gastrocnemii also increase their activity during the braking phase in t4. In t5, the perturbation is evoked 45±16 ms before the right touch-down. The duration of the braking phase seems not long enough to allow the adjustments and the soleus activity is still increased during the push-off phase in t5.

The Figure 4-2B shows that the tibialis anterior also increases its activity during the braking phase, close to a significant level. It has been shown that co-contractions could help to enhance gait stability after the foot touch-down by stiffening the ankle joint (Seyedali et al. 2012, Shinya et al. 2009). Thus the increased activity of the triceps surae associated with the similar increased activity of the tibialis anterior could contribute to stabilize the ankle joint. Even if we could not exclude this hypothesis, we rather suggest that the increase of the triceps surae activity during the braking phase contributes to bring back the ankle to its control position. Further investigations are
needed to clarify the role of the tibialis anterior in the control of stability after the perturbations evoked during mid-late swing.

4.5 Conclusion

After the perturbations evoked in early swing of running, the ankle is brought back to its control position without extra-EMG activity probably due the passive elasticity of the ankle muscles. After the perturbations evoked in mid-late swing, the ankle geometry is still altered at the time of foot touch-down and an extra-EMG activity of the ankle muscles is observed during the stance phase, probably designed to bring back the foot as fast as possible to its control position. Our results confirm that the foot touch-down is a critical moment during locomotion.

References


Chapter 5 - Pilot study: Ipsi- and contralateral effect of a large ankle dorsiflexion perturbation evoked during the early ipsilateral swing phase of running

Abstract

In this pilot study, we investigated the bilateral effect of a large sudden right ankle dorsiflexion evoked during the early swing phase of running for one subject. We analyzed the running pattern immediately after the perturbation and the electromyographic activity of ipsi- and contralateral ankle and knee muscles.

The perturbation resulted in an increase of the right ankle dorsiflexion of at least 10 degrees. The ankle was still in a dorsiflexed position at the time of the following right touch-down when compared to control steps but no modification of the running pattern greater than 10% was observed on the following first right step after the perturbation. In the ipsilateral leg, no clear modification of the EMG activity was observed during the early and late reflex responses but an increased EMG activity (>10%) was observed for the triceps surae and rectus femoralis muscles during the braking phase after the perturbation. This extra-EMG activity could contribute to the return of the body segments from a perturbed position at the foot touch-down to a normal position at the next toe-off. In the contralateral leg, only an early reflex response was observed in the semimembranosus.
5.1 Introduction

In Chapters 1-4, an increased activity of the triceps surae and a modification of the vertical impact were observed after the perturbation when the ankle was still more dorsiflexed at the time of TD. We discussed that this increased triceps surae activity could be mediated by supra-spinal centers to bring the ankle back to its control position and that the modification of the vertical impact could be a passive consequence of the lower limb geometry at touch-down. Indeed we observed a significant correlation between the increase of ankle dorsiflexion at touch-down and the modification of the vertical impact parameters. However due to the low coefficient of determination of these correlations ($r^2 = 0.10$ to 0.23), it is clear that the ankle geometry at touch-down is not the unique factor to explain the modifications of the vertical impact of the foot. It should be noted that the perturbations inducing a more dorsiflexed ankle at touch-down were evoked mainly in late swing (t4-t5), i.e. the time between the perturbation and the foot touch-down is reduced, compared to perturbations evoked in early swing of running. For these early perturbations, the ankle was brought back to its control position at the time of foot touch-down (Fig. 1-2 in Chapter 1) and nearly no adjustment of the running pattern was observed during the first step after the perturbation (Table 1-1 in Chapter 1). The first purpose of this pilot study is to evoke larger perturbations in early swing than those previously evoked in Chapters 1 to 4 and to observe if the running pattern is modified after such larger early perturbations in
order to dissociate the effect of the factors ‘time of perturbation’ and ‘ankle geometry at touch-down’.

In Chapter 3, we showed that there was no adjustment of the triceps surae stretch reflex in the ipsilateral leg after early perturbations. We hypothesized that the inhibition of the triceps surae stretch reflex is probably centrally predetermined (Scohier et al. 2014). However supra-spinal pathways could influence differently the responses in the contralateral leg during the early swing phase of running and we did not evaluate this. The early right swing phase coincides to the left stance phase and thus the contralateral triceps surae is active at this time (Fig. 5-1). Previous studies showed that a stimulus applied to one leg can evoke a reflex response with functional relevance in the contralateral triceps surae during walking (Duysens et al. 1991, Stubbs et al. 2011, Gervasio et al. 2013). Stubbs et al. (2011) observed a phase-dependency of the short-latency crossed response in human soleus. Indeed a short-latency facilitation was observed following an ipsilateral tibial nerve stimulation at 63% of the gait cycle while no response was observed at 70% and a short-latency inhibition was observed from 80% to 100% of the gait cycle. Little is known about this crossed response after a mechanical perturbation during running. The second purpose of this chapter is to measure the responses in the contralateral leg after early perturbations.
Figure 5-1. Muscle activity during two consecutive cycles (empty bars for the right muscles and solid bars for the left muscles). The swing and stance phases are represented at the top. TD = touch-down; TO = toe-off. The data come from one of our subjects.

Here, we realized a pilot study in which we applied to one subject ankle dorsiflexions in early swing with a greater amplitude than those evoked previously. We analyzed the running pattern and the electromyographic activity of ipsi- and contra-lateral ankle and knee muscles. In addition we also measured the angular position of the ankle and knee joints.

5.2 Methods

One healthy young men (age=26 years, body mass=64kg, height=1.82m), free of lower leg injuries, participated in this pilot study. The subject was informed of the experimental conditions and provided his written consent to participate. Experiments were
performed according to the Declaration of Helsinki and approved by
the local ethics committee.

The data were collected during a new session but with a
similar experimental protocol to the one of Chapter 1-4. The subject
ran on the instrumented treadmill at a speed of 2.8 m.s\(^{-1}\) while
equipped with the powered exoskeleton on his right leg (Fig. 1-
1A&B). Perturbations (n = 12) were evoked to the right ankle at the
beginning of the right swing phase, corresponding to the first 40% of
the left step duration (i.e. \(t_1\) and \(t_2\) as defined in Chapter 1). The
perturbations consisted of a dorsiflexion of \(~50\) ms duration followed
by a plateau of \(~150\) ms before ankle release.

The same biomechanical parameters as those presented in the
previous chapters were calculated and compared between control and
perturbed steps, i.e. the contact (\(t_c\), ms), flight (\(t_f\), ms) and total (\(T\), ms)
durations of the step; the maximal amplitude of the negative fore-aft
(\(F_{y,\text{brake}}\), N), of the positive fore-aft (\(F_{y,\text{push}}\), N) and of the vertical
(\(F_{z,\text{max}}\), N) ground reaction forces; the step length (\(L_{\text{step}}\), mm); the
amplitude (\(F_{z,i}\), N), the time (\(t_{z,i}\), ms) and the mean loading rate (\(G_{z,i}\,
N.m.s^{-1}\)) of the vertical impact.

As previously, the angular position of the ankle was measured
by the optical encoder placed in the pivot of the exoskeleton (1 kHz
sampling rate, Avago Technologies®; HEDS-9200). Additionally, the
knee angle was evaluated by means of a camera (100 Hz sampling,
Basler® piA 140-210 gc) and three reflective markers. The camera
was placed in parallel to the treadmill. The three markers were
retroreflective half spheres of 2 cm diameter fixed directly to the skin
with adhesive on the greater trochanter, the lateral femoral condyle
and the lateral malleolus. The data were collected by the software eLynx® and analyzed by the software Lynzone1.7.1®. The lower limb was modelized in two segments with the coordinates (X, Y) from each reflective marker and the knee angle was calculated as the angle between the thigh and the lower leg.

The muscular activity was measured by a wireless system (1kHz sampling rate, BTS© Free-Emg). After the skin was shaved and cleaned, a pair of surface EMG electrodes, separated by 2 cm, was positioned over the following ipsi- and contra-lateral leg muscles: rectus femoris (RF), semimembranosus (SM), medial gastrocnemius (MG), soleus (Sol) and tibialis anterior (TA). The EMG activity was analyzed for both legs during the two ‘reflex windows’ (40-90 and 90-140) defined in Chapter 3 and only for the ipsilateral muscles during two specific phases (braking and push-off) defined in Chapter 4. Because EMG activity was measured only for one subject, EMG activity values were not normalized and the absolute values are presented thereafter.

The values observed after the perturbation were compared to those measured during the corresponding period of the control cycle.

5.3 Results

5.3.1 Effect of the perturbation on the right ankle and knee angles

The average right ankle dorsiflexion was characterized by a rise time of 55±15 ms, an absolute amplitude of 16.1±2.5 deg, a relative amplitude of 12.8±2.5 deg, an absolute speed of 307±69
deg.s\(^{-1}\) and an hold time \(\sim 150\) ms. The mean delay between the perturbation and the next touch-down \(R_{\text{pert TD}}\) was 285±28 ms (range from 316 to 237 ms, Fig. 5-2). An example is illustrated for a perturbation with a delay of 243 ms before \(R_{\text{pert TD}}\) in Fig. 5-3A.

![Figure 5-2. Typical trace of the vertical ground reaction force in function of time.](image)

The arrows show the specific timing of each perturbation \((n = 12)\). In the text, the timing of each perturbation is referred as the delay between the perturbation (arrow) and the next touch-down (black solid circle).

The ankle was still in a dorsiflexed position at the time of the following \(R_{\text{pert TD}}\) when compared to control steps: +4.4±2.7 deg (Fig. 5-3C). However, the right ankle dorsiflexion was not anymore modified at \(R_{\text{pert TO}}\) (\(R_{\text{pert TO}}\)). The knee joint angle was not modified by the perturbation (see typical trace in Fig. 5-3B).
Figure 5-3. Typical traces of the effect of a perturbation on the right ankle (A) and knee (B) joint angles. The control stride (dashed trace) and the perturbed stride (continuous trace) are superimposed and synchronized on the right TD (time 0, vertical interrupted line). The dashed arrow shows the perturbation onset. The relative amplitude (1) of the perturbation was obtained by subtracting the ankle angular displacement of the control step from the absolute amplitude (2) of the perturbation. C: Relative right ankle dorsiflexion at specific times after the perturbations, i.e. at the end of the rise time (grey bar) and at the following toe-offs and touch-downs ($L_{pert}$ TO, $R_{pert}$ TD, $R_{pert}$ TO and $L_{+1}$ TD; black bars) as indicated. The values are expressed as the difference between the right ankle position at these specific times and its position at the corresponding time of the control step. Bars represent mean±s.d. The arrow shows the mean perturbation onset time. Note the time scale is the same in Panels A, B & C.

5.3.2 Immediate effect of the perturbation on the running pattern (Table 5-1)

The perturbations were evoked during the early swing phase of the right step which corresponds to the stance phase of the left step. No modification greater than 10% was observed either on the left step or on the following right step after the perturbation.
Table 5-1. Effect of the perturbations on the biomechanical parameters.

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The absolute differences (Δ) of each parameter are shown as the mean±standard deviation (n = 12) for the left and right perturbed step compared to the corresponding control. No modification was greater than 10%. The parameters are defined in the Methods of the Chapter 1.
5.3.3 Modulation of the ipsi- and contralateral leg muscles activity during early and late reflex responses (Figure 5-4)

In the ipsilateral leg muscles (right side), no clear modification of the EMG activity was observed after the perturbation during the early and late reflex responses. In the contralateral leg muscles (left side), the EMG activity was clearly modified in the semimembranosus during the early reflex response, increasing from 230±164 to 294±188 µV (+28%).

Figure 5-4. Mean leg muscles activity during the 40-90 (A) and 90-140 (B) reflex windows for rectus femoris (RF), semimembranosus (SM), medial gastrocnemius (MG), soleus (Sol) and tibialis anterior (TA). Contralateral (left) muscles at the left; ipsilateral (right) muscles at the right.
5.3.4 Modulation of the ipsilateral leg muscles activity during the braking and push-off phases (Figure 5-5)

During the braking phase of the first right step after the perturbation, we observed a clear increase of the activity for the rectus femoralis (+11%), the medial gastrocnemius (+12%) and the soleus (+13%) muscles. The activity of the ipsilateral muscles was not clearly modified during the push-off phase.

![Figure 5-5. Mean ipsilateral (right) leg muscles activity during the braking and push-off phases for rectus femoris (RF), semimembranosus (SM), medial gastrocnemius (MG), soleus (Sol) and tibialis anterior (TA).](image)

5.4 Discussion

5.4.1 Running pattern and implications of the ankle geometry at touch-down

In this pilot study, large and fast ankle dorsiflexions were applied at the right ankle from 316 to 237 ms before the right foot
contact (early perturbations), i.e. at the beginning of the left step. No modification of the running pattern was observed on the left step after the perturbation. At the time of the following right touch-down, the right ankle was still in an enhanced dorsiflexion. The amplitude of this modification (+4.4 deg) is quite similar to the one observed previously after late perturbations (+5.6 and +4.8 deg for t4 and t5, see Chapter 1). In Chapter 1, we observed a larger number of small modifications after late perturbations (Table 1-1) and we showed that the vertical impact was clearly modified. Here, only few small modifications (<10%) are observed. In Chapter 1, we hypothesized that the vertical impact could be a passive consequence of the altered geometry at touch-down but here the vertical impact is not modified despite the altered ankle geometry at touch-down. In this pilot study, the altered geometry at touch-down is due to a perturbation evoked earlier during the swing phase and the effect of the perturbation on the kinematics could be different. Other parameters not measured in our study could have influenced the vertical impact: the position of the centre of mass of the whole body at initial ground contact, the foot placement, the position of the shank, and so on ... (De Wit et al. 2000, Klute and Berge 2004). In order to understand the determinants of the vertical impact, the global geometry should be further investigated.

5.4.2 Activity of the ipsilateral muscles during the right contact phase

The results of this pilot study showed an increase of about 10% of the right medial gastrocnemius and soleus muscles activity during the braking phase while these muscles are the most active (Fig.
5-5). This increase is similar to the one described in Chapter 4 after the late perturbations (see Fig. 4-2). We also observed an increase of about 10% of the right rectus femoralis during the braking phase. The rectus femoralis is a bi-articular muscle and its function is extension of the knee and flexion of the hip. Because our results showed an unmodified trajectory of the knee joint, the increase of the rectus femoralis probably contributes to increase the hip flexion. As discussed previously, the extra-EMG activity of the triceps surae together with this of the rectus femoralis could contribute to bring back the body segments from a perturbed position at the foot touchdown to its normal position at the next toe-off (Fig. 5-3).

5.4.3 Ipsi- and contralateral early and late reflex responses

As observed in the Chapter 3 for early perturbations, the subject showed no early/late reflex response in the ipsilateral (right) triceps surae and tibialis anterior muscles. In addition, we observed no response in the additional ipsilateral leg muscles investigated (rectus femoris and semimembranosus). In Chapter 3, we discussed that the suppressed early reflex response was due to presynaptic inhibition; we suggested that supra-spinal pathways contribute to this suppression and that the major part of the inhibition is probably centrally predetermined. We hypothesized that the ipsilateral triceps surae late reflex response after a perturbation was facilitated at critical moments during running, probably by supra-spinal centers.

The early right swing phase of running could be a critical moment for the left leg because at this time, the left foot is in contact
with the ground and most of the contralateral (left) muscles are active. The sudden increase of dorsiflexion of the swinging foot could be interpreted as a threat to the stability of the body that should be controlled by the contralateral muscles. As observed in walking (Dietz et al. 1989, Duysens et al. 1991, Stubbs and Mrachacz-Kersting 2009, Stubbs et al. 2011, Gervasio et al. 2013), a contralateral triceps surae stretch reflex could be elicited after a mechanical or electrical perturbation of the ipsilateral leg. This crossed response likely has a functional relevance. Indeed, it can be reversed when an opposite reaction is required (Gervasio et al. 2013) and its short-latency response is phase-dependent (Stubbs et al. 2011).

In our pilot study, except an increased response in the left semimembranosus in 40-90, no clear reflex response was observed after the perturbation in the contralateral muscles (Fig. 5-3). First, a response in the contralateral leg, i.e. here the left leg, could originate from the ipsilateral leg, i.e. here the right leg wearing the exoskeleton, probably through crossed spinal interneurones (Stubbs and Mrachacz-Kersting 2009). Thus, the stimulation of the alpha motoneurones in the contralateral leg could be induced by an increased discharge of the muscle spindles in the ipsilateral leg. Here, the sudden stretch of the right triceps surae muscles is evoked at a non-critical time for the right leg. Consequently, the gamma motoneurones could downregulate the excitability of the right triceps surae muscle spindles at this time. Shimba et al. (2010) showed that the soleus stretch reflex was significantly larger in passive standing than in supine posture and discussed that it is possible that the CNS regulates the gamma motoneurones activation in order to decrease the responsiveness of the
muscle spindles to the stretch. Second, a response in the contralateral leg could also originate from the contralateral leg itself; this one being indirectly perturbed (Dietz et al. 1989, Duysens et al. 1991). It is suggested that the reflexes in the contralateral leg could have a functional role in the maintenance of stability during human locomotion (Tax et al. 1995, Haridas et al. 2008). Here, it is possible that the perturbation was not destabilizing enough for the foot on the ground to induce a triceps surae response in the contralateral leg. However, we observed a clear early reflex response in the contralateral semimembranosus. This muscle has a double function: flexion of the knee and extension of the hip. The flexion of the knee does not seem to be modified by the increase of the semimembranosus activity. The extension of the hip can not be evaluated as we did not measure the hip kinematic. In any case, the contralateral semimembranosus response could show that the semimembranosus plays a role in the control of dynamic stability after the perturbation by adjusting the hip flexion-extension.

References


Conclusion and perspectives

In this study, we evoked a sudden ankle dorsiflexion of about 10 deg and with a speed greater than 100 deg.s$^{-1}$ during the swing phase of running. A powered exoskeleton (< 1kg) attached to the right leg was designed to deliver a well-defined perturbation. This perturbation induces a stretch of the triceps surae muscles and we observed at rest an early stretch reflex response in these muscles. We showed that the exoskeleton did not modify running variability and symmetry.

This study was intended to analyse the modifications of the running pattern after a mechanical perturbation and to investigate the phase-dependency of the triceps surae stretch reflex responses during the swing phase of running. To our knowledge, this is the first study investigating the triceps surae stretch reflex excitability through a mechanical ankle dorsiflexion during running. The present discussion is the opportunity to bring together the modifications of biomechanical parameters and muscle responses, reflex or not, in order to have an overview of the recovery strategies.

c.1 Recovery strategy

The perturbation was not too destabilizing and none of our subjects stumbled or fell after the perturbation. Whatever the timing of the perturbation, we observed appropriate adjustments, as previously observed after various kinds of perturbations during walking.
(Weerdesteyn et al. 2004, Nakazawa et al. 2004, van der Linden et al. 2007, Schillings et al. 2000) and running (Grimmer et al. 2008, Müller et al. 2010, Haudum et al. 2012). Most of the modifications occurred on the first step and in a lesser extent on the second step after the perturbation. The adjustments were appropriate because the subjects were able to continue a stable locomotion on the treadmill.

Eng et al. (1994) showed in walking that a sudden perturbation evoked at different times during the cycle can lead to an identical recovery strategy achieved by different patterns of muscle activation. In our study, the recovery strategy could consist in maintaining the step length and the step duration as constant as possible. We showed that these two parameters were the most symmetric and stable ones in control treadmill running. They were maintained quite constant after the perturbation whatever its timing, while other time-dependent adjustments were observed after a perturbation evoked in early-, mid- or late swing of running.

Evoked at the beginning of the swing phase (0-40% of the left step), the perturbation induced only small modifications of the running pattern whether the ankle is already brought back to its ‘control’ position at touch-down (Chapter 1) or not (larger perturbations, Chapter 5 – Pilot study). In addition, no modification of the leg muscles investigated was observed either in the reflex windows or in the pre-stance and push-off phases. An increase of leg muscles activity (rectus femoralis, medial gastrocnemius and soleus) was observed during the braking phase only after the largest perturbations, when the ankle was not returned to control values at
touch-down. After the largest perturbations, the subject showed also an early reflex response in the contralateral semimembranosus but not in the triceps surae. The contralateral reflex response could contribute to maintain the dynamic stability during running (Tax et al. 1995, Haridas et al. 2008). Further investigations are needed to evaluate the crossed reflex response in running.

After the perturbations evoked at mid-swing (40-60% of the left step), the ankle was still more dorsiflexed at touch-down (+2.4 deg), few biomechanical parameters were modified and the soleus activity was increased during the braking phase only.

Evoked in late swing (60-100% of the left step), the perturbation led to a clear increase of the ankle dorsiflexion at touch-down (~ 5 deg) associated with a greater number of modifications of the biomechanical parameters including a modified vertical impact of more than 10%. We also observed more frequent adjustments of the muscular responses: in t4, a late reflex response for the gastrocnemii and an increased activity during the braking phase for the triceps surae; in t5, an early reflex response for the lateral gastrocnemius, a late reflex response for the lateral gastrocnemius and soleus, and finally an increased activity during the braking and push-off phases for the soleus.

In a few words, our results show a suppression of the triceps surae early reflex response during the swing phase of running and a time-dependent late reflex response that could be useful to control the ankle trajectory. The vertical impact is the only strong modification of
the running pattern and appears when the perturbation is evoked in late swing.

c.2 Suppression of the triceps surae early stretch reflex response during the swing phase

At rest, we observed an early reflex response in the triceps surae after the sudden ankle dorsiflexion while it was suppressed during the swing phase of running. This is in agreement with previous studies. For example, Courtine et al. (2007) stimulated percutaneously the spinal cord at the T11–T12 level during running and showed a suppression of the monosynaptic responses in the triceps surae during swing while they were facilitated during the stance phase and just prior to touch-down when the ankle extensors were activated.

We suggest that the suppression is due to presynaptic inhibition that could be mediated by the active tibialis anterior. Indeed, the TA Ia afferents could reduce the excitability of the triceps surae α motoneurones during the swing phase when the triceps surae is silent (Hultborn et al. 1987). Supra-spinal pathways could also contribute to reduce the early reflex response (see Dietz 1999), through for example an increase of presynaptic inhibition and/or a downregulation of the gamma motoneurones activation (Shimba et al. 2010). According to Lavoie et al. (1997), the major part of the triceps surae inhibition is probably predetermined through supra-spinal pathways.

Literature shows that an increased speed of perturbation increases the triceps surae short-latency stretch reflex amplitude
(Berardelli et al. 1982, Gollhofer et al. 1998, Cronin et al. 2009) but our early response was also suppressed after the fastest perturbations evoked in one subject in early swing. Finley et al. (2013) recently demonstrated that the acceleration of the applied perturbation rather than its speed affects the amplitude of the stretch reflex components in the triceps surae. In future studies, the acceleration should be controlled and sudden ankle dorsiflexion with greater acceleration should be investigated.

c.3 Functional role of the late reflex response

After perturbations during gait, the main response appears at a latency of around 85 to 90 ms corresponding to our late reflex response. According to Duysens et al. (2008), this late response brings a meaningful global response to the perturbation. In running, we observed a late reflex response in the triceps surae when the perturbation was evoked in the late swing, i.e. when the late response coincided approximately with the braking phase. This late reflex response seems to be triggered after touch-down, which is considered as a critical period of the running cycle (Christensen et al. 2001, van der Linden et al. 2007). After these late perturbations, the ankle was not back to its control position at touch-down. Yet, the foot trajectory seems to be accurately controlled in gait (Ivanenko et al. 2002). So, the late reflex response induces an increase of the plantar-flexion that could contribute to bring back the ankle to its control position through an active regulation triggered at touch-down.
Thus, we hypothesize that the triceps surae late reflex response is facilitated after a perturbation at critical moments during running, probably by supra-spinal centers. During lower limb loading, a variety of sensory receptors can be activated, such as Golgi tendon organs, cutaneous receptors of the foot and spindles from stretched muscles (Duysens et al. 2000). The expected sensory feedback can be compared with the actual sensory feedback at a transcortical and/or cerebellar level. At a cortical level, there is a continuous comparison between the expected feedback and the actual feedback of the somatosensory receptors. Evidence for a cortical contribution in the long-latency reflex response have been demonstrated (Petersen et al. 1998, Christensen et al. 2001, Mrachacz-Kersting et al. 2006, Taube et al. 2006). At the cerebellar level, there is also a comparison between the afferent feedback and the predicted sensory feedback (Wolpert et al. 1998). It has been shown that the long latency reflex response in the hand muscles of patients suffering from cerebellar disorders is different from the normal values (Claus et al. 1986). The contribution of the cerebellum in the soleus late reflex response could be clarified by comparing the adjustments after this kind of perturbation in patients with cerebellar disorders.

c.4 Determinants of the vertical impact of the foot at touch-down

The last point we want to discuss concerns the modification of the vertical impact of the foot at touch-down that we observed after the perturbations evoked in late swing. In running, the collision of the foot with the ground induces high impact forces during the first 50 ms
of a step. Large and rapid impact forces, resulting in a high loading rate, have been associated with an increased risk of developing an overuse injury of the lower extremity (for a detailed review, see Hreljac 2004). This is why a lot of studies investigated the determinants of the vertical impact showing that it is affected by multiple factors including running speed, lower leg geometry at touch-down, step frequency and footwear (Nilsson and Thorstensson 1989, Gerritsen et al. 1995, Hreljac 2004, Hobara et al. 2012, Lieberman et al. 2010, Willy and Davis 2014). It is difficult to investigate the influence of each factor separately. For example, in habitually minimalist shod runners, the lower leg geometry at touch-down is modified and the step frequency also increased (Belkacem et al. 2013).

In our study, we observed a decreased loading rate of the vertical impact peak. Because they were unchanged, running speed, step frequency and footwear can not explain the modification of the impact. Thus, the decreased loading rate is probably explained by a modified lower leg geometry at touch-down. However, according to the results of footwear studies (Huyghe et al. 2012, Willy and Davis 2014), we could expect an increased loading rate due to the increased ankle dorsiflexion at touch-down. The discordance with these studies could come possibly from the specificity of our study in which the lower leg geometry modifications are due to a sudden perturbation and not to a planned strategy and/or from other modifications of the lower leg geometry. More than the position of each segment, their acceleration relative to the others contributes to the vertical impact (Bobbert et al. 1991, Bobbert et al. 1992) and it was not measured in
our study. Moreover, the increased ankle dorsiflexion at touch-down observed in our study is probably a passive consequence of the sudden perturbation rather than an active adaptation strategy. This differs from most of the studies that investigate the determinants of the vertical impact where the ‘perturbation’ is not sudden. For example, barefoot running induces a modified lower leg geometry at touch-down (De wit et al. 2000) but in this type of study, the joint configuration of the leg at touch-down can be prepared during the swing phase. Komi et al. (1987) showed a higher preactivation level of gastrocnemius muscle for the barefoot condition than for the shod condition.

Our data do not allow to highlight the mechanism responsible for the decreased loading rate of the vertical impact. However, we suggest that this decreased loading rate observed in our study is a passive consequence of the altered lower leg kinematic at touch-down induced by the perturbation. Indeed after the sudden perturbation that subjects could not anticipate, no modification in the lower leg muscles activity was observed during pre-stance and the vertical impact appears too early to be modified by the increased triceps surae activity observed during the braking phase. So the vertical impact is a passive modification that could be associated with the lower leg geometry. Indirectly, we can assume that the late reflex response contributes to bring back the vertical impact to control values by correcting the ankle geometry. In future investigations, it would be interesting to realize a complete kinematic analysis to understand the determinants of the vertical impact in human running after this kind of perturbation.
References


