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Romain Bechet

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THÈSE

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Romain Bechet

CHARACTERISATION OF ANTICIPATORY MUSCLE ACTIVATIONS DURING MOTOR TRANSITIONS

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devant la Commission d'Examen

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For those who want to change the world,

R.

Abstract

Human movements result from a complex coordination of the nervous, muscular, and skeletal systems. Understanding motor coordination requires proper consideration of each system characteristics. When at least one system is defective, human mobility is largely impaired, leading to dependency. A fundamental understanding of human movement coordination is necessary to build adapted devices or rehabilitation programs for populations with mobility impairments. Particularly, the objectives the nervous system needs to satisfy when executing movement remain unclear.

To adapt their movements relative to both internal and external constraints, humans can predict the consequences of these constraints, and thus program anticipatory muscle activations, providing favourable conditions for movement execution. To better understand these favourable conditions, we propose a new framework of motor transitions to better characterise how the nervous system manages the distinct changes in external force. We then reviewed the different roles of anticipatory muscle activations using this new framework in two different contexts: anticipation for balance-movement coordination, and anticipation of ground contact. First, we characterised the mechanical consequences of anticipatory muscle activations and showed that motor transitions are a period of desired mechanical instability with a different balance-movement coordination than during steady-states (such as walking or standing). However, the complete understanding of balance regulation, in particular the conditions provided by free segments, during motor transitions is still lacking. When reviewing anticipation of contact, we showed that the literature only states that anticipatory muscle activations generate stiffness to prepare the whole-body upward acceleration during contact. Some kinematic configurations of the lower-limb at the instant of contact reduce the magnitude of external force at contact, and help protect the skeletal system. However, the conditions required to achieved these kinematic configurations remain unknown.

To improve our knowledge of the favourable conditions provided by anticipatory muscle activations, two experimental situations have been set up. First, motor transitions during walking were analysed to determine the contribution of the free segments. We modified the inertial parameters of the trunk by adding rigid masses, to highlight the role of upper-body

segments in balance-movement coordination. We showed that the trunk first increases the state of mechanical instability, and once the transition is initiated, contributes to regulate this instability. Second, we analysed anticipatory kinematic adjustments during different landing contexts. We showed that anticipatory muscle activations have kinematic consequences before ground contact. These adjustments may serve to provide conditions to achieve a given kinematic configuration at contact, and to cope both with gravity and estimated consequences of ground contact to protect the skeletal system. As a direct consequence of these anticipatory joint flexions, we showed that the foot was accelerated upward before contact to reduce the upward acceleration required at the beginning of contact. Moreover, we recorded two muscle activations before contact, and we suggested that the first one creates favourable conditions to prepare the joint flexions we described.

Combining these two experimental situations, we suggest that anticipatory processes provide different *favourable conditions* to the movement execution, and may represent objectives that the nervous system needs to satisfy when executing a movement. Since motor transitions are ubiquitous in daily-life, these conditions are necessary to movement execution and may be incorporated in future adapted devices and rehabilitation programs for population with mobility impairments.

Keywords: Coordination ; Anticipation ; Transitions ; Neuromuscular ; Movement

Résumé

Les mouvements humains dépendent d'une coordination des systèmes nerveux, musculaire et squelettique. La compréhension de la coordination motrice nécessite la considération des caractéristiques de chaque système. Quand un des systèmes est défectueux, la mobilité humaine est largement dégradée et mène à la dépendance. La compréhension fondamentale de la coordination motrice est nécessaire afin de proposer des dispositifs adaptés aux populations avec des déficits de la mobilité. En particulier, les objectifs que le système nerveux doit satisfaire restent sous-étudiés.

Pour adapter les mouvements aux contraintes internes et externes, les humains peuvent prédire les conséquences de ces contraintes et programmer des activations musculaires anticipées permettant d'apporter des conditions favorables au mouvement. Pour mieux comprendre ces conditions favorables, nous avons développé le cadre des transitions motrices afin de mieux caractériser la manière dont le système nerveux gère le changement de force extérieure. Nous avons ensuite examiné les activations musculaires anticipées en utilisant ce cadre dans deux contextes : l'anticipation pour la coordination de l'équilibre et du mouvement, et l'anticipation d'un contact. Nous avons premièrement caractérisé les conséquences mécaniques des activations musculaires anticipées et montré que les transitions motrices sont une période d'instabilité mécanique désirée et une coordination entre l'équilibre et le mouvement différente d'un état stable (comme la marche ou le maintien d'une posture). Cependant, les conditions apportées par l'utilisation des segments libres restent incomplètes. En examinant l'anticipation du contact, nous avons montré que la littérature présente les activations musculaires anticipées uniquement dans le but de générer de la raideur et accélérer le corps vers le haut durant le contact. Pourtant, des configurations cinématiques du membre inférieur à l'instant du contact réduisent la force de réaction du sol nécessaire, et protège le système squelettique. Cependant, les conditions nécessaires afin d'arriver à ces configurations cinématiques restent inconnues.

Pour étendre nos connaissances quant aux conditions apportées par les processus anticipés, deux situations expérimentales ont été mises en place. Premièrement, nous avons analysés des transitions motrices durant de la marche pour déterminer la contribution des segments libres. Nous avons modifié les paramètres inertiels du tronc en ajoutant des masses, afin

de mettre en évidence le rôle des segments du haut du corps dans la coordination entre l'équilibre et le mouvement. Nous avons montré que le tronc augmente tout d'abord la condition d'instabilité mécanique, et, une fois la transition initiée, régule cette instabilité. Deuxièmement, nous avons montré que les activations musculaires ont une conséquence cinématique avant le contact avec le sol lors de tâches de réception. Ces ajustements peuvent servir à créer les conditions nécessaires pour atteindre une certaine configuration cinématique au contact. Ces ajustements permettent de faire face aux conséquences prédites du contact et protéger le système squelettique. Nous avons également montré que ces ajustements permettent d'accélérer le pied vers le haut avant le contact pour réduire l'accélération nécessaire au début du temps de contact. De plus, nous avons enregistré deux activations musculaires avant le contact, et avons suggéré que la première crée des conditions favorables afin de préparer les flexions précédemment décrites.

En combinant les deux situations expérimentales, nous suggérons que les processus anticipés fournissent des *conditions favorables* au mouvement, et pourraient représenter les objectifs que le système nerveux doit satisfaire. Les transitions motrices étant omniprésentes dans la vie quotidienne, ces conditions sont nécessaires à l'exécution des mouvements et peuvent être incorporées dans les futurs dispositifs d'aide à la mobilité.

Mots clés: Coordination ; Anticipation ; Transitions ; Neuromusculaire ; Mouvement

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Acronyms

ACL Anterior Cruciate Ligament.

APA Anticipatory Postural Adjustments.

BFLH Biceps Femoris Long Head.

CoM Centre of Mass.

CoP Centre of Pressure.

EMG Electromyography.

GRF Ground Reaction Forces.

MTU Muscle Tendon Units.

SM Semi Membranous.

SPM Statistical Parametric Mapping.

ST Temi Tendinosus.

Nomenclature

- $[x, y, z]^T$ (3×1) Transpose of the row vector $[x, y, z]$
- $\delta\Theta_k$ (3×1) Variation of joint angle of the k^{th} degree of freedom
- $\delta\Theta_{k_i}$ (3×1) Variation of joint angle of the k^{th} degree of freedom of the i^{th} joint
- δL_{MTU} (1) Variation of muscle tendon unit length
- ω_0 (1) The angular eigenfrequency of a pendulum
- \vec{H}_M (3×1) Time derivative of internal whole-body angular momentum
- $\vec{\kappa}$ (3×1) Coefficient of cancellation of internal whole-body angular momentum with respect to the whole-body centre of mass
- $\vec{\omega}_i$ (3×1) Angular velocity of the i^{th} segment
- \vec{a}_M (3×1) Linear acceleration of the whole-body centre of mass
- \vec{F}_E (3×1) New external force
- \vec{F}_G (3×1) Ground reaction force
- \vec{H}_0 (3×1) Global whole-body angular momentum with respect to the origin of the global reference frame
- \vec{H}_M (3×1) Internal whole-body angular momentum with respect to the whole-body centre of mass
- \vec{OE} (3×1) Position of the application point of the new external force
- \vec{OM}' (3×1) Position of the whole-body centre of mass in the transverse plane on the ground
- \vec{OM}_i (3×1) Position of the centre of mass of the i^{th} segment

NOMENCLATURE

| | |
|----------------------------|--|
| \overrightarrow{OM} | (3 × 1) Position of the whole-body centre of mass |
| \overrightarrow{OP} | (3 × 1) Position of the centre of pressure |
| $\overrightarrow{v_M}$ | (3 × 1) Linear velocity of the whole-body centre of mass |
| $\overrightarrow{v_{M_i}}$ | (3 × 1) Linear velocity of the centre of mass of the i^{th} segment |
| × | Cross product between two vectors |
| d | (1) Number of degree of freedom for the given joint |
| dt | (1) Variation of time |
| H_M^i | (3 × 1) Contribution of the i^{th} segment to the internal whole-body angular momentum with respect to the whole-body centre of mass |
| h_p | (1) Height of the participant |
| I_b | (3 × 3) Inertia tensor of a barbell with respect to its centre of mass |
| I_i | (3 × 3) Inertia tensor of the i^{th} segment with respect to its centre of mass |
| j | (1) Number of joints crossed by the muscle tendon unit |
| l | (1) Effective pendulum length |
| l_b | (1) Length of the barbell |
| m | (1) Mass of the whole-body |
| m_b | (1) Mass of the barbell |
| m_i | (1) Mass of the i^{th} segment |
| m_p | (1) Mass of the participant |
| n | (1) Number of segments of the multi-body model |
| r_b | (1) Radius of the barbell |
| r_k | (3 × 1) Moment arm of the muscle tendon unit with respect to the k^{th} degree of freedom |
| r_{k_i} | (1) Moment arm of the muscle tendon unit with respect to the i^{th} joint and the k^{th} degree of freedom |
| $xCoM$ | (3 × 1) Extrapolated centre of mass |

NOMENCLATURE

CHAPTER 1

General Introduction

As human technologies take on more of
the characteristics of nature, nature
becomes a more useful teacher

Steven Vogel (Cats' Paws and Catapults:
Mechanical Worlds of Nature and
People)

1.1 Elements of history

The complexity and adaptability of human movement has always intrigued scientists. We can go as far back as Aristotle (384-322 BC), who established that movement required a cause to change the state of the system. Centuries later, Leonardo da Vinci (1452-1519) provided detailed descriptions of the human anatomy and started to investigate how muscles produce force. Giovanni Alfonso Borelli (1608-1679) first applied mechanical laws to study human and animal movement. He computed muscle forces exerted on the skeletal system, and understood the roles of lever arms in the skeletal system, dedicated to motion rather than pure force production. Few decades later, Isaac Newton (1642-1727) described the three laws of motion and the universal law of gravity, that considerably defined the study of human movement.

At the beginning of the twentieth century, Nikolaï Bernstein (1896-1966) introduced fundamental concepts of human movement such as motor coordination and redundancy. First, he defined the degrees of freedom, as the number of independent variables required to define the configuration of a given joint. He showed that the human skeletal system has more degrees of freedom than necessary to perform any given movement, that he referred to as the degrees of freedom problem for the nervous system. Given that there is also more muscles than necessary to act on each degree of freedom, that he referred to as motor redundancy, there is an infinite number of muscle activation sets to execute any given movement. Thus, to execute any movement, the nervous system must choose one solution, in terms of trajectory, and then choose one set of muscle activations. These two motor control problems are the bases of motor coordination, which he defined as the processes leading to **choose one solution of muscles acting together, among the infinite possibilities to execute a movement** (Bernstein, 1967). To understand motor coordination, one must be able to determine which variables the nervous system considers to perform a movement.

1.2 Motivations

Movements enable humans to interact and navigate in the world. The ability to move is the results of a complex coordination between different systems -the nervous, muscular, skeletal, respiratory and circulatory- working together (Dickinson et al., 2000). One fundamental ability of humans is mobility, defined as the **ability to move, with or without assistance devices** (Reijnierse et al., 2023). The ability to move is vital: daily energy expenditure (Manini et al., 2006) and the ability to walk (Studenski et al., 2011) are correlated with life expectancy. We often take our mobility for granted until something impedes its execution: when at least one of the systems enabling mobility dysfunctions, mobility is impaired, leading to loss of autonomy and, ultimately, dependence.

First, the decrease in muscles capabilities, for example through ageing, limits mobility (Montero-Odasso et al., 2022). Second, dysfunction of the nervous system, such as spinal cord injury, limits the use of some limbs, also restricting mobility (Nene et al., 1996). Third, alteration of the skeletal system such as osteoarthritis reduces walking abilities

(Winter et al., 2010). Apart from physical consequences of decrease in mobility, there are cognitive consequences directly related to a decrease in the quality of life in elderly (Schoene et al., 2019; Selikson et al., 1988), and lead to large costs to society (Schultz, 1992). To improve mobility, rehabilitation programs (Means et al., 2005), and partial assistance exoskeleton have been proposed (Dellon & Matsuoka, 2007; Grimmer et al., 2019; Wu, 2021). However, lack of confidence and fear of falling with these devices lead to a decrease in mobility and social activities (Miller et al., 2001; Hamza et al., 2020). Yet, the understanding of coordination of movement is necessary to provide assistance and adequate mobility restoration to population with mobility impairments (van der Woude et al., 2021). Therefore, the control strategies implemented must resemble the control of human movement (Baud et al., 2021).

1.3 Approach

We start from the premise that understanding fundamentals of movement generation and control is necessary to simulate and produce adequate movements. Before one can say to have understood complex systems containing information processing steps, such as human movement, Marr (1982) proposed that we must precisely understand three sequential distinct levels of analysis: the computational, the representation and algorithm, and the hardware implementation (table 1.1).

Table 1.1: The three levels of understanding according to Marr (1982). The first row is a copy of page 25 from his book. The two other rows are applications of his theory to human movement.

| | Computational theory | Representation and algorithm | Hardware implementation |
|--|--|---|--|
| Details of the three levels by Marr (1982) | What is the goal of the computation, why is it appropriate and what is the logic of the strategy by which it can be carried out? | How can this computational theory can be implemented? In particular, what is the representation for the input and output, and what is the algorithm for the transformation? | How can the representation and algorithm be realised physically? |
| Application for human movement | What are the goals of the movement? Purpose and constraints of the movement | How is the movement planned and programmed? Motor commands and control strategies | How the different systems enable to realise the movement? Neuromuscular processes |

At the computational theory level, one must understand both the computation goal, and its appropriateness and adequacy to the context in which the system operates. Applied to human movement, this level involves defining the problem the nervous system is trying to solve, *i.e.* the objectives that must be reached to execute a given movement. At the

1.3. APPROACH

representation and algorithm level, one must understand how the output from computational theory can be implemented, *i.e.* understand the relationship between the inputs and the outputs of the system. Applied to human movement, this level involves the relationship between the objectives defined at the first level and the motor commands required to execute it. Namely, this level requires to choose a solution of the degrees of freedom and abundance problems exposed by [Bernstein \(1967\)](#). Finally, at the hardware implementation level, one must understand how the system realises the output from the representation and algorithm level. Applied to human movement, this level involves the understanding of all processes implicated in the movement execution, such as neural inputs, muscle force production inside muscle fibres, or force transmission to the skeletal system.

For any complex system, [Marr \(1982\)](#) stated the importance of carefully understanding the computational level first, to better inform the representation and implementation levels. Indeed, outputs of the computational level drives the other two levels. Without a clear understanding of the computational theory level, it is difficult to fully grasp why an algorithm is chosen, and objectively determine their objectives and constraints, or how they are implemented physically. To understand human movement and propose adequate assistive devices and rehabilitation programs to people with mobility impairments, a full understanding of the objectives the nervous system tries to satisfy is required.

However, the computational level remains understudied in the context of human movements. For example, in studies with upper-limb movements, authors stated that the movement goal (and thus the role of the computation performed by the nervous system) is to "move the upper-limb towards the target" ([Kawato, 1988](#); [Uno et al., 1989](#)). Based on this assumption, authors tested different models of hand trajectory (detailed in chapter 2), and reproduced the trajectories of experimental data. However, using this approach of making general hypotheses about the objectives of the task, these authors probably simplified the computational theory level and missed some of the objectives the nervous system must satisfy when executing a whole-body movement, such as balance maintenance.

Another solution to determine the computation objectives would be to observe specific movement adaptations during experimental situations with distinct change of state, and infer on what could be the purposes of movement. For example, [Belenkii et al. \(1967\)](#) recorded activations of trunk and lower-limb muscles preceding the activation of the deltoid during arm raising. This result suggests that, during the simple task of arm raising, the objective of the movement is not only the upper-limb trajectory but also to ensure balance maintenance. This situation illustrates that there are other goals when executing a movement that may even precede the beginning of the movement. Indeed, because the human body is a multi-body system, mechanical interactions are created upon the movement of one body segment, disturbing the positions of adjacent segments and eventually whole-body balance. Thus, because these perturbations can be predicted, the system required *favourable conditions* provided for proper movement execution. Another example of these *favourable conditions* is the surprising and sagging feelings following an unexpected step-down while walking. After foot contact, the whole-body centre of mass is driven for-

ward and/or downward by a change of velocity. In that context, the main concern shortly becomes to regain balance over all other things. The unexpected hole on the road, or staircase step of a different height, fooled the predictive capacity of the nervous system, leading to inadequate segment configuration and muscle activations when touching the ground. Ultimately, this leads to inadequate linear and angular momenta that need to be quickly reduced. This second situation illustrates the necessity of the *favourable conditions* provided by anticipatory muscle activations during transitioning and unsteady situations. Investigating the *favourable conditions* provided by anticipatory muscle activations may enable to identify what are the other goals considered by the computational theory level when programming a movement. Moreover, motor transitions (as we will define them) are ubiquitous in day-to-day movements. Yet, the way the nervous system controls motor transitions remains poorly understood (Biewener & Daley, 2007; Jindrich & Qiao, 2009), but are necessary to provide solutions improving mobility (Ijspeert, 2014). Finally, motor transitions are also when the most common falling situations occur in elderly (Robinovitch et al., 2013) making these *favourable conditions* also critical for better fall prevention.

1.4 General outline of the thesis

The general approach of this thesis is to use the context of voluntary motor transitions to investigate anticipatory muscle activations and infer on the *favourable conditions* they provide for movement execution. In chapter 2, we start by explaining how anticipatory muscle activations generate *favourable conditions*. We will show that anticipatory processes have been investigated in two principal, yet different, contexts: anticipation for balance-movement coordination and anticipation of contact. In this thesis, we considered both contexts, with the objective to extract similarities that could lead to a wider understanding of anticipatory processes dedicated to movement execution. After reviewing each context independently, we point out the gaps in the literature and define the specific objectives of the thesis aiming to fill those gaps. In chapter 3, we detail the two experimental protocols used in this thesis, one for each context. In chapter 4, we present results relative to the study of balance-movement coordination. In chapters 5 to 7, we present three complementary studies relative to anticipation of contact. Finally, in chapter 8, we discuss the combination of the different results, and highlight perspectives to the importance of anticipatory processes for proper movement execution and ensuring mobility to everyone.

According to requirements of the doctoral school, each chapter will end with a three-pages minimum French summary.

1.5 French summary

1.5.1 Éléments historiques

La complexité et l’adaptabilité du mouvement humain a toujours intrigué les scientifiques. Depuis Aristote (384-322 avant JC), établissant qu’un mouvement nécessite un changement d’état du système étudié. Plusieurs siècles plus tard, Léonard de Vinci (1452-1519) a fourni des descriptions détaillées de l’anatomie humaine et a commencé à rechercher comment les muscles produisent de la force. Giovanni Alfonso Borelli (1608-1679) a été le premier à appliquer les lois mécaniques à l’étude du mouvement humain et animal. Il a calculé les forces musculaires exercées sur le système squelettique, et a compris et détaillé le rôle de levier du système squelettique, qui permet d’avantage le mouvement que la production de force pure. Quelques décennies plus tard, Isaac Newton (1642-1727) a décrit les trois lois du mouvement et la loi universelle de la gravité, qui ont considérablement défini l’étude du mouvement humain.

Au début du vingtième siècle, Nikola Bernstein (1896-1966) a introduit les concepts fondamentaux à l’étude du mouvement humain, tels que la coordination et la redondance motrice. Premièrement, il a défini les degrés de liberté, comme étant le nombre de variables indépendantes nécessaires pour caractériser la configuration d’une articulation. Il a montré que le système squelettique du corps humain possède plus de degrés de liberté que nécessaire pour effectuer n’importe quel mouvement, qu’il nommera le problème des degrés de liberté pour le système nerveux. Etant donné qu’il y a également plus de muscles que nécessaire pour agir sur chaque degré de liberté, défini comme étant la redondance motrice, il y a une infinité de combinaisons d’activations musculaires pour effectuer un mouvement donné. Pour effectuer un mouvement, le système nerveux doit donc choisir une solution en termes de trajectoire, puis choisir une combinaison d’activations musculaires. Ces deux problèmes fondamentaux du contrôle moteur sont la base de la coordination, qu’il définit comme étant les processus menant aux choix d’une solution d’un ensemble de muscles agissant ensemble, parmi une infinité de possibilités, pour exécuter un mouvement (Bernstein, 1967). Pour comprendre la coordination, nous devons être capables de déterminer quelles variables le système nerveux considère afin d’effectuer un mouvement.

1.5.2 Motivations

Les mouvements permettent aux humains d’interagir et de naviguer dans le monde. Cette mobilité est le résultat d’une coordination complexe entre différents systèmes -nerveux, musculaires, squelettique, respiratoire et circulatoire, agissant ensemble (Dickinson et al., 2000). La mobilité, capacité fondamentale pour les humains, est définie comme la capacité de se mouvoir, avec ou sans assistance (Reijnierse et al., 2023). La mobilité est vitale : la dépense énergétique quotidienne (Manini et al., 2006) et la capacité de marcher (Studenski et al., 2011) sont corrélées à l’espérance de vie. Nous prenons généralement pour acquis notre mobilité jusqu’à ce qu’un élément imprévu n’empêche son exécution : quand au moins un des systèmes qui permet la mobilité dysfonctionne, menant à la perte d’autonomie et au final, à la dépendance.

Premièrement, la baisse des capacités musculaires, par exemple suite au vieillissement, limite notre mobilité (Montero-Odasso et al., 2022). Deuxièmement, la dysfonction du système nerveux, comme la lésion de la moelle épinière, empêche l'utilisation de certains membres, restreignant également la mobilité (Nene et al., 1996). Troisièmement, l'altération du système squelettique tel que l'arthrose réduit les capacités de marche (Winter et al., 2010). En plus des conséquences physiques de la diminution de la mobilité, des conséquences psychologiques sont présentes, directement liées à la diminution de la qualité de vie chez les personnes âgées (Schoene et al., 2019; Selikson et al., 1988), et entraînent des coûts importants pour la société (Schultz, 1992). Pour améliorer la mobilité, des programmes de rééducation (Means et al., 2005) et de l'assistance partielle comme avec l'utilisation d'exosquelettes ont été proposés (Dellon & Matsuoka, 2007; Grimmer et al., 2019; Wu, 2021). Cependant, un manque de confiance et une peur de chute avec ces produits mènent à une diminution de la mobilité et des interactions sociales (Miller et al., 2001; Hamza et al., 2020). La compréhension de la coordination du mouvement est donc nécessaire afin de proposer une assistance adéquate et de permettre la mobilité aux populations concernées (van der Woude et al., 2021), avec des stratégies de contrôle du mouvement qui ressemblent au contrôle du mouvement humain (Baud et al., 2021).

1.5.3 Approche

Nous commençons par le principe qu'une compréhension fondamentale de la génération et du contrôle du mouvement est nécessaire pour simuler et produire des mouvements. Avant de pouvoir affirmer que nous comprenons un système qui traite de l'information comme le mouvement humain, Marr (1982) a proposé que nous devons récemment comprendre trois niveaux d'analyse distincts et successifs : le niveau calculatoire, le niveau de représentation et d'algorithme, et le niveau d'implémentation (table 1.1).

Au niveau calculatoire, nous devons comprendre le but du calcul qui va être réalisé, et son adéquation avec le contexte dans lequel le système opère. Appliqué au mouvement humain, ce niveau implique de définir le problème que le système nerveux essaie de résoudre, c'est-à-dire les objectifs qui doivent être réalisés lors de l'exécution du mouvement. Au niveau de représentation et d'algorithme, nous devons comprendre comment les objectifs définis au niveau calculatoire peuvent être implémentés, c'est-à-dire comprendre la relation qui existe entre les variables d'entrée et de sortie du système. Appliqué au mouvement humain, ce niveau implique la relation entre les objectifs définis au premier niveau et les commandes motrices nécessaires pour atteindre ces objectifs. Concrètement, à ce niveau, le système nerveux doit faire un choix pour répondre aux problèmes des degrés de liberté et de la redondance motrice exposée par Bernstein (1967). Enfin, au niveau de l'implémentation, nous devons comprendre comment les variables de sortie du niveau précédent sont appliquées. Appliqué au mouvement humain, ce niveau implique de comprendre tous les processus impliqués dans l'exécution du mouvement, de la commande nerveuse à la production de force au sein des fibres musculaires, à la transmission des forces au système squelettique.

1.5. FRENCH SUMMARY

Pour n'importe quel système complexe, Marr (1982) met en avant l'importance de la compréhension du niveau calculatoire, afin de mieux informer les niveaux suivants. Sans une compression claire du niveau calculatoire, il apparaît difficile de vraiment comprendre pourquoi un algorithme particulier est choisi, et de déterminer objectivement ses objectifs et contraintes, ou comment l'implémenter. Pour comprendre le mouvement humain et proposer une assistance adéquate aux personnes dans le besoin, la compréhension complète des objectifs que le système nerveux tente de satisfaire est alors nécessaire.

Cependant, le niveau calculatoire reste assez peu étudié dans le contexte du mouvement humain. Par exemple, lors d'études sur des mouvements du membre supérieur, les auteurs indiquent généralement que l'objectif du mouvement (et donc le but du calcul réalisé par le système nerveux) est de « déplacer le membre supérieur en direction de la cible (Kawato, 1988; Uno et al., 1989). En se basant sur cette hypothèse, les auteurs ont pu tester différents modèles de trajectoire de la main (détaillé dans le chapitre 2), et ont reproduit les trajectoires provenant de données expérimentales. Cependant, en faisant des hypothèses aussi générales sur l'objectif de la tâche, les auteurs ont probablement simplifié le niveau calculatoire et oublié des objectifs que le système nerveux doit également satisfaire durant l'exécution d'un mouvement du corps complet, comme la gestion de l'équilibre.

Une autre solution pour déterminer les objectifs du niveau calculatoire est d'observer des adaptations du mouvement lors de situations expérimentales avec des changements nets d'état du corps complet, et inférer sur ce que pourraient être les objectifs du mouvement. Par exemple, Belenkii et al. (1967) ont enregistré des activations des muscles du tronc et du membre inférieur avant l'activation du deltoïde durant une tâche de lever de bras. Ce résultat suggère que, lors d'une simple tâche impliquant le membre supérieur, les objectifs du mouvement ne sont pas uniquement caractérisés en termes de trajectoire du membre supérieur, mais impliquent également de maintenir l'équilibre du corps complet. Cette situation illustre que plusieurs objectifs sont présents lors de la réalisation du mouvement, et précèderaient même le début du mouvement. En effet, étant donné que le corps humain est un système multi-corps, des interactions mécaniques sont générées suite au mouvement d'un segment, perturbant la position des segments adjacents et éventuellement l'équilibre du corps complet. Puisque ces perturbations peuvent être prédites, le système nécessite des *conditions favorables* pour l'exécution du mouvement. Un autre exemple de ces *conditions favorables* est les sentiment de surprise et d'affaissement lors d'un changement de hauteur imprévu en marchant. Après le contact du pied au sol, notre centre de masse est entraîné vers l'avant et/ou vers le bas par un changement de vitesse. Dans ce contexte, la principale préoccupation est rapidement de retrouver l'équilibre. Le trou non prévu sur la route, ou la marche d'une hauteur différente (la 7ème pour monter au troisième étage de l'aile Ouest de Pprime) a trompé la capacité prédictive du système nerveux, menant à une configuration posturale et des activations musculaires non adaptées à la situation au moment de toucher le sol. Au final, cela mène à une quantité de mouvements linéaires et angulaires du corps complet non adaptés à la tâche, qui doivent rapidement être diminués. Cette situation illustre la nécessité des *conditions favorables* apportées par des activations

musculaires anticipées durant des transitions entre deux états distincts. Rechercher ces *conditions favorables* apportées par les activations musculaires anticipées pourrait permettre d'identifier quels sont les objectifs considérés dans le système calculatoire lors de la programmation du mouvement. De plus, les transitions motrices (comme nous allons les définir) sont des situations omniprésentes durant les mouvements de la vie quotidienne. Pourtant, la manière dont le système nerveux gère ces transitions reste assez peu compris (Biewener & Daley, 2007; Jindrich & Qiao, 2009), mais nécessaire pour proposer une assistance aux personnes à mobilité réduite (Ijspeert, 2014). De plus, les transitions motrices sont les situations où les chutes des personnes âgées sont les plus présentes (Robinovitch et al., 2013), rendant les *conditions favorables* cruciales pour une meilleure prévention des chutes.

1.5.4 Plan général de la thèse

L'approche générale de cette thèse est d'utiliser le contexte des transitions motrices volontaires afin d'investiguer les activations musculaires anticipées et d'inférer sur les *conditions favorables* qu'elles apportent lors de l'exécution du mouvement. Dans le chapitre 2, nous commençons par expliquer comment ces activations musculaires anticipées apportent des *conditions favorables*. Nous montrons que les processus anticipés ont été étudiés dans deux différents contextes : l'anticipation pour la coordination entre l'équilibre et le mouvement, et l'anticipation d'un contact. Dans cette thèse, nous allons considérer les deux contextes, avec l'objectif de faire ressortir des similarités qui pourraient mener à une compréhension plus large des processus anticipés. Après une revue indépendante de chacun des contextes, nous mettons en avant les manques de la littérature et définissons les objectifs spécifiques de la thèse. Dans le chapitre 3, nous détaillons les deux protocoles expérimentaux utilisés dans cette thèse, un pour chaque contexte d'anticipation. Dans le chapitre 4, nous présentons les résultats relatifs à l'étude de la coordination entre l'équilibre et le mouvement. Dans les chapitres 5,6 et 3, nous présentons trois études complémentaires sur l'anticipation du contact. Enfin, dans le chapitre 8, nous discutons la combinaison des différents résultats, et mettons en avant des perspectives sur l'importance de la considération de ces processus anticipés pour assurer la mobilité de chacun.

En accord avec les exigences de l'école doctorale, chaque chapitre se terminera avec un résumé en Français d'au moins trois pages.

1.5. FRENCH SUMMARY

CHAPTER 2

Literature Review

The progress of science has been largely
matter of discovering what questions
should be asked

Steven Weinberg (To explain the whold,
the discovery of modern science)

Part of this chapter (section 2.3) has been presented at the 47th Congress of Société de Biomécanique in Monastir (Bechet et al., 2022).

Another part of this chapter (section 2.2.1.3) is currently under review in the *Gait & Posture* journal.

2.1 Human movement coordination, motor control and anticipation

Movement enables humans to navigate and interact with the environment. Movements result from a complex coordination of the nervous, muscular and skeletal systems. More than 600 muscles are activated or inhibited, rotating, gliding and/or stabilising more than 200 degrees of freedom to displace segments and the whole-body in space, all of while while staying balanced (figure 2.1). The main challenge in motor control is to understand the principles used by the nervous system to execute, regulate, and adapt movements to the environment. Overall, coordination has been defined as mastering the degree of freedom problem, namely, choosing one solution of muscles acting together, among the infinite possibilities to execute a movement (Bernstein, 1967). To be robust, motor control theories must consider the characteristics and interactions between the different components of the neuro-musculo-skeletal system. Just to mention a few, the multi-body and redundant musculo-skeletal system enables humans to perform a large variety of movements, but questions the criteria used by the nervous system to choose one solution among others to execute the movement. Additionally, the movement of one segment creates mechanical interactions to adjacent segments that will influence the movement execution (Hollerbach & Flash, 1982). These mechanical interactions disturb the whole-body balance, which is already limited due to a limited surface and an elevated whole-body Centre of Mass (CoM) that requires constant muscle force production (Morasso & Sanguineti, 2002; Loram & Lakie, 2002). In the sensori-motor system, noises and delays prevent to accurately and timely determine the movements performed (figure 2.1). Thus, quick movements cannot be corrected in due time (Franklin & Wolpert, 2011). Furthermore, the electromechanical delay, the delay between muscle activation and muscle force production (Cavanagh & Komi, 1979) adds an additional delay between the intention and the force production. These mechanical interactions, the noise and the different delays present in the neuro-musculoskeletal system need to be considered by the nervous system when executing movement. If they are not properly taken into account, it can lead to imbalance, incorrect coordination of body segments, or movements that are not precise enough. Thus, the nervous system must find solutions to deal with these constraints.

2.1.1 Internal Models

To deal with these constraints, the internal model theory proposed that the nervous system would use different internal models to plan, execute and control movements (Kawato, 1999). Internal models are neural mechanisms that simulate and predict the dynamics of the whole-body and its environment (Kawato, 1999). First, inverse model used models of the limbs involved in movements to plan the trajectory of the desired movement, and then generate the motor commands (even if no evidence clearly suggests that this happens sequentially) (Kawato, 1988; Atkeson, 1989; Shadmehr & Mussa-Ivaldi, 1994). To plan the trajectory of the desired movement, the majority of inverse models were developed under the framework of optimisation: a scalar value would be used to quantify the different solu-

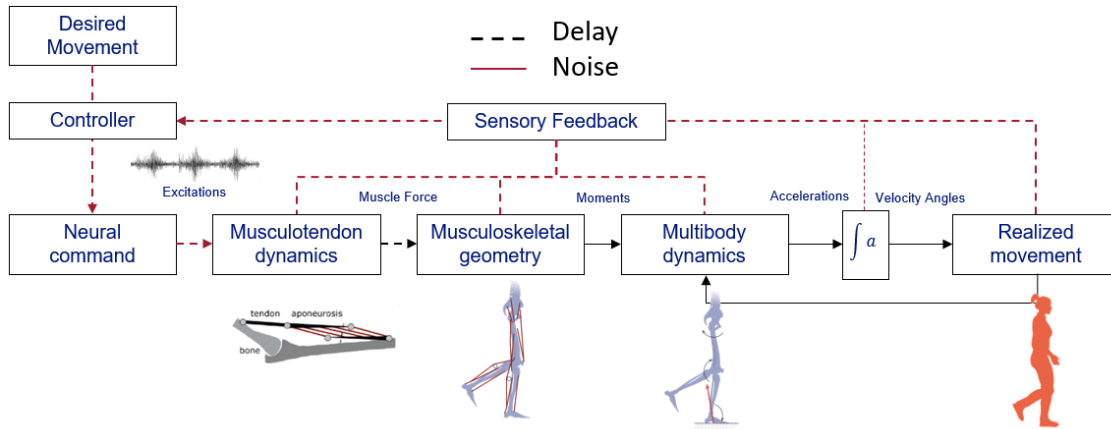


Figure 2.1: Schematic diagram of movement control. From a desired movement to perform, the controller (the nervous system) programs neural motor commands to contract or relax muscles, putting the skeletal system in motion. Moving segments create mechanical interactions to adjacent segments. Finally, all segment displacements enable to realise the desired movement. Sensory feedbacks are present at each step, and can be used by the nervous system to adapt motor commands and realise the movement. Dashed lines and red lines represent delays and noise in the sensori-motor system, respectively (Franklin & Wolpert, 2011). Diagram adapted and completed from Seth et al. (2018).

tions to achieve a given task (Abend et al., 1982) and chose the *best solution* depending on (a) given parameter(s). Different cost functions were tested during upper-limb movements for movement trajectory: minimisation of jerk (Flash & Hogan, 1985), minimisation of torque change (Uno et al., 1989; Kawato, 1988), minimisation of intervention (Todorov & Jordan, 2002), or energy minimisation (Alexander, 1997) reviewed in Todorov (2004). In the case of energy minimisation, it should be noted that the motor generations step is simplified, with equal activation of every muscles included in the model (Alexander, 1997). Next, when the movement trajectory is determined, motor generations, *i.e.* the degree of activation of each muscle, is mainly performed through minimisation of energy (Anderson & Pandy, 2001), or muscle force (Pandy et al., 1995). Finally, to enable online adjustments of the performed movement, optimal feedback control has been suggested, where feedback gains are adjusted during the execution of a movement to optimise the cost function, adapt the movement to the environment (Todorov, 2004) and provide the flexibility of motor behaviour observed by Bernstein (1967).

Optimal feedback control requires a good estimation of the current state, that is not possible due to delays and noise present in the sensori-motor system (Faisal et al., 2008): noise prevents from accurate state estimation, and due to delays, the estimation made is not appropriately timed. To overcome these constraints, it has been suggested that humans and animals can predict the consequences of their own actions. von Holst & Mittelstaedt (1971) proposed the principle of *reafference*, *i.e.* the sensory afference that should be caused by a self-initiated movement. The principle of reafference was first used to explain the vestibulo-ocular reflex, enabling to stabilise gaze during voluntary-initiated head rotations. Since the motion of the head is programmed, its consequences can be expected and eye movements

2.1. HUMAN MOVEMENT COORDINATION, MOTOR CONTROL AND ANTICIPATION

can be adjusted to stabilise gaze. von Holst & Mittelstaedt (1971) proposed that an efference copy (*i.e.* a copy of motor commands) is used to predict the sensory consequences of the movements, and used to differentiate the sensory information due to the voluntary movements, and the sensory information coming from the external environment. They further suggested that this distinction enables the nervous system to not stabilise against a voluntarily-initiated movement, which would be counter-productive.

Few decades later, these findings were generalised under the term *forward* model (Wolpert et al., 1998). Forward models are predictors of sensory consequences of a given motor commands, and enable to overcome delays in the sensori-motor system (Miall et al., 1993), serving both state estimation and prediction, based on initial or previous state of the limb involved (*i.e.* joint positions, velocities and accelerations) and the efferent copy (Wolpert et al., 1995). Because inverse and forward models may be coupled for motor control, it enables to adapt motor commands depending on the predictions made by forward models (Wolpert et al., 1998). As it was described for the vestibulo-ocular reflex, the prediction of a future state enables to provide adequate adjustments for the task, eye movements in this case. Further evidence of forward models existence came from analyses of coordination during simple motor tasks with the upper-limb. For instance, when participants held an object between their index and their thumb, and were instructed to elevate the object (through an elbow flexion), authors found that the grip force is precisely controlled so that it is greater than the minimal force required to prevent slip by a small safety margin, confirming the existence of internal models in the nervous system to adapt the grip force (figure 2.2a) (Johansson & Westling, 1984). Moreover, the change in load and grip forces were correlated, as well as the timing of both maximal forces (Flanagan & Wing, 1993), suggesting that the nervous system uses forward model to predict the consequence of the forthcoming movement on the interaction between the fingers and the object. Overall, the relationship between both internal models (inverse and forward) enables to coordinate a voluntarily-initiated movement and the required adjustments to counteract perturbations arising from this movement, enabling proper timing between different actuators of a same movement (figure 2.2b) (Kawato, 1999). This ability to perform smooth movements, thanks to the temporal and spatial adaption of movements to the objectives and constraints of the task led to the assumption that *anticipation* is crucial for performance in human movements (Schmidt, 1968).

2.1.2 Motor anticipation

A general definition of an anticipatory system is "*a system containing a predictive model of itself and/or of its environment, which allows it to change state at an instant in accord with the model's predictions pertaining to a later instant*" (Rosen, 2012). Anticipatory systems are present and necessary in every fields, from sociology to philosophy, through engineering and biology (Poli, 2010).

In the previous section, we showed that humans have the predictive capability of an anticipatory system. However, prediction does not necessarily lead to anticipation. Here, we

2.1. HUMAN MOVEMENT COORDINATION, MOTOR CONTROL AND ANTICIPATION

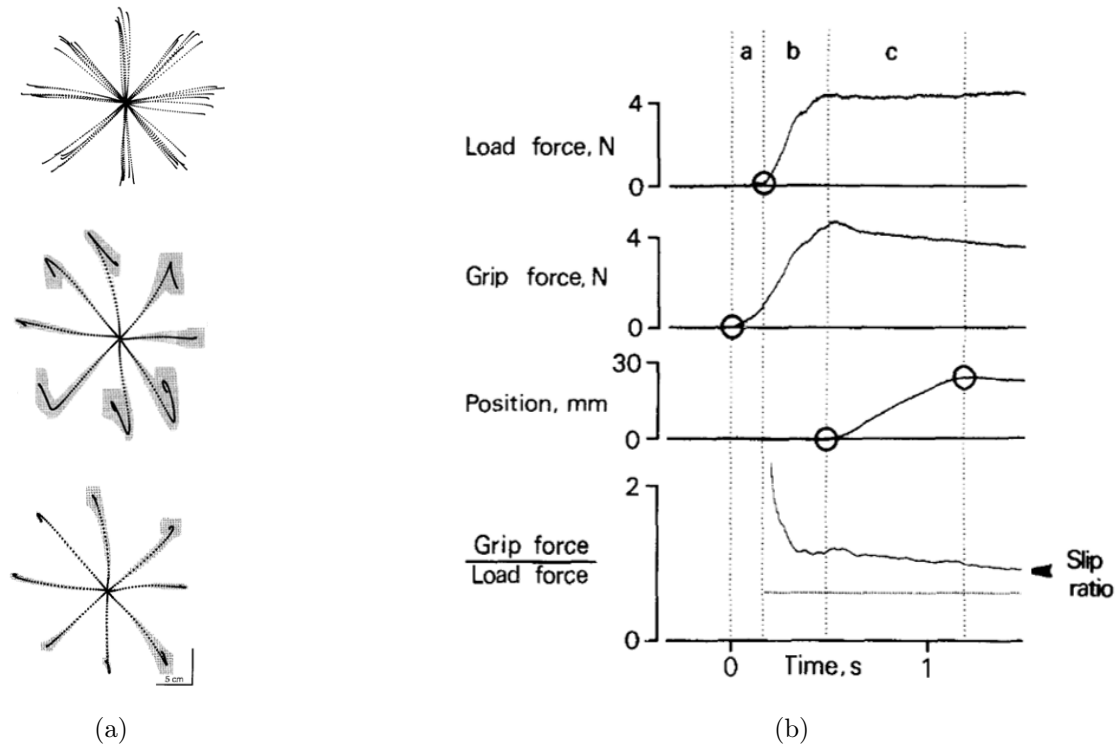


Figure 2.3: (a) From top to bottom, hand trajectories during reaching movements in a null force field; average and standard deviation of hand trajectories during the first reaching movement in the presence of an unknown force field; average and standard deviation of the hand position during the 250th trial in the presence of a known force field. Dots represent measurements each 10ms, adapted from [Shadmehr & Mussa-Ivaldi \(1994\)](#)

(b) Load and grip forces during a vertical movement of the upper-limb while holding an object. The grip force increases in anticipation of the load force. The ratio between the grip and the load forces is larger than the ratio that would lead the object to slip between fingers, indicated by the horizontal line on the bottom panel; adapted from [Johansson & Westling \(1984\)](#)

2.1.3 Two contexts of anticipation

In the scientific literature, motor anticipation have been studied through muscle activation patterns in two main, yet different, contexts: through *Anticipatory Postural Adjustments (APA)* occurring before a voluntarily-initiated movement, and through muscle *pre-activations* measured before an external perturbation that can be timely predicted. First, *APA* refer to changes of posture preceding the initiation of a movement (reviewed in [Massion \(1992\)](#) and [Bouisset & Do \(2008\)](#)). As first introduced and suggested in [Belenkii et al. \(1967\)](#), changes of posture induced by *APA* would ensure maintenance of balance despite the balance perturbation due to movement execution. For example, an arm raising perturbs balance, and requires *APA* before initiation of the arm movement to maintain balance ([Belenkii et al., 1967](#)). Then, muscle pre-activations before a predicted event have largely been described through an increase in joint stiffness, generally in motor tasks with large momentum. For instance, the increase in joint stiffness is suggested to help the whole-body prepare for the forthcoming impact during landing tasks, as reviewed in [Santello \(2005\)](#). When the landing is immediately followed by a jump, *i.e.* during a drop-jump,

the role of measured muscle pre-activations was suggested to enable the muscle to act as a spring, as reviewed in [Fukutani et al. \(2021\)](#). Thus, different muscle functions seem to be used in anticipation of a predictable perturbation to provide these *favourable conditions* for movement execution. In the following sections, we will review separately these two body of literature to identify gaps in the interpretation of the favourable conditions provided by anticipatory muscle activations. In the [Anticipation for balance-movement coordination](#) section, we generalise the effect of anticipatory muscle activations on balance during different types of movement. In the [Anticipation of contact](#) section, we review how both anticipatory muscle activations and postural configuration enable to cope with a predictable contact with an external support. In these sections and in the rest of the manuscript, we will use the term **anticipatory muscle activations** instead of *APA* and *pre-activations*, to remain consistent with our definition of motor anticipation, and because they both rely on a prediction made by the nervous system and begin before the movement or the contact. In each section, we will define how anticipatory phases can be determined in the given motor situation.

2.2 Anticipation for balance-movement coordination

The ability to maintain balance is often taken for granted. It is only when a condition impedes its control that the vital role it plays in our mobility and quality of life is appreciated. Failing to maintain balance during movements leads to falls, a loss of confidence and, ultimately, loss of mobility, and decrease in quality of life.

It has long been suggested that movement execution disturbs balance maintenance, and that appropriate muscle activations are required to compensate for these disturbing forces ([Bernstein, 1967](#); [Akert, 1981](#)). According to this view, balance maintenance and voluntarily-initiated movements are considered as separate processes that need to be coordinated to enable efficient motor actions ([Massion, 1992](#); [Bouisset & Do, 2008](#)). Yet, understanding the underlying processes of balance-movement coordination remains challenging.

In this context, our overview of the current understanding of balance-movement coordination focuses on the mechanical consequences of muscle activations during the critical, anticipatory phase of voluntarily-initiated motor transitions. Voluntarily-initiated movements reflect how the nervous system predicts and integrates the mechanical consequences of a movement to ensure balance, because we assume these consequences can be predicted through internal models. Instead, when the mechanical consequences cannot be accurately predicted, for example, if a person unexpectedly trips while walking at a steady velocity, the predictive capacity of the nervous system is fooled. This can lead to both inadequate muscle activations and segment configuration and, ultimately, result in a fall. This situation illustrates the critical role of anticipation during motor transitions to ensure balance while moving.

This review section is organised into three sections. In the first section, we introduce three key concepts of balance-movement coordination: balance, through the three main balance

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mechanisms; motor transitions, through a new mechanical framework; and anticipation, through the early muscle activations related to the motor transitions performed. In the second section, we review the biomechanical contributions of the anticipatory muscle activations identified in the literature during motor transitions, through the prism of the three balance mechanisms. In the third section, we discuss the role of these anticipatory muscle activations in balance-movement coordination, we highlight gaps in the literature, and suggest new perspectives for bridging them.

2.2.1 Main concepts relative to balance-movement coordination

2.2.1.1 Maintenance of balance and the three mechanisms

Balance has originally been related to the regulation of posture, i.e., the ability to maintain the whole-body in a desired segmental configuration (Horak & Macpherson, 1996). From this perspective, balance is described by considering the position of the whole-body CoM relative to the base of support (i.e., the area surrounding all contact points with the environment) (Winter, 1995). However, maintaining balance is rarely limited to the maintenance of one posture. Mechanically, it is insufficient to only consider the position of the whole-body CoM when it is spatially displaced, especially with a modification of the base of support. It is also necessary to consider the linear momentum of the whole-body CoM, because its velocity enables the determination of future whole-body CoM positions (Pai & Patton, 1997), which characterise the maintenance of balance (Bruijn & van Dieën, 2018; Hof et al., 2005). To generalise to all situations, we define balance mechanisms as muscle activations that create forces that aim to accelerate or decelerate the whole-body CoM, with kinematic consequences that correspond to the objective(s) of the task and, ultimately, prevent the whole-body from falling (Winter, 1995).

Human balance is usually modelled using an inverted pendulum, where the whole-body CoM oscillates around a single point: the Centre of Pressure (CoP), representing the point of application of Ground Reaction Forces (GRF) (Winter, 1995). By computing the sum of external moments of a linearised inverted pendulum around the projection of the whole-body CoM in the transverse plane on the ground (M') (2.1); Hof (2007) proposed three complementary balance mechanisms involved in motor tasks, which all can contribute to modifying whole-body CoM acceleration: (1) ‘moving the CoP’, (2) ‘counter-rotating’ segment(s), and (3) ‘applying new external forces(s)’ (figure 2.4). The whole-body CoM acceleration can then be computed along the antero-posterior and medio-lateral axes (equation (2.2)). See Nomenclature page [xix](#) for definition of all variables. Because $m.l$ is constant for a linearised inverted pendulum, only the numerators are used to describe the three balance mechanisms.

$$(\overrightarrow{OP} - \overrightarrow{OM}') \times \overrightarrow{F}_G - \dot{\overrightarrow{H}}_M + (\overrightarrow{OE} - \overrightarrow{OM}') \times \overrightarrow{F}_E = [0, l, 0]^T \times m \cdot \overrightarrow{a}_M \quad (2.1)$$

$$\begin{bmatrix} a_{M_x} \\ a_{M_y} \\ a_{M_z} \end{bmatrix} = \begin{bmatrix} -\frac{(OP_x - OM'_x)F_{G_y} - \dot{H}_{M_z} + (OE_x - OM'_x)F_{E_y} - (OE_y - OM'_y)F_{E_x}}{m \cdot l} \\ 0 \\ -\frac{(OP_z - OM'_z)F_{G_y} - \dot{H}_{M_x} + (OE_y - OM'_y)F_{E_z} - (OE_z - OM'_z)F_{E_y}}{m \cdot l} \end{bmatrix} \quad (2.2)$$

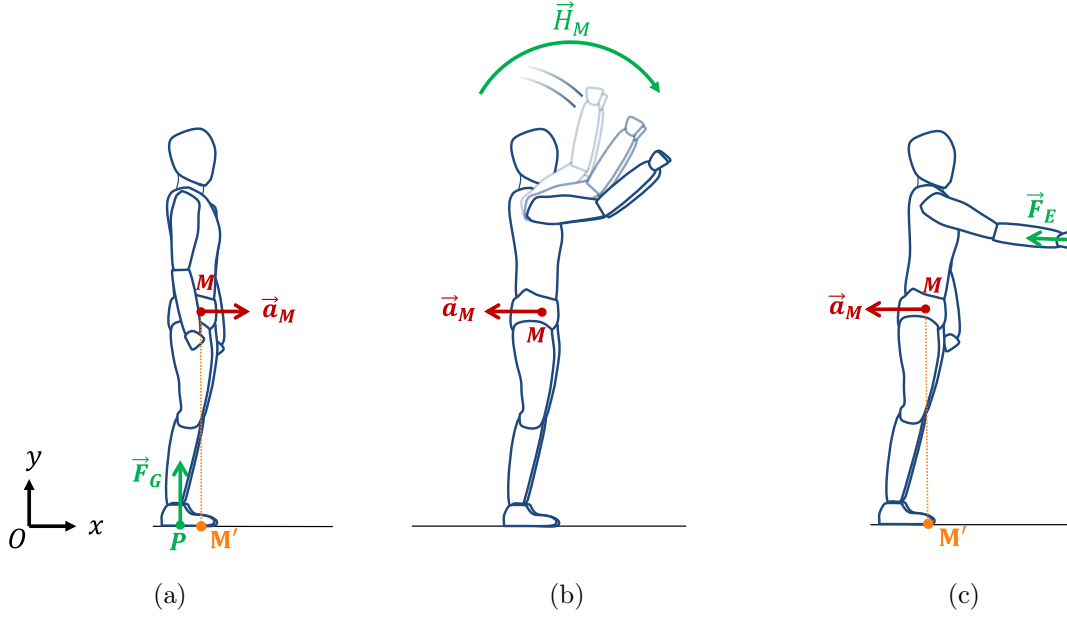


Figure 2.4: Schematic representation of the three balance mechanisms that contribute to modifying whole-body CoM acceleration (red point M) (Hof, 2007), here illustrated in the antero-posterior direction. (a) Moving the Centre of Pressure (P) location within the base of support to modify the distance between the CoP and the projection of the whole-body CoM in the transverse plane on the ground (M'). (b) Counter-rotating segments (trunk, upper limbs, etc.) modifies internal whole-body angular momentum (\vec{H}_M). (c) Applying a new external force (\vec{F}_E) extends the area of the base of support, and makes it possible to modify the external forces applied to the whole body. Green arrows represent the balance mechanisms responsible for whole-body CoM acceleration, and red arrows represent whole-body CoM acceleration (\vec{a}_M).

CoP Mechanism The ‘moving the CoP’ mechanism refers to all muscle actions that contribute to changing the CoP location within the base of support. Mechanically, changing the CoP location misaligns the weight and external force vectors, and accelerates the whole-body CoM in the opposite direction (Winter, 1995). The contribution of this mechanism to whole-body CoM acceleration depends on the distance between P (the CoP) and M' (the whole-body CoM), and the magnitude of the GRF (2.3).

$$\overrightarrow{a}_M = (\overrightarrow{OP} - \overrightarrow{OM}') \times \overrightarrow{F}_G \quad (2.3)$$

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Counter Rotating mechanism The ‘counter-rotating’ mechanism refers to all muscle actions that contribute to rotating body-segment(s) that are not directly in contact with a surface. When a whole-body movement is performed, it modifies the *global* whole-body angular momentum (H_O), which is the sum of the *internal* whole-body angular momentum (H_M) and its translational component (equation (2.4)).

$$\vec{H}_O = \vec{H}_M + \vec{OM} \times m \cdot \vec{v}_M \quad (2.4)$$

H_M represents the rotation of all body segments about the whole-body CoM, in a colinear reference frame, translated with respect to the global reference frame, whereas the second term illustrates the displacement of the whole-body CoM in a global reference frame. H_M can be computed using (2.5):

$$\vec{H}_M = \sum_{i=1}^n [I_i \cdot \vec{\omega}_i + (\vec{OM}_i - \vec{OM}) \times m_i (\vec{v}_{M_i} - \vec{v}_M)] \quad (2.5)$$

The first term in the square brackets is the angular momentum of the i^{th} segment about its centre of mass, and the second term represents the transfer of the momentum of the i^{th} segment to the whole-body CoM, the most used reference point. The literature reports that H_M can also be computed about a point of the foot that approximates the CoP, reflecting the whole-body rotation relative to the ground (Liu et al., 2022). As long as the reference point M belongs to the whole-body, it does not change the modulus of the internal angular momentum but it does change the relative contribution of each segment.

According to equation (2.1), linear whole-body CoM acceleration is modified by the time derivative of H_M . The counter-rotation of segments thus modifies whole-body CoM acceleration, especially when M is outside the base of support (Otten, 1999).

Applying an external force The ‘applying new external force(s)’ mechanism refers to muscle actions involved in taking at least one additional support, relative to an initial configuration, which add external force(s) that act on the whole-body. Compared to the ‘moving the CoP’ mechanism, this mechanism modifies the area of the initial base of support, increasing the amplitude to shift the CoP location and, therefore, to modify whole-body CoM acceleration (Hof, 2007). Well-known examples of this mechanism are hand placement (figure 2.4c) and foot placement, which is largely used to maintain balance while walking (see Bruijn & van Dieën (2018) for a review). The contribution of this mechanism to whole-body CoM acceleration can be quantified using equation (2.6):

$$\vec{a}_M = (\vec{OE} - \vec{OM}') \times \vec{F}_E \quad (2.6)$$

This equation is similar to equation (2.3), with the differences that the distance $\vec{OE} - \vec{OM}'$ can be larger than the distance $\vec{OP} - \vec{OM}'$.

2.2.1.2 Motor transitions: a new mechanical framework

A transition is classically defined as a “change of a current state” (Cambridge Dictionary, 2024), and a state of balance can be characterised by the whole-body CoM acceleration. Thus, in the context of human movement, we can consider a balance state to be steady when the whole-body CoM acceleration is near zero, meaning that the whole-body CoM velocity remains fairly constant (because a strictly zero whole-body CoM acceleration is impossible in humans) (Granacher et al., 2012). Classical examples of steady balance states are ‘*postures*’, where the objective is to maintain the whole-body CoM velocity close to zero, and cyclic ‘*movements*’, such as walking or running, during which there is little change in whole-body CoM velocity during a cycle, and little deviation in whole-body CoM velocity from one step to another, despite the presence of small perturbations (Dingwell & Kang, 2006).

Here, we define a motor transition as a movement phase modifying an initial steady balance state to reach another, final, steady balance state, i.e., when whole-body CoM acceleration increases or decreases to change whole-body CoM velocity (Breniere & Do, 1986; Jian et al., 1993). Analysis of motor transition requires the identification of the onset and end of a change in a steady balance state. We propose that a motor transition starts when the whole-body leaves an initial steady balance state (i.e., when there is a noticeable and continuous increase or decrease in whole-body CoM acceleration), and ends when the whole-body reaches a final steady balance state (i.e., when whole-body CoM acceleration once again approaches zero). When whole-body CoM acceleration cannot be properly computed, change in a steady balance state can also be identified by exploring the causes of the motor transition, namely through external forces acting on the whole body, or whole-body linear and angular momentum.

Because motor transitions are periods when whole-body CoM acceleration changes, they offer an excellent model to study balance-movement coordination. Here, we identify four mechanical types of motor transition relative to their initial and final states (i.e., required whole-body CoM velocity) (figure 2.5): i) posture to posture, ii) posture to movement, iii) movement to posture, and iv) movement to movement.

2.2.1.3 Anticipation

During voluntarily-initiated motor transitions, anticipatory muscle patterns have been defined as muscle activations or inhibitions preceding the prime mover (*i.e.* the segment responsible for the voluntary movement) muscle activation (Massion, 1992). Although prime mover muscle activation onsets have been clearly identified when the muscle is not involved in balance maintenance, (e.g., during upper-limb pointing tasks (Bouisset & Zattara, 1981)), a posture to posture transition), it is much more difficult to identify prime mover muscle activation onset when muscles are already actively contributing to the initial steady balance state. Thus, anticipatory activation of prime movers cannot always be used to identify the onset of voluntarily-initiated movements. Consequently, we suggest that biomechanical variables that start to change before the onset of voluntarily-initiated

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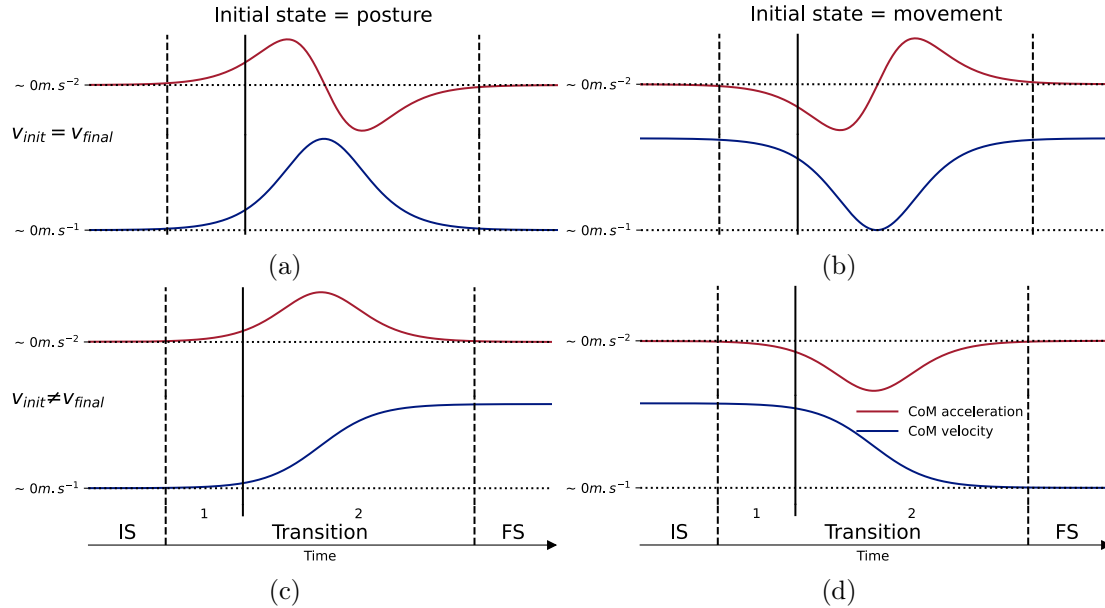


Figure 2.5: Schematic representation of whole-body CoM acceleration (red) and velocity (blue) during four types of motor transitions. On the top row, transitions have identical initial and final whole-body CoM velocities. (a) Posture to posture: a transition between two postures, such as upper-limb pointing or sit-to-stand tasks. (b) Movement to movement: a transition between two cyclic movements, such as a change of direction during walking. On the bottom row, transitions have different initial and final whole-body CoM velocities. (c) Posture to movement: a transition between an initial posture and a final movement, such as gait initiation. (d) Movement to posture: a transition between an initial movement and a final posture, such as gait termination. Horizontal black arrow represents the interval between the initial state (IS) and final state (FS), i.e., when whole-body CoM acceleration is near zero. The ‘Transition’ interval represents the motor transition phase. The interval (1) represents the anticipation phase of the motor transition, i.e., the change of whole-body CoM acceleration occurring before the onset of the prime mover muscle activation (see the Anticipation subsection) represented by the vertical black line. The subinterval (2) represents the remaining of the motor transition.

movements, such as changes in the pattern of external forces and/or external moments (and therefore changes in whole-body CoM acceleration) (subinterval (1) in figure 2.5), could be more appropriate for all types of transitions. In turn, for the purposes of this review, we define anticipation as muscle patterns that have mechanical consequences on the whole-body CoM, starting before the onset of the voluntary movement (*e.g.*) raising the upper limb of lifting the foot to initiate gait). This definition enables to consider the delay between muscle activation and muscle force production (Cavanagh & Komi, 1979), without considering it as anticipation.

2.2.2 Evidence of anticipatory muscle activations modulating balance mechanisms during voluntary initiated motor transitions

In this section, we review evidence from experimental studies that recorded anticipatory muscle activations during voluntarily-initiated motor transitions. We organise this literature according to the mechanical consequences of anticipatory muscle activations, through

the prism of the three balance mechanisms (figure 2.4), and focus our analysis on the anticipatory phase of the identified motor transitions (corresponding to subinterval (1) in figure 2.5). Because not all studies directly quantified the modulation of each balance mechanism, in some cases we use the results of other studies to infer the modulated balance mechanism(s).

2.2.2.1 The 'Moving the CoP' mechanism

The mechanical consequences of anticipatory muscle activations on the CoP have been largely investigated in the sagittal plane, during motor transitions starting from a posture, such as upper-limb pointing (posture to posture) (Bouisset & Zattara, 1981), gait initiation, or squat jump (posture to movement) (Crenna & Frigo, 1991; Le Pellec & Maton, 1999; Lepers & Brenière, 1995). The main anticipatory pattern of the lower-limb muscles, preceding the onset of prime mover muscle activation is described as: activation of the tibialis anterior, coupled with inhibition of the soleus (Bouisset & Zattara, 1981; Crenna & Frigo, 1991; Le Pellec & Maton, 1999; Lee, 1980) (table 2.1). Studies also showed that the amplitude of this anticipatory pattern is modulated by the movement velocity and/or the weight of the object to lift, the two components of whole-body linear momentum (Brenière et al., 1987; Horak et al., 1984; Lee et al., 1987). The mechanical consequence of this anticipatory muscle pattern is to shift the CoP backward. According to equation (2.3), this backward CoP shift is thought to generate forward whole-body CoM acceleration to initiate the voluntary movement (figure 2.4a) (Bancroft & Day, 2016; Bouisset & Zattara, 1987; Breniere & Do, 1986; Lepers & Brenière, 1995; Polcyn et al., 1998).

The mechanical consequences of anticipatory muscle activations on the CoP have also been investigated in the frontal plane. During gait initiation (posture to movement), the anticipatory muscle pattern responsible for the frontal displacement of the CoP has been described as a brief activation of the gluteus medius on the swing foot side, quickly followed by decreased activation of the tibialis anterior on the swing foot side, and the activation of the gastrocnemius medialis and gluteus medius on the stance foot side (Brunt et al., 1991; Mickelborough et al., 2004) (table 2.1). This pattern is thought to have two consecutive mechanical consequences. The first is to shift the CoP towards the swing foot, accelerating the whole-body CoM towards the stance foot (2.3). The second is to progressively shift the CoP towards the stance foot, decelerating the whole-body CoM, enabling the swing foot unloading and lifting, while avoiding a fall towards the stance lower-limb side.

In summary, the 'moving the CoP' mechanism has been extensively studied during motor transitions starting from a posture. In this case, anticipatory muscle patterns are dedicated to modifying the location of the CoP, and changing the distance between M' and P to accelerate the whole-body CoM (2.3). However, the second term, representing the GRF vector in (2.3), is generally not considered in studies, probably because it is not expected to change much during transitions with small momentum (posture to posture, and posture to movement).

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2.2.2.2 The 'Counter-rotating' mechanism

During the motor transitions described in the previous section, other anticipatory muscle activations, that may not contribute to CoP displacement, have been reported (Hodges et al., 1999; Ceccato et al., 2009; Farinelli et al., 2021).

During bilateral shoulder flexions (posture to posture), activations of the erector spinae preceding the activation of the deltoid anterior (the prime mover) have been recorded, resulting in a trunk extension preceding the onset of shoulder flexion. The opposite biomechanical consequence has been reported during bilateral shoulder extension, with a small trunk flexion preceding the onset of shoulder extension, despite the non-systematicity of a rectus abdominis activation preceding deltoid posterior activation (Hodges et al., 1999). Although the latter authors did not quantify H_M , we suggest that these rotations could illustrate a 'counter-rotating' mechanism. Even with small angular displacements, the large inertial parameters of the trunk segment should impact the whole-body CoM acceleration.

The following sequence of trunk muscle activations, preceding tibialis anterior activation, has also been reported during gait initiation (posture to movement): activation of the bilateral rectus abdominis and obliquus abdominis, accompanied by a non-systematic inhibition of the swing side erector spinae (Farinelli et al., 2021). While these activations are likely to rotate the trunk forward, the authors did not quantify trunk kinematics during this early period preceding gait initiation. During the remainder of the anticipatory phase of gait initiation preceding foot off, authors have reported activations of the rectus and obliquus abdominis, and the erector spinae (Ceccato et al., 2009; Farinelli et al., 2021) (table 2.2).

Authors who have quantified trunk kinematics during the gait initiation motor transition have reported results that seem to have contradictory effects on H_M . Specifically, some have shown a forward trunk flexion preceding foot-off (Ceccato et al., 2009; Laudani et al., 2006) (table 2.2). This observation suggests that H_M should be directed in a forward rotation in the sagittal plane during gait initiation. However, H_M is mostly directed in a backward rotation in the sagittal plane before the foot-off during a stepping task (posture to posture transition with change in base of support) (Begue et al., 2019), with the most important contribution coming from the trunk segment (Begue et al., 2021). This point could be clarified by identifying whether the recorded trunk flexion follows that of the pelvis, or if there is a dissociation between trunk and pelvis segments. More research is needed to determine whether these early trunk muscle contractions contribute to a modulation of H_M and, therefore, to the control of whole-body CoM acceleration.

Authors reported that around the time of maximal backward CoP shift, the erector spinae of the swing side are activated (Ceccato, 2009; Farinelli et al., 2021), and have suggested that these activations serve to limit trunk inclination towards the stance foot side, and direct it towards the swing foot side (Ceccato, 2009). This trunk inclination should reduce the amplitude of H_M directed in a rotation towards the stance lower-limb in the frontal plane. However, during a stepping task, some authors have reported an increase in H_M

directed in a rotation towards the stance lower-limb in the frontal plane (Begue et al., 2019). As for sagittal plane observations, these conclusions seem contradictory, and future studies are required to precisely assess the contribution of the ‘counter-rotating’ mechanism to different types of motor transitions.

In summary, the mechanical consequences of anticipatory muscle activations on H_M have not been directly investigated during motor transitions. We are only able to infer this mechanism from anticipatory muscle activations and resultant kinematics recorded during motor transitions with small momentum (posture to posture, and posture to movement). Based on a limited number of studies, we suggest that anticipatory trunk muscle activations could modify H_M , but direct evidence remains fragmentary. Notably, it remains unknown if these anticipatory muscle activations rotate the trunk, for small trunk orientation adjustments, or act to stiffen and stabilise the upper-body, particularly because of the importance of stabilising the head (Laudani et al., 2006; Pozzo et al., 1990). Given the large inertial parameters of the trunk segment, its potential contribution to whole-body CoM acceleration cannot be neglected in the characterisation of balance maintenance (2.5). The contribution of the ‘counter-rotating’ mechanism to whole-body CoM acceleration remains to be investigated during different types of motor transitions, notably to determine the role of the ‘counter-rotating’ mechanism relative to whole-body CoM acceleration and, by extension, to general balance maintenance. Because the contribution of the ‘counter-rotating’ mechanism to whole-body CoM acceleration has not been directly investigated, our conclusions remain speculative. This contribution still needs to be examined across various types of motor transitions, notably to clarify the role of the ‘counter-rotating’ mechanism relative the whole-body CoM acceleration and, by extension, its impact on overall balance maintenance.

2.2.2.3 The ‘Applying new external force(s)’ mechanism

The ‘applying new external force(s)’ mechanism relates to motor transitions starting from a movement (i.e. movement to posture and movement to movement). In this case, there is a modification of the base of support, for example, adapting foot placement when walking on uneven terrain (Matthis et al., 2018). Because using the hand(s) for additional support rarely occurs during voluntarily-initiated motor transitions, and because it is central in balance maintenance during walking (Bruijn & van Dieën, 2018), we only selected studies that considered modification of the foot placement.

The literature reported two distinct muscle activation mechanisms enabling to modify foot placement. The first mechanism used to modify foot placement is *muscle activations of the swing lower-limb*. These muscle activations contribute to modifying the joint angles and the foot position (Roelker et al., 2019). Notably, it has been suggested that the gluteus medius actively modulates medio-lateral foot placement during gait (Rankin et al., 2014) (table 2.3). During change of direction (movement to movement), other authors reported that humans regulate the medio-lateral positioning of their foot one step before changing direction, when asked to change direction early in the gait cycle (Patla et al.,

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1999) (table 2.3). Analysing a right turn, they argued that the reduction in whole-body CoM acceleration in the outward direction (the left side) was explained by a reduction in the penultimate step width (equation (2.6)) (the right foot placement). Furthermore, they suggested that this mechanical solution facilitates an increase in whole-body CoM acceleration in the intended direction (the right side), in addition to the lateral force this position enables.

The second mechanism used to modify foot placement is *muscle activations of the stance lower-limb* (Roelker et al., 2019). While walking, foot placement is closely related to the current position and velocity of the whole-body CoM (Bruijn & van Dieën, 2018). Authors have recorded biceps femoris activations during the penultimate step, before a change of direction (Hase & Stein, 1999). The same authors argued that these activations helped to limit hip extension, reducing the forward velocity of the whole-body CoM and, consequently, reducing the step length before changing direction. Similarly, during gait termination, activations of both soleus and vastii have been recorded prior to foot contact (Bishop et al., 2004; Hase & Stein, 1998). Other authors have suggested that while these activations may contribute to the last foot placement, they could also be related to the increase in GRF measured during gait termination, the other parameter in equation (2.6) (Jaeger & Vanitchatchavan, 1992).

In summary, the ‘applying new external force(s)’ mechanism makes a particularly important contribution to motor transitions that start with a movement. Foot placement can be modulated through muscle activations of both stance and swing lower-limbs, acting to modify the distance between M' and E (the position of the CoP when the foot touches the ground). However, anticipatory muscle activations have been little investigated during motor transitions, and the evolution of the GRF vector has rarely been considered (equation (2.6)). Overall, this balance mechanism has received much less attention in the literature compared to the two others, probably because it is more difficult to identify the transition onset. Thus, it seems that more research is needed to clarify which muscle activations contribute to changing foot placement during voluntarily-initiated motor transitions.

2.2.3 Discussion and perspectives

Our objective was to provide an overview of the mechanical consequences of anticipatory muscle patterns identified during motor transitions that contribute to balance-movement coordination. We proposed a new framework for motor transitions that aims to generalise the identification of anticipatory period. In this framework, we classified motor transitions into four types based on their initial and final states. During the anticipatory period, we propose that this framework enables to identify the contribution of the three balance mechanisms proposed by Hof (2007) -moving the CoP, counter-rotating, and applying new external force(s)- to the whole-body CoM acceleration. The role of each mechanism can thus be discussed according to the whole-body CoM acceleration required for each transition (figure 2.5). Consequently, this approach allows to infer on the *favourable conditions*

anticipatory muscle activations provide for successful transition execution.

Using this new framework, we showed that the mechanical consequences of anticipatory muscle activations have been extensively described in terms of the ‘moving the CoP’ mechanism, and mostly during motor transitions starting from postures. The mechanical consequences of anticipatory muscle activations on the other two balance mechanisms (‘counter-rotating’ segments and ‘applying new external force(s)’) have received much less attention in the literature, probably because of the difficulty of linking muscle activations to variation in H_M , and identifying activation onset of the muscle(s) contributing to changing the foot placement, respectively. Here, we discuss the potential contribution of the identified anticipatory muscle activations to balance-movement coordination, through the prism of changes in whole-body CoM acceleration.

2.2.3.1 Motor transitions: a period of required instability

The relative positions of the CoP and the whole-body CoM have been extensively used to characterise balance. During a posture, the distance between M' and P must remain small to minimise whole-body CoM acceleration (equation (2.3)) (Winter, 1995). During a movement, the foot is placed such that a steady velocity can be maintained (Bruijn & van Dieën, 2018). In contrast, during motor transitions, the evidence we report here suggests that anticipatory muscle activations contribute to the opposite mechanical objectives. During motor transitions starting from a posture, anticipatory muscle activations contribute to shifting P away from M' , whereas during motor transitions starting with a movement, foot placement is shifted away from the theoretical foot position required to maintain a steady balance state. In both cases, the resulting whole-body CoM acceleration helps reaching the final state, by inducing acceleration during transitions starting from a postural state and deceleration during transitions starting from a movement (tables 2.1 and 2.3). Thus, the nervous system seems to create a situation of mechanical instability (by modifying the whole-body CoM acceleration), which provide favourable conditions helping initiating or terminating whole-body movements, and transition between two steady balance states (Brenière et al., 1987; Lepers & Brenière, 1995). During motor transitions starting with a movement, such as a change of direction, this instability has been demonstrated by quantifying H_M . The more medial penultimate foot placement has been related to a larger magnitude of H_M , illustrative of mechanical instability in the frontal plane (Nolasco et al., 2019). This evidence strongly suggests that the anticipatory muscle activations responsible for the ‘moving the CoP’ and the ‘applying new external force(s)’ mechanisms contribute to a short period of mechanical instability to initiate the motor transition.

In addition, this required mechanical instability appears to be modulated as a function of the intended motor task (*i.e.* the final state of the transition). During reaching tasks (posture to posture) in different directions, it has been suggested that anticipatory muscle activations contribute to accelerating the whole-body CoM towards the target, and do not play a role in balance maintenance during this phase (Leonard et al., 2009). During stepping (posture to posture), other authors have reported that the whole-body CoM

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acceleration caused by the CoP shift is tuned to the planned foot placement, in both sagittal and frontal planes (Bancroft & Day, 2016). These modulations support arguments that instability is required to facilitate reaching the final state.

The latter observation is aligned with recent control theory, which suggests that humans modulate their initial postural state depending on the movement they expect to perform (the final state) (Le Mouel & Brette, 2017; Le Mouel et al., 2019). In this theory, the relative positions of M' and P are adjusted in anticipation of a motor transition, in such a way that the ‘moving the CoP’ mechanism enables the motor transition to be initiated (equation (2.3)). However, our review showed that the literature has focused on modulating the distance between M' and P , rather than the magnitude of external force vectors (the GRF in equation (2.3), and the new external force in equation (2.6)). Although this vector may not change much during motor transitions with small momentum (for instance during a posture to posture transition), it can have a much larger impact during motor transitions with large momentum, such as a change of direction (movement to movement) while running.

When investigating upper-limb movements, some authors have suggested that it is necessary to abandon the maintenance of the initial state to initiate a movement (Cluff & Scott, 2016; Scott, 2016). Our evidence of the required mechanical instability reported above also supports this hypothesis in motor transitions that require whole-body balance maintenance. Moreover, one study investigated voluntary sways and shoulder flexion (posture to posture), and reported a decrease in muscle activations stabilising the CoP position, resulting in an increase in whole-body CoM acceleration (Klous et al., 2011). In another study, vestibular-stabilising responses to electrical stimulations were reported to be proactively down-regulated before different types of motor transitions (Tisserand et al., 2018). In the light of our proposed mechanical framework, the abandonment of the initial balance state is likely to be necessary to enable the period of required instability to transition from one state to another.

In summary, our evidence suggests that ‘moving the CoP’ and ‘applying new external force(s)’ mechanisms do not have the same role in steady balance states and motor transitions: they ensure balance during steady movements, but contribute to increase mechanical instability in the early phases of a motor transition creating favourable conditions helping the nervous system to switch from the initial to the final steady balance state.

2.2.3.2 ‘Counter-rotating’, a stabilising mechanism during motor transitions?

In the previous section, we presented evidence which suggests that anticipatory muscle activations related to ‘moving the CoP’ and ‘applying new external force(s)’ mechanisms generate mechanical instability required to a motor transition. This mechanical instability, which is characterised by an increase in whole-body linear and angular momenta, challenges balance, and can lead to falls (Cummings & Nevitt, 1989; Simoneau & Krebs, 2000). Since it is very unlikely that the ankle muscles alone can regulate balance (Loram & Lakie, 2002; Morasso & Sanguineti, 2002), especially if the distance between M' and P is large

equation (2.3)), other mechanisms may limit excessive increases in whole-body linear and angular momenta during motor transitions. In practice, the three balance mechanisms are not mutually exclusive, and can complement each other, depending on the objective of the task and biomechanical constraints (Hof, 2007; Leestma et al., 2023; Tisserand et al., 2023; van Leeuwen et al., 2022). During motor transitions, the ‘counter-rotating’ mechanism may contribute to balance modulation. For instance, an anticipatory ‘counter-rotating’ mechanism has been used to minimise H_M so that robots and computer animated avatar can transition without falling (Kajita et al., 2003; Rabbani et al., 2018).

In human movements, however, the role of the ‘counter-rotating’ mechanism remains unclear (table 2.2). On the one hand, authors have reported a trunk rotation in the opposite direction from the resultant movement during shoulder flexions and extensions (posture to posture) (Hodges et al., 1999). During stepping (posture to posture), the trunk contribution to H_M in the sagittal plane is in the opposite direction to that of the stance limb (Begue et al., 2021), and that of an inverted pendulum. On the other hand, anticipatory trunk muscle activations and the associated trunk kinematics have been found to be directed towards that of the voluntary movement during reaching tasks (posture to posture) (Stamenkovic et al., 2021), or in the final steady state direction during the penultimate step in a change of direction task (movement to movement) (Nolasco et al., 2019). In these cases, the trunk seems to contribute to increase whole-body mechanical instability to initiate the motor transition. These different contributions of the ‘counter-rotating’ mechanism to balance-movement coordination could, therefore, depend on the objectives and characteristics of the task (*i.e.* the final state of the transition). Based on our review of the literature, we suggest that more research is necessary to clarify the role of the ‘counter-rotating’ mechanism in balance-movement coordination. Specifically, it is important to investigate the contribution of the ‘counter-rotating’ mechanism to the whole-body CoM acceleration, to determine whether this contribution facilitates or opposes the acceleration required for the transition.

One limitation of studying the ‘counter-rotating’ mechanism is that it is difficult to address the consequences of anticipatory muscle activations on H_M variation. Here, we were only able to infer the impact that anticipatory trunk muscle activations should have on H_M , based on studies that only quantified the consequences of trunk kinematics. A step towards a better understanding of the ‘counter-rotating’ mechanism could be the quantification of each segment’s angular momentum to H_M during different transitions, such as in the work of Nolasco et al. (2019). This would make possible to differentiate between segments generating H_M that contribute to initiating the movement, and segments generating H_M that contribute to regulating balance. A second step could be to use musculoskeletal modelling to quantify the contribution of muscle activations to variation in H_M (Neptune & McGowan, 2011, 2016), given that the link between muscle activations and segment dynamics is not straightforward. This would make it possible to study direct cause and effect relationships between muscle activations and H_M , notably taking internal coupling and whole-body dynamics into account.

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2.2.3.3 Practical perspectives

In daily life, the “*forces we exert on the environment during (loco)motion are anything but constant*” (Dickinson et al., 2000). Given the definition of motor transitions that we propose here (i.e., movement phases during which muscles produce forces that aim to change whole-body CoM acceleration), they are ubiquitous in our day-to-day movements. Changes of direction alone represent up to 50% of our walking steps (Glaister et al., 2007). These motor transitions are therefore vital for every human to move safely, and interact with the world. For instance, most falls in older people occur following ineffective motor transition phases, *i.e.* when the whole-body CoM acceleration resulting from internal perturbation becomes excessive (Robinovitch et al., 2013).

The three balance mechanisms that we identify are not mutually exclusive; instead, they are complementary processes that act together to modulate whole-body CoM acceleration (Fettrow et al., 2019), and their respective contributions can be analytically separated (Hof, 2007). Thus, we suggest that quantifying the contribution of each of the three mechanisms to balance-movement coordination could help to improve our understanding of the balance problems experienced by people with balance deficits during motor transitions. For example, it has been reported that during stepping, older people have a larger range of H_M in the sagittal plane compared to their younger counterparts (Begue et al., 2021). Furthermore, after tripping, older people were found to be less able to control H_M , using their upper-limbs to prepare for impact instead of reducing H_M (Roos et al., 2008), and placed their recovery limb less accurately (Pijnappels et al., 2005), compared to their younger counterparts. Therefore, older people may be less able to adjust their whole-body CoM acceleration, because of a smaller contribution of the ‘counter-rotating’ mechanism. However, these conclusions remain speculative due to the limited evidence on the contribution of the ‘counter-rotating’ mechanism. Another limitation is that the linearised inverted pendulum neglects the contribution of the ‘counter-rotating’ mechanism in the transverse plane (equation (2.2)). Future studies should identify specific situations in which individuals rely on the ‘counter-rotating’ mechanism to regulate the whole-body CoM acceleration, as well as the extent to which its use is affected by aging or various pathologies. Quantifying the role of the ‘counter-rotating’ mechanism in balance-movement coordination could help determining if training to enhance this mechanism should be included in future fall-prevention and rehabilitation programs.

A better understanding of balance-movement coordination during motor transitions could also benefit other populations with mobility impairments, such as amputees or exoskeleton users. Amputees lack balance confidence, decreasing their mobility (Miller et al., 2001). For example, a neural prosthesis was developed to mimic the ‘moving the CoP’ mechanism of the residual lower-limb during simple posture to posture transitions (Fleming et al., 2023). While this is an encouraging step towards improved mobility for amputees, the prosthetic ankle was limited to only one type of motor transition with small momentum, and its control is based on residual limb muscle activations. The latter point limits its potential adaptation, given the asymmetric control involved in the ‘moving the CoP’ mechanism.

For lower-limb exoskeleton users, a balance controller is required to safely perform motor transitions (Hamza et al., 2020). Recently, hip exoskeletons were developed to modulate step width, and ensure balance during steady walking (Alili et al., 2024). In an able-bodied population using a lower-limb exoskeleton, trunk motion and arm movements have been used to detect gait initiation (Alaoui et al., 2020), gait termination, and change of direction intentions (Alaoui, 2021). Hence, combining the intention to perform a motor transition with an adaptation of the foot placement could enhance mobility in lower-limb exoskeleton users. However, to achieve this objective, more research is needed to adapt foot placement to motor transitions, while considering the abilities of different populations, notably the capacity to use the ‘counter-rotating’ mechanism.

Finally, as a broader perspective, we propose that anticipatory muscle activations provide *favourable conditions* to the motor transition execution: the required mechanical instability and maintenance of balance. A better understanding of these *favourable conditions* may be beneficial for populations with balance deficits. Indeed, if we can better characterise these *favourable conditions*, then we can better understand motor transition and therefore assess more precisely which mechanisms are impaired in these populations, to provide more adapted rehabilitation programs or assistive devices.

2.2.3.4 Conclusion

The new mechanical framework we proposed for the study of motor transitions may help to better identify the underlying processes involved in balance-movement coordination. Studies have shown that anticipatory muscle activations modify whole-body CoM acceleration during the four types of motor transition. However, we demonstrated that anticipatory muscle activations have mainly been interpreted in terms of only one mechanism, namely ‘moving the CoP’, and during motor transitions involving small whole-body momentum (for instance during a posture to posture transition). Based on the interpretation of whole-body CoM acceleration resulting from anticipatory muscle activations, we suggest that transitions are a period of required mechanical instability that facilitates the shift from one steady balance state to a final steady balance state. This mechanical instability seems to mainly be the result of two balance mechanisms: ‘moving the CoP’ and ‘applying new external force(s)’. It appears that the ‘counter-rotating’ mechanism may be more dedicated to balance regulation, but this assumption remains to be verified, and its action may also depend on the objective and the characteristics of the task. Motor transitions are essential to ensuring mobility, and can lead to falls if they are not properly executed. We therefore suggest that improving our understanding of balance-movement coordination during motor transitions would help in developing better rehabilitation programs and/or supporting devices.

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Table 2.1: Summary of the anticipatory muscle activations, biomechanical consequences, and proposed role in balance movement coordination for the ‘moving the CoP’ mechanism during transitions starting from a posture. The activations, biomechanical consequences and proposed role in the sagittal plane encompass both upper-limb raising (posture to posture) and gait initiation (posture to movement) tasks, whereas the activations described in the frontal plane are only reported during gait initiation.

| ‘Moving the CoP’ | Transitions starting from a posture (e.g., upper-limb raising, gait initiation) | |
|---|---|---|
| | Sagittal Plane | Frontal Plane |
| Evidence of anticipatory muscle activations | Tibialis anterior activation and soleus inhibition (Bouisset & Zattara, 1981; Crenna & Frigo, 1991; Le Pellec & Maton, 1999; Lee, 1980) | Sequentially, (1) Brief swing side Gluteus Medius activation, (2) Decreased swing side Tibialis Anterior activation (Brunt et al., 1991; Mickelborough et al., 2004) |
| Biomechanical consequences of anticipatory muscle activations | Backward shift of the CoP, accelerating the whole-body CoM forward (Breniere & Do, 1986; Bancroft & Day, 2016; Bouisset & Zattara, 1987; Polcyn et al., 1998) | Sequentially, (1) Shift the CoP towards the swing foot, accelerating the CoM towards the stance foot, (2) and shift the CoP towards the stance foot, decelerating the CoM towards the swing foot (Brunt et al., 1991; Mickelborough et al., 2004) |
| Proposed role in the balance-movement coordination | Required mechanical instability to help initiating the transition. Whole-body CoM acceleration required to perform the transition | Whole-body CoM acceleration required to perform the transition and enabling the initiation of the voluntary movement and maintaining balance |

Illustration

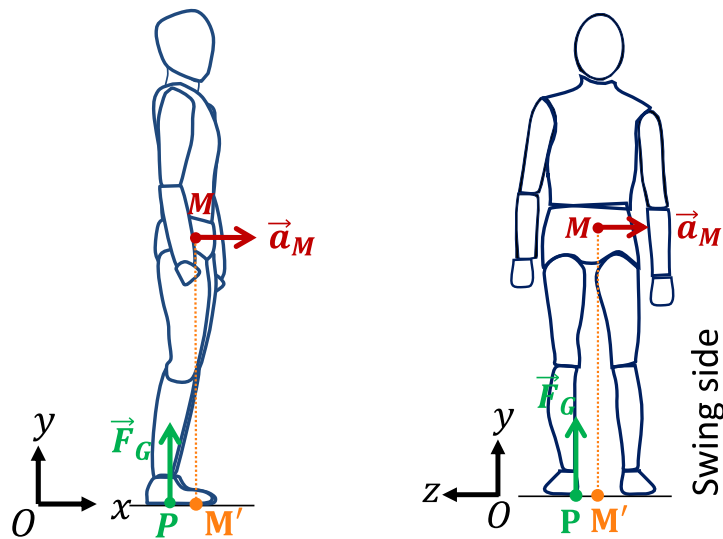
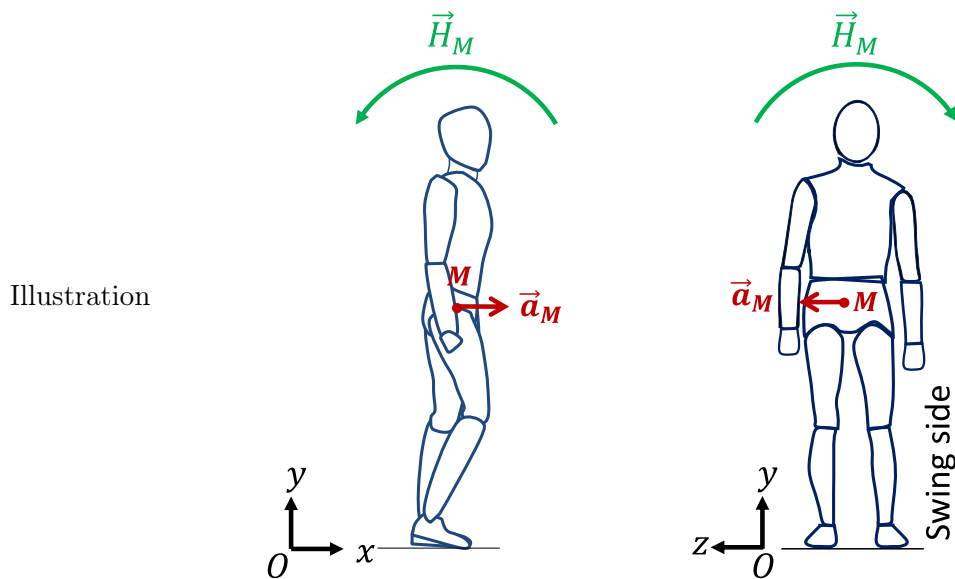


Table 2.2: Summary of the anticipatory muscle activations, biomechanical consequences, and proposed role in balance movement coordination for the ‘counter-rotating’ mechanism during transitions starting from a posture. The activations, biomechanical consequences and proposed role in the sagittal plane encompass both upper-limb raising (posture to posture) and gait initiation (posture to movement) tasks, whereas the activations described in the frontal plane are only associated with gait initiation.

| ‘Counter-rotating’ | Transitions starting from a posture (e.g., upper-limb raising, gait initiation) | |
|---|--|---|
| | Sagittal Plane | Frontal Plane |
| Evidence of anticipatory muscle activations | Bilateral activation of rectus abdominis and obliquus abdominis, with a non-systematic inhibition of swing erector spinae (Ceccato et al., 2009; Farinelli et al., 2021) | Activation of erector spinae of the swing side (Ceccato et al., 2009; Farinelli et al., 2021) |
| Biomechanical consequences of anticipatory muscle activations | Trunk Flexion (Ceccato et al., 2009; Laudani et al., 2006), but H_M is directed in a backward rotation (Begue et al., 2019) | Limit trunk lateral inclination towards the stance foot side (Ceccato et al., 2009), and direct H_M in rotation towards the swing foot side (Begue et al., 2019). |
| Proposed role in the balance-movement coordination | Unclear - The dissociation between pelvis/lower-limb and trunk should be further clarified in future studies | Limit the increase in HM directed in a rotation towards the stance lower-limb side, probably to limit the increase in H_M and maintain balance |

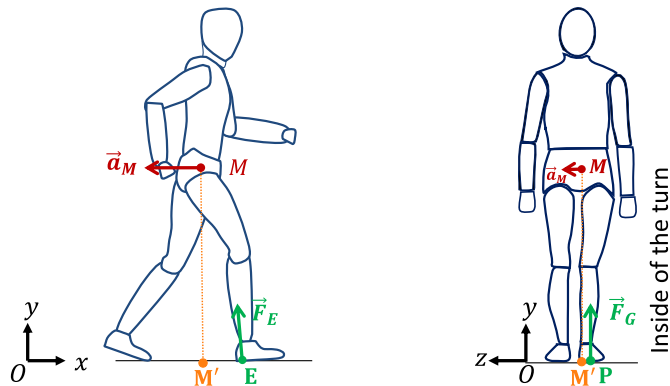


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Table 2.3: Summary of the anticipatory muscle activations, biomechanical consequences, and proposed role in balance movement coordination for the ‘applying an external force’ mechanism during transitions starting from a movement. The activations, biomechanical consequences and proposed role in the sagittal plane are mainly associated with gait termination (movement to posture) or to reducing whole-body CoM velocity before changing direction (movement to movement), while those in the frontal plane are mainly associated with change of direction (movement to movement).

| ‘Applying an external force’ | Transitions starting from a movement (e.g. gait termination, change of direction) | |
|---|--|---|
| | Sagittal Plane | Frontal Plane |
| Evidence of anticipatory muscle activations | (1) Penultimate stance biceps femoris activation (Hase & Stein, 1999), and (2) Swing soleus and vastii activation (Hase & Stein, 1998; Bishop et al., 2004) | Activation of gluteus medius [48] (not directly assessed during motor transitions)(Rankin et al., 2014) |
| Biomechanical consequences of anticipatory muscle activations | (1) Reduce gait velocity and step length (Hase & Stein, 1998; Bishop et al., 2004) and (2) Increase in GRF during the last step (Jaeger & Vanitchatchavan, 1992) | Reduction in the penultimate step width to reduce the CoM acceleration in the outward direction (Patla et al., 1999) |
| Proposed role in the balance-movement coordination | Required mechanical instability to help initiating the transition. Whole-body CoM deceleration required to perform the transition | Required mechanical instability to help initiating the transition. Whole-body CoM deceleration required to perform the transition |

Illustration



2.3 Anticipation of contact

In the previous section, we used a linearised inverted pendulum model to infer on the whole-body CoM acceleration because it reflects whole-body balance. By definition, the whole-body CoM vertical position never changes in a linearised inverted pendulum. Thus, no acceleration along the vertical axis can be inferred from this model. However, when interacting with the environment, we must also consider the ubiquitous gravity external force, constantly accelerating the whole-body downward, requiring constant muscle activity to remain upright. Moreover, when humans pose a foot or a hand on an external support, a large external force is required to accelerate the segment in contact with the external support upward. If muscles are not activated (or not sufficiently activated), all joints would flex or extend and the whole-body may collapse. Moreover, an ineffective consideration of gravity and change in external force leads to both overuse and acute injuries, such as osteoarthritis or low back pain or patellofemoral pain (Dufek & Bates, 1991; Collins & Whittle, 1989; De Bleecker et al., 2020); and upper-limbs fractures (DeGoede et al., 2003) or anterior cruciate ligament ruptures (Chia et al., 2022), respectively.

Here, the aim is to provide an overview of the anticipatory muscle activations in the context of a predictable contact enabling to accelerate the whole-body CoM upward or limit the magnitude of GRF, to cope with gravity. In the first section, we present two main concepts required to study anticipation of contact: the integration in our mechanical framework of motor transition and the prediction of the instant of contact. In the second section, we present anticipatory muscle activations to accelerate the whole-body CoM (or the object) upward, during the forthcoming contact time. In the third section, we present the different strategies to limit the transient force, and we highlight the gaps in the literature to suggest new perspectives for bridging them.

2.3.1 Main concepts relative to anticipation of contact

2.3.1.1 Integration in the mechanical framework of motor transitions

In *Anticipation for balance-movement coordination*, we focused on the anticipatory muscle activations influencing the position of the foot, and modifying the whole-body CoM acceleration, mainly in the transverse plane (equation (2.6)). Here, we focus on the anticipatory muscle activations dedicated to prepare coping with a transient external force, to accelerate the whole-body upward, and to remain upright (or to maintain a given posture). Different experimental paradigms were used to study how humans cope with the gravity external force such as landing on the feet (Jones & Watt, 1971b), arresting a forward fall with hands (DeGoede & Ashton-Miller, 2002) or catching a ball (Lacquaniti & Maioli, 1989)). These experimental paradigms are special cases of *Motor transitions: a new mechanical framework* we presented before (figure 2.6). A main advantage of these experimental paradigms is that anticipatory phases are easily identified as the time before contact between feet and ground, hand and ground, and ball and hand, respectively. This time can be identified with the distinct change in transient external force brought by the contact. However, the whole-body CoM acceleration can differ from zero during steady

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balance states, but remains constant, such as during a free-fall situation (figure 2.6). Anticipatory period is identified when the whole-body CoM acceleration is constant, before contact. Therefore, and in the same way as in [Anticipation for balance-movement coordination](#), we define anticipatory muscle activations as activations which have biomechanical consequences *preceding the instant of contact* between the body of interest and the external object/environment (*i.e.* the contact between the foot or the hand with an external support or object). The intensity of the transition can be characterised using the time rate change of linear momentum between the onset and the end of the transition.

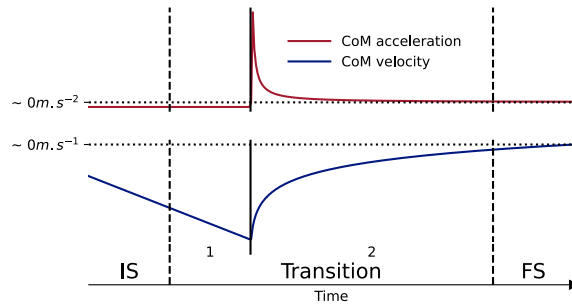


Figure 2.6: Adaptation of the framework of motor transitions in the context of anticipation of contact. Here, the whole-body CoM acceleration (in red) is not null during the initial state, because the whole-body is in the air. Horizontal black arrow represents the interval between the initial state (IS) and final state (FS), *i.e.* when whole-body CoM acceleration is near zero. The ‘Transition’ interval represents the motor transition phase. The interval (1) represents the anticipation phase of the motor transition, *i.e.* the change of whole-body CoM acceleration occurring before the onset of the prime mover muscle activation (see the [Anticipation](#) subsection) represented by the vertical black line. The subinterval (2) represents the remaining of the motor transition.

Here, we mainly focus on landing on the feet because it was largely investigated in the literature and because it is a whole-body task involving full-body weight, as opposed to arresting falls with hands, where a part of the GRF is applied to the feet. We use the term *landing contexts* to refer to all tasks containing a landing, such as landing from a jump, landing from a drop (*i.e.* drop-landing), landing from a drop and immediately performing a jump (*i.e.* drop-jumping), and performing multiple jumps (*i.e.* repetitive jumps). Although we focus mainly on landing tasks, an understanding of the mechanisms of anticipation of contact is essential to understand common mechanisms involved in a broader variety of movements, such as walking or running.

2.3.1.2 Prediction of contact

In [Anticipation for balance-movement coordination](#), we showed that anticipatory muscle activations are programmed based on a prediction made by the efferent copy of the motor commands required to perform the movement. In the case of contact with an external support (*i.e.* the ground or an object), the prediction cannot arise from the same principle. It has been suggested that humans use an internal model of gravity for their own movement ([Merfeld et al., 1999](#)) and when interacting with an external event such as catching a free-

falling ball (McIntyre et al., 2001; Indovina et al., 2005). This internal model would enable humans to predict both the timing of an event and the forces required to account for gravity consequences in the desired movement. Therefore, by accurately predicting the timing and magnitude of an additional external force, anticipatory muscle activation can be programmed to prepare muscles to develop enough force to accelerate the whole-body or the object upward (Lacquaniti & Maioli, 1989).

2.3.2 Evidence of anticipatory muscle activations to accelerate upward

Fifty years ago, Jones and Watt suggested that stretch reflex responses alone would occur too late to accelerate the whole-body upward during a step-down (Jones & Watt, 1971b). In other words, the consequences of gravity must be anticipated by muscle processes engaged during the air-time phase preceding ground contact. Accordingly, Jones & Watt (1971b,a); Arampatzis et al. (2001); Podraza & White (2010) described activations of the main lower-limb muscles (*e.g.* rectus femoris, vastii, hamstrings, soleus, and gastrocnemii) starting 50 to 150 ms before ground contact during drop-landing and drop-jumping tasks, and interpreted these activations as preparation for muscle to develop large forces starting from ground contact. Similarly, Dietz & Noth (1978); Dietz et al. (1981) described activation of main upper-limb muscles (*e.g.* biceps and triceps brachii) 100 to 300 ms before ground contact when landing from a forward fall. When analysing the task of catching a ball, Lacquaniti & Maioli (1989) recorded activations of extensor carpi radialis and flexor carpi radialis before the contact between the ball and the hand, in addition to the biceps and triceps brachii. It should be noted that, even if reflex responses alone cannot accelerate the whole-body or the ball upward, they do, however, play a significant role and must not be neglected. Using protocols with false information about the ground contact time, Duncan & McDonagh (2000) and Zuur et al. (2010) suggested that both anticipatory muscle activations *and* reflex muscle activations contribute to muscle activity dedicated to accelerate the whole-body upward during ground contact.

The impact of the time rate change of linear momentum has been largely studied using the experimental paradigms listed above. Linear momentum was manipulated by modifying the velocity at contact -manipulating drop height, gravity intensity, or drop slope-, by modifying the change of velocity during contact -through the change of instruction, for example between a drop-landing and a drop-jumping-, or by modifying the mass of the object or of the whole-body. The literature agrees to describe an increase of the anticipatory muscle activation amplitude with the increase of whole-body CoM velocity during drop-landing (Jones & Watt, 1971a; Santello & McDonagh, 1998; Peng et al., 2011; Lesinski et al., 2017; Helm et al., 2019, 2020; Waldvogel et al., 2023) and during landing on hands after a forward fall (Dietz et al., 1981). Moreover, during ball catching, the two components of the ball linear momentum (*i.e.* mass and velocity at contact) lead to an increase of anticipatory muscle activation amplitude (Lacquaniti & Maioli, 1989). Next, anticipatory muscle activation amplitudes are larger with an increase in time rate change of linear momentum, observed by comparing drop-jumping and drop-landing tasks (Dyhre-Poulsen et al., 1991; Leukel et al., 2011; Waldvogel et al., 2023), and by comparing drop-jump

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with decreasing ground contact time (Arampatzis et al., 2001). Moreover, when studying drop-jumping tasks with different rebounding height, Arai et al. (2013) recorded larger anticipatory tibialis anterior activation amplitude. Finally, the anticipatory muscle activation amplitudes were correlated with the eccentric action of the muscle during ground contact (Avela et al., 1996; Ishikawa & Komi, 2004). In summary, it is clear that humans use anticipatory muscle activations to prepare their muscles to decrease the amount of vertical velocity accumulated during the air-time phase of dropping movements.

The literature proposed that the role of these anticipatory activations is to increase the muscle and joint stiffnesses to accelerate the whole-body centre of mass upward while on the ground, reviewed in Santello (2005). This assumption has been confirmed by musculoskeletal modelling, where co-activation of muscles around the ankle joint was related to larger joint stiffness and smaller joint range of motion during contact (DeMers et al., 2017); and in animal models (turkey), where Konow & Roberts (2024) established a relationship between gastrocnemius anticipatory activations and gastrocnemius force before ground contact. The more anticipatory muscle activation amplitude, the most joint stiffness and the less the joint rotation amplitude (Butler et al., 2003), resulting in an important upward acceleration of the whole-body CoM, characterised by a low variation of the whole-body CoM vertical position (Arampatzis et al., 2001). As a result, Horita et al. (2002) proposed two strategies for drop-jumping: a *bouncing* strategy, with larger anticipatory muscle activations and resulting knee joint stiffness, and an *absorbing* strategy, with lower anticipatory muscle activations and knee joint stiffness. With the results presented before, we can place these strategies onto a continuum, from the most bouncing type to the most absorbing type, also containing drop-landing strategies, and suggesting that drop-landing and drop-jumping contains similar motor strategies.

In addition to reduce joint flexion excursions during ground contact, anticipatory muscle activations also enable to stabilise joints in other planes (Wikstrom et al., 2006). This stabilisation is important to cope with external forces because, due to the multi-body structure of the whole-body, the vertical component of GRF also contains a significant transverse (shear) component (Collins & Whittle, 1989). This transverse component is a significant risk factor of lower-limb injuries (Hewett et al., 2005; Ross et al., 2005; Zazulak et al., 2007). To reduce injury risks, joint excursions in frontal and transverse planes must be limited shortly after ground contact, when GRF are the largest. Whereas quadriceps muscles activation reduces knee joint flexion, the co-activation of quadriceps and hamstrings muscles increases knee joint stability (Baratta et al., 1988). In vitro studies suggested that hamstrings contraction reduces the knee internal rotation and the Anterior Cruciate Ligament (ACL) strain during quasi-static (Li et al., 1999; MacWilliams et al., 1999) and landing situations (Withrow et al., 2008). Since a muscle can produce larger magnitude of force during an eccentric contraction (Westing et al., 1991), Withrow et al. (2008) suggested that the strain of the ACL can be reduced by eccentric hamstring activations during landing tasks. They suggested that increasing hip flexion during ground contact would lengthen the bi-articular hamstrings Muscle Tendon Units (MTU), enabling

to reduce the ACL strain, but it has not been observed experimentally. Therefore, joint configuration at contact, and the time evolution of joint angles before contact, appear to be crucial to stabilise joints and protect the musculo-skeletal system, but have not been characterised yet. Moreover, the amount of force muscles can produce is multi-factorial (Zajac & Gordon, 1989). One key factor influencing the moment produced by a muscle at a given joint is its moment arm (Pandy, 1999). For mono-articular muscles, moment arms vary depending on joint configuration. For bi-articular muscles, such as rectus femoris, biceps femoris, semi tendinous and membranous for instance, moment arms depend on the two joints muscles span, which make it much more difficult to estimate. Force production capability of a bi-articular muscle thus depends on six degrees of freedom (the rotation around each axis for each joint) rather than three for mono-articular muscles. Joint configuration at contact thus appears important to enable muscles to produce large force and stabilise joints in presence of large GRF.

The majority of the literature suggests that these anticipatory muscle activations are time locked to the expected contact time (Jones & Watt, 1971a; Greenwood & Hopkins, 1976a; Dyhre-Poulsen et al., 1991; Duncan & McDonagh, 2000; Arampatzis et al., 2001; McDonagh & Duncan, 2002; Santello, 2005). This suggests that the rise in Electromyography (EMG) signal preceding contact, *i.e.* corresponding to the first motor commands, is manipulated by the nervous system to reach a larger value at contact, when the time rate change of linear momentum increases. However, when studying unexpected dropping tasks, (*i.e.* when instant of contact could not be predicted, some authors found that the timing of activation is rather related to the release time (Liebermann & Goodman, 2007; Konow & Roberts, 2024). This discrepancy may arise from two factors. First, when studying unexpected drop-landing in the lower and upper-limbs tasks, some authors recorded another burst of EMG, earlier than the one already identified (Greenwood & Hopkins, 1976b; Borrelli et al., 2020). This burst was related to the release time, was characterised as the consequence of a startle reaction, and its amplitude seemed to be related to the rate of change of vertical acceleration experienced (Greenwood & Hopkins, 1976b). Thus, it is possible that authors suggesting that timing of muscle activation is related to the release time indeed recorded consequences of a startle reaction to the drop release. Second, algorithms used to detect EMG onsets differ between studies (Santello & McDonagh, 1998; Liebermann & Goodman, 2007), which may explain differences in timings between studies (Hodges & Bui, 1996; Carvalho et al., 2023). For example, Liebermann & Goodman (2007) used a correlation function between the increase in EMG and time in the air, excluding neuromuscular factors indicating muscle activation contrary to methods using thresholds for example (Hodges & Bui, 1996). Moreover, authors did not specify if they only searched multiple muscle activations during the anticipatory period. Onsets of muscle activations in the literature ranged from 50 to 150 ms before ground contact, but air time preceding contact during a drop-landing task from more than 0.20 m is longer than 150 ms, and may thus enable multiple muscle activation before contact, as confirmed by the startle reaction recorded during unexpected landing tasks (Greenwood & Hopkins, 1976b). Whether multiple anticipatory activations can be present and play a biomechanical role in anticipation

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of a ground contact remains to be investigated.

In summary, it is clear that humans use anticipatory muscle activations *before* contact, to prepare their muscles to accelerate the whole-body upward *during* contact, depending on the expected amount of time rate change in linear momentum. Evidence suggest that anticipatory muscle activations are timed according to the expected contact time, but earlier muscle activations potentially due to startle reactions make this identification difficult. Finally, the kinematic consequences of these earlier muscle activations have not been investigated.

2.3.3 Strategies to limit the external force magnitude

In the previous section, we provided evidence that anticipatory muscle activations enable to accelerate the whole-body CoM upward during ground contact. However, minimising the impact of external forces is also important to protect the skeletal system and thus reduce injuries when experiencing a contact with an external support (Dufek & Bates, 1991; Devita & Skelly, 1992). This trade-off can be obtained by reducing the time rate change of linear momentum at the onset of ground contact. Consequently, a body of literature focused on kinematic landing techniques used by humans to minimise impact external force(s). During walking and running, impact forces are mainly determined by initial foot and leg orientation (Gerritsen et al., 1995), which in turn is mainly influenced by knee joint flexion at contact (Lafortune et al., 1996). It was further confirmed that technique, *i.e.* joint configuration and/or coordination, significantly influences the time rate change of GRF during running (Lieberman et al., 2010). During drop-landing tasks, which imply more momentum than running, Devita & Skelly (1992); Podraza & White (2010) showed that when humans experience lower GRF and joint moments with larger hip and knee joint flexion at ground contact. Simulating single-leg landings, Wakabayashi et al. (2021) also found that larger knee joint flexion at ground contact reduce the GRF. These joints configurations are suggested to enable a larger work production by the hip and knee joints during contact, but also require larger muscle activations (Devita & Skelly, 1992; Podraza & White, 2010).

These studies suggest that the joint configuration at ground contact is a determinant factor to protect the skeletal system. However, these studies quantified kinematics only *starting from* ground contact. To reach the flexed lower-limb joints configuration described at ground contact, humans can either (1) spend the whole air-time phase with joints in the final desired flexed configuration or (2) initiate joint flexions during the air-time phase preceding ground contact. Only the ankle joint was characterised during the air-time phase before ground contact and showed little to no kinematic adjustments, suggesting the first solution is used for the ankle joint (Santello & McDonagh, 1998; Santello, 2005). However, potential anticipatory kinematics adjustments of the hip and knee joints before ground contact have not been characterised. One study reported possible hip and knee angular velocity at ground contact, negatively correlated to the peak of vertical GRF (Yu et al., 2006). However, the results reported in this paper indicate a large heterogeneity in the hip

and knee angular velocity between participants: flexion angular velocity was not present in every participant at ground contact, some participants even presented extension angular velocity at ground contact; and the authors did not quantify any joint kinematics during the air-time phase. Yet, the presence of hip and knee angular velocity at ground contact in some participants might suggest that hip and knee joint flexions are initiated before ground contact. Hip and knee joint angles have been plotted during the last 100 ms before ground contact, where they seem to flex before ground contact (Devita & Skelly, 1992; Horita et al., 2002). But these results were obtained from limited 2D kinematic chain models, with few markers, approximating the hip joint centre to the great trochanter, which can affect both hip and knee joint flexion angle computation (Della Croce et al., 2005). Thus, it remains to clarify whether anticipatory kinematic adjustments exist at the hip and knee joints, and if there is a relationship between the anticipatory muscle activations and the temporal evolution of these lower-limb joint kinematic adjustments before ground contact.

If knee and hip joint flexion angles at contact enable to reduce the magnitude of GRF, one can assume that these joint flexion angles would increase when drop-landing from higher heights. However, there is no consensus on such relationship in the literature. McNitt-Gray (1991) and Yeow et al. (2010) did not find significant difference in hip and knee joint flexion angle at ground contact between different drop heights. More recently, Helm et al. (2020) and Waldvogel et al. (2023) described an increase in knee joint flexion angle at ground contact with an increase in drop height and gravity, respectively. The discrepancy may arise from little change in joint angles with increase in drop height. Indeed, Yeow et al. (2009b) described a natural logarithmic regression relationship between drop height (0.15 to 1.05 m) and knee joint flexion angle, meaning that knee joint flexion angle increase is low per drop height increase. For instance, when drop-landing from 0.3 and 0.6 m, the increase in knee joint flexion is only about 3 °.

Moreover, authors reported that hip and knee joint angles were more flexed at ground contact during drop-jumping (where the magnitude of GRF must be larger) compared to drop-landing (Hovey et al., 2021; Mache et al., 2013; Waldvogel et al., 2023). This joint configuration, associated with larger anticipatory muscle activations than in drop-landing, may favour the quick extension of the lower limb to initiate the following jump. Therefore, it remains to determine how flexed hip and knee joints at contact may contribute to reduce the magnitude of GRF during landing, but but also contribute to produce larger GRF during drop-jumping. The explanation may come from the quantification of the air-time kinematic adjustments. A main gap in the literature is to determine whether anticipatory muscle activations recorded in anticipation to contact have other mechanical consequences than the increase in stiffness, such as joint rotations.

In summary, whole-body joint configuration at ground contact is important to reduce GRF magnitude experienced during contact and protect the skeletal system. During activities with moderate momentum, it was suggested that joint flexion at contact can reduce the magnitude of GRF. However, studies of activities with larger momentum do not fully confirm this hypothesis. One possible explanation is the absence of characterisation of the

2.4. SUMMARY AND GOALS OF THE THESIS

anticipatory joint kinematics. Some evidence suggests that joint flexion angular velocity at contact may decrease the magnitude of GRF, but has to be confirmed.

2.3.4 Conclusion

In this section, we characterised how anticipatory muscle activations enable to cope with gravity during contact with an external support. We first described anticipatory muscle activations recorded during anticipation of contact, and noticed that their role was attributed to the increase in muscle and joint stiffnesses, to accelerate the whole-body CoM (or an object) upward. Amplitude of anticipatory muscle activations increases when the time rate change of linear momentum increases during the transition, to adapt joint stiffness. We then described kinematic configurations observed *at* the instant of contact that were associated to reduced GRF magnitude, which may consecutively contribute to protect the skeletal system. These two objectives are opposite and may not be achieved in all situations. We showed that the cause-effect relationship between the joint configuration and the magnitude of GRF remains unclear, and proposed that quantifying joint kinematics during anticipation of contact -as a consequence of anticipatory muscle activations- may clarify this relationship. Quantify anticipatory joint kinematics would also enable to understand MTU kinematics during anticipatory phase, and the configuration of bi-articular muscles to produce force and protect joints in presence of large GRF.

2.4 Summary and goals of the thesis

In this chapter, we showed that anticipation is necessary for executing efficient movements, because it enables to adapt movements to the conditions and constraints of the task. Analysis of the literature revealed that anticipation have been studied in two main, yet different, contexts during which there is a change in external forces acting on the whole-body: balance-movement coordination and anticipation of contact with an external support. Since these situations are ubiquitous in day-to-day life as well as in sport movements, anticipation must be clearly understood to ensure mobility for everyone, and to reduce sport-related risk injury. Based on this change in external forces acting on the whole-body, we introduced a mechanical framework of motor transitions to study anticipation, and describe situations in which which change of external forces acting on the whole-body are large and discrete, to better understand how the nervous system designs *favourable conditions* for movement execution through the use of anticipatory muscle activations.

The review of mechanical consequences of anticipatory muscle patterns during motor transition modifying balance-movement coordination illustrated the requirement of the nervous system to create a mechanical instability, which appears to be one of the *favourable conditions* for movement execution when a change of whole-body CoM velocity is intended. Balance-movement coordination is different during motor transitions than during steady balance states, suggesting this period must be studied with a different view. The contribution of the 'counter-rotating' mechanism is less clear during anticipatory phases of motor

transitions, either the action of different segments contribute to increase the mechanical instability or contribute to reduce the mechanical instability at a specific instant of the transition. The specific cases in which one or the other solution is used by humans has to be clarified, to help in developing better rehabilitation programs and supporting devices.

The review of mechanical consequences of anticipatory muscle activation preceding contact with an external support showed that anticipatory muscle activations are present, and have been characterised in terms of increasing muscle and joint stiffnesses. This increase in stiffness surely contributes to generate *favourable conditions* to accelerate the whole-body CoM upward *during* contact. However, since most studies only analysed periods *starting from* ground contact, consequences of anticipatory muscle activations *before* contact remain largely unexplored. In addition, the effect of joint configuration at contact remains unclear. Flexed lower-limb joint angles may help reducing the amount of GRF during contact in whole-body landing tasks, but the literature reported conflicting results on this interpretation. One possible reason is that coordination between multiple joints has not been considered. One way to explore the coordination between two adjacent joints is to quantify bi-articular MTU lengths. Moreover, joint angles influence muscle moment arms, which consequently influence force production capabilities. Some configurations, arising from anticipatory kinematic adjustments, may thus favour joint stabilisation, but remain to be investigated.

Thus, the global aim of the thesis is to complete the fundamental understanding on the underlying mechanisms the nervous system uses anticipatory muscle activations to generate *favourable conditions* during motor transitions. Given the gaps identified in this chapter, the four following objectives were established for this thesis:

- **First, to better characterise the use of the 'counter rotating' mechanism during motor transitions.** It remains unclear if the 'counter rotating' mechanism contributes to increase or decrease the necessary mechanical instability during motor transitions. In particular, the trunk is a segment with large inertial parameters, thus has a large influence in the whole-body dynamics. By comparing conditions with added masses to the trunk, we seek to highlight how the trunk is used to generate *favourable conditions* during motor transitions. This objective is covered in chapter 4.
- **Second, to characterise the kinematic consequences of anticipatory muscle activations before contact with the ground.** We studied drop-landing tasks because of the many advantages offered by this experimental paradigm: the contact time is easy to identify for both participants during the task and experimenters during data analysis; there is enough time before contact to observe potential kinematic changes; linear momentum is large at contact, suggesting that anticipatory actions are necessary to protect the skeletal system, and the change in linear momentum is easy to modify by modulating the drop-height and/or the task. By comparing different tasks involving drop-landing from different drop heights, we seek to understand how the nervous system modulates anticipatory muscle activations and resulting

2.4. SUMMARY AND GOALS OF THE THESIS

kinematic adjustments prior to contact to generate *favourable conditions* to the both the task and its constraints. This objective is covered in chapter 5.

- Third, to **characterise if there is different periods of anticipation before contact**. The majority of the literature quantified only one period of muscle activation before contact. Only during unexpected landing tasks a second **EMG** burst was recorded, and interpreted as a startle reaction. By computing all muscle activation periods before contact and analysing lower-limbs kinematics, we seek to determine whether multiple periods of anticipatory muscle activations exist, and to determine whether they could contribute to create additional *favourable conditions* to cope with gravity. Moreover, by comparing drop-landing tasks from different drop heights, we seek to determine if these additional periods of activation are related to the expected contact time or to the drop time. This objective is covered in chapter 6.
- Fourth, to **characterise the **MTU** lengths changes due to anticipatory kinematic adjustments**. Bi-articular **MTU** lengths are the result of coordination between two joint rotations. Through the characterisation of bi-articular **MTU** lengths, we seek to understand whether the nervous system coordinates multiple joints to create *favourable condition* to the task. Moreover, by characterising muscle moment arms at before and at contact, we aim to identify joint configurations favouring muscle force production and joint stabilisation. This objective is covered in chapter 7.

2.5 French summary

2.5.1 Coordination motrice, contrôle moteur et anticipation

Dans ce chapitre, nous avons montré que l'anticipation est nécessaire pour exécuter des mouvements de manière efficace, parce que cela permet d'adapter le mouvement aux conditions et contraintes de la tâche. L'analyse de la littérature a montré que l'anticipation a été étudiée dans deux principaux contextes durant lesquels il y a un changement distinct de forces extérieures agissant sur le corps complet : la coordination entre l'équilibre et le mouvement et l'anticipation d'un contact. Étant donné que ces situations sont omniprésentes, aussi bien dans la vie quotidienne que lors des activités sportives, l'anticipation doit être plus précisément comprise pour assurer la mobilité pour tout le monde, et réduire le risque de blessure. Basé sur le changement de forces extérieures agissant sur le corps complet, nous avons introduit le cadre de travail des transitions motrices afin d'étudier l'anticipation, de décrire les situations durant lesquelles il y a un changement net et important de forces extérieures, pour mieux comprendre comment le système nerveux apporte des *conditions favorables* pour l'exécution du mouvement grâce à l'utilisation d'activations musculaires anticipées.

2.5.2 Anticipation pour la coordination entre l'équilibre et le mouvement

Nous avons ensuite fait une revue de littérature des conséquences mécaniques des activations musculaires anticipées durant des transitions motrices, modifiant la coordination entre l'équilibre et le mouvement. Premièrement, nous avons détaillé les trois mécanismes qui permettent de réguler l'équilibre du corps complet, en modifiant l'accélération du corps complet : le déplacement du centre des pressions, le mécanisme de contre-rotation et l'application d'une nouvelle force extérieure. Le mécanisme du déplacement du centre des pressions a été le plus étudié, et consiste en la modification de la position du centre des pressions par rapport à la projection du centre de masse du corps complet au sol, afin d'accélérer le centre de masse du corps complet dans la direction opposée. Le mécanisme de contre-rotation concerne la rotation des segments qui ne sont pas en contact avec un support extérieur, et modifie la quantité de mouvement angulaire du corps complet. Ce mécanisme permet de modifier l'accélération du centre de masse du corps complet, notamment lorsque la projection du centre de masse du corps complet au sol est en dehors de la base de support. Le mécanisme d'application d'une nouvelle force extérieure implique les actions de pas de rattrapage ou d'appui du membre supérieur contre un support externe. Son fonctionnement est le même que la mécanique de déplacement du centre des pressions, sans que le déplacement du centre des pressions ne soit restreint par la taille de la base de support.

Après avoir détaillé la contribution des trois mécanismes durant des transitions motrices, nous avons montré que le système nerveux crée un état d'instabilité mécanique, qui apparaît comme étant une des *conditions favorables* à l'exécution du mouvement quand il y a un changement de vitesse du centre de masse du corps complet. La coordination entre l'équilibre et le mouvement est différente lors d'une transition motrice par rapport à un

2.5. FRENCH SUMMARY

état d'équilibre stable, ce qui suggère que les transitions motrices doivent être étudiées avec un point de vue différent. Nous avons montré que la contribution du mécanisme de contre-rotation ne fait pas consensus durant la période d'anticipation des transitions motrices : soit les actions des différents segments libres contribuent à augmenter l'instabilité mécanique, soit à réduire cette instabilité mécanique à un instant clé de la transition. Le détail des instants où les humains utilisent ce mécanisme pour augmenter ou limiter l'instabilité reste à être clarifié, pour aider à l'élaboration de programmes de rééducation ou le développement d'appareils d'assistance.

2.5.3 Anticipation du contact

Ensuite, nous avons fait une revue des conséquences mécaniques des activations musculaires anticipées précédant un contact avec un support extérieur. Nous avons tout d'abord adapté le cadre de travail des transitions motrices pour l'appliquer à ce cas-là. Ensuite, nous avons montré que les activations musculaires anticipées ont principalement été caractérisées en termes d'augmentation de la raideur musculaire et articulaire du membre inférieur. Cette augmentation de raideur devrait contribuer à générer des *conditions favorables* pour accélérer le centre de masse du corps complet vers le haut *durant* le contact. Cependant, étant donné que la majorité des études ont uniquement analysé la période débutant par le contact avec le sol, les conséquences des activations musculaires anticipées *avant* le contact avec le sol restent non explorées. De plus, l'effet de la configuration articulaire lors du contact reste flou. Toucher le sol avec des articulations du membre inférieur fléchies pourrait aider à réduire le pic de force de réaction du sol durant le contact, mais la littérature reporte des résultats non consensuels à ce propos. Une des raisons possibles est que la coordination entre plusieurs articulations du membre inférieur n'a pas été considérée. Une solution pour caractériser la coordination entre deux articulations adjacentes serait de quantifier les longueurs des complexes musculo-tendineux bi-articulaires. De plus, les angles articulaires influencent les bras de levier des muscles, qui représentent l'avantage mécanique d'un muscle et influence sa capacité de production de force. Certaines configurations, provenant d'ajustements cinématiques anticipés, pourraient alors favoriser la stabilisation des articulations face à d'importantes forces extérieures, mais cela reste à explorer.

2.5.4 Objectifs de la thèse

Ainsi, l'objectif global de la thèse est de compléter la compréhension fondamentale des mécanismes sous-jacents par lesquels le système nerveux utilise les activations musculaires anticipatives pour générer des conditions favorables lors des transitions motrices. Étant donné les manques identifiés dans ce chapitre, les quatre objectifs suivants ont été établis pour cette thèse :

- Premièrement, de mieux caractériser l'utilisation du mécanisme de contre-rotation durant des transitions motrices. Cela reste à déterminer si le mécanisme de contre-rotation contribue à augmenter ou à diminuer l'état d'instabilité mécanique nécessaire

pour effectuer une transition motrice. En particulier, le tronc est un segment avec d'importants paramètres inertiels, et a donc une forte influence sur la dynamique du corps complet. En comparant des conditions avec différentes masses ajoutées au tronc, nous avons cherché à mettre en évidence comment le tronc est utilisé pour générer des *conditions favorables* à l'exécution du mouvement durant des transitions motrices. Cet objectif est traité dans le chapitre 4.

- Deuxièmement, de caractériser les conséquences cinématiques des activations musculaires anticipées avant un contact avec le sol. Nous avons étudié différentes tâches de réceptions car elles offrent plusieurs avantages : l'instant de contact est facilement identifiable, aussi bien pour le participant que pour les expérimentateurs durant la phase d'analyse des données ; il y a suffisamment de temps avant le contact pour observer des potentiels ajustements cinématiques ; le changement de quantité de mouvement linéaire est important au contact, ce qui suggère que des actions anticipées sont nécessaires pour protéger le système squelettique ; la variation de quantité de mouvement linéaire est facilement modifiable en modulant la hauteur du saut et/ou la tâche. En comparant différentes tâches impliquant des réceptions de plusieurs hauteurs différentes, nous avons cherché à comprendre comment le système nerveux module les activations musculaires anticipées et les ajustements anticipés avant le contact pour générer des *conditions favorables* aussi bien à la tâche qu'à ses contraintes. Cet objectif est traité dans le chapitre 5.
- Troisièmement, de mieux caractériser les différentes périodes d'anticipation avant un contact. La majorité des études n'ont quantifié qu'une seule période d'activation musculaire avant un contact. Uniquement durant des tâches de réceptions non prévues, une seconde activation musculaire a été enregistrée et interprétée comme une réaction de sursaut. En identifiant toutes les activations musculaires avant le contact et en analysant les ajustements cinématiques du membre inférieur, nous avons cherché à déterminer si plusieurs périodes d'activation musculaires existent, afin de déterminer si elles peuvent contribuer à créer de nouvelles *conditions favorables* pour faire face à la gravité. De plus, en comparant des réceptions depuis plusieurs hauteurs, nous avons cherché à déterminer si ces nouvelles périodes d'activation musculaires sont programmées à partir de l'instant estimé du contact ou du début de la chute. Cet objectif est traité dans le chapitre 6.
- Quatrièmement, de caractériser les variations de longueurs des complexes muscles-tendons dues aux ajustements cinématiques anticipés. Les muscles bi-articulaires sont le résultat de la coordination de deux articulations. En caractérisant les variations de longueurs des muscles bi-articulaires, nous avons cherché à comprendre si le système nerveux coordonne plusieurs articulations afin de créer des *conditions favorables* à la réalisation de la tâche. De plus, en caractérisant les bras de levier musculaires avant et au contact avec le sol, nous avons cherché à identifier des configurations articulaires favorisant la capacité de production de force et donc la stabilisation de l'articulation. Cet objectif est traité dans le chapitre 7.

2.5. FRENCH SUMMARY

CHAPTER 3

Methods

Probability is not a mere computation of odds on the dice or more complicated variants; it is the acceptance of the lack of certainty in our knowledge and the development of methods for dealing with our ignorance

Nassim Nicholas (Fooled by randomness)

3.1 First experiment: Balance-movement coordination

3.1.1 Participants

Thirteen healthy participants (characteristics in table 3.1) were recruited for this study. All participants gave informed consent to the protocol in accordance with the institutional guidelines set by the Declaration of Helsinki. Exclusion criteria were: any musculoskeletal injury of the lower-limb during the six months preceding the experiment, any neurological impairment that could affect balance and coordination, and any contraindication to the practice of physical activity. All procedures were approved by the University ethics committee (CER-TP 2022-04-02).

Table 3.1: Participants characteristics for the study on balance-movement coordination, with average, standard deviation, minimal and maximal values of female, male, and total participants.

| | Female n = 4 | Male n = 9 | Total n = 13 |
|----------------------------------|---------------------------------|---------------------------------|---------------------------------|
| | average \pm std [min; max] | average \pm std [min; max] | average \pm std [min; max] |
| Age (<i>years</i>) | 22.8 \pm 1.7 [21; 25] | 23.8 \pm 5.0 [21; 37] | 23.5 \pm 4.2 [21; 37] |
| Height (<i>m</i>) | 1.61 \pm 0.02 [160; 164] | 1.77 \pm 0.07 [167; 185] | 1.72 \pm 0.09 [160; 185] |
| Body mass (<i>kg</i>) | 64.1 \pm 4.9 [60.2; 71.3] | 71.9 \pm 9.3 [62.0; 90.6] | 69.5 \pm 8.8 [60.2; 90.6] |
| BMI (<i>kg.m⁻²</i>) | 24.7 \pm 2.2 [23.2; 27.9] | 23.0 \pm 3.4 [20.4; 31.3] | 23.5 \pm 3.1 [20.4; 31.3] |

3.1.2 Protocol

The participants first performed a standing trial. They then performed five functional movements bilaterally, rotating each degree of freedom of the hip, knee, shoulder, lumbar and neck to compute joint centres. Then, participants initiated gait with their preferred stepping foot and walk up to a mark placed five meters away. After familiarisation, initial medio-lateral and antero-posterior feet location were marked in the force plates to ensure the repeatability of the initial states between trials and conditions (figure 3.1a), and their first stepping foot landing position was marked, to ensure the repeatability of the task. This was chosen because foot landing position has been correlated with whole-body **Centre of Mass (CoM)** velocity at first foot-off (Bancroft & Day, 2016). Participants initiated gait in three conditions, presented in a randomised order: a control condition, a condition with 6 % and a condition with 13 % of their body mass added to the trunk segment. The additional masses consisted of rigid barbells placed at shoulder level, evenly distributed between the front and the back of the trunk (figure 3.1a). Some non rigid masses, placed at the same place, were also used, to adjust the mass to each participant’s body mass. Participants performed three trials in each condition and were familiarised with the task and the added masses before any recording. Participants also performed other tasks during

this experiment (stepping, change of direction and walking on a beam, all with the three same conditions) that will not be detailed in this manuscript.

3.1.3 Measurements

The three-dimensional **Ground Reaction Forces (GRF)** and torques were recorded by ten force plates (400×600 mm, Sensix, Poitiers, France) sampled at 2000 Hz. Participants initiated gait with each foot over one force plate, the other eight force plates were used to record the first few steps (figure 3.1a). Fifty four reflective markers were placed on the participants' body, 36 on anatomical body landmarks and 18 as technical markers (figure 3.1b), detailed in table 3.4. Additional markers were placed on the barbells endpoints to quantify their position and inertial parameters. Markers three-dimensional trajectories were recorded by an optoelectronic system composed of 19 cameras (T40, Vicon, Oxford, UK) sampled at 200 Hz. Participants were also equipped with surface electromyographic electrodes on the leg and lower-back muscles, that will not be considered in this manuscript. All three measurement systems were synchronised using Vicon Nexus 2.12 (Vicon, Oxford, UK).

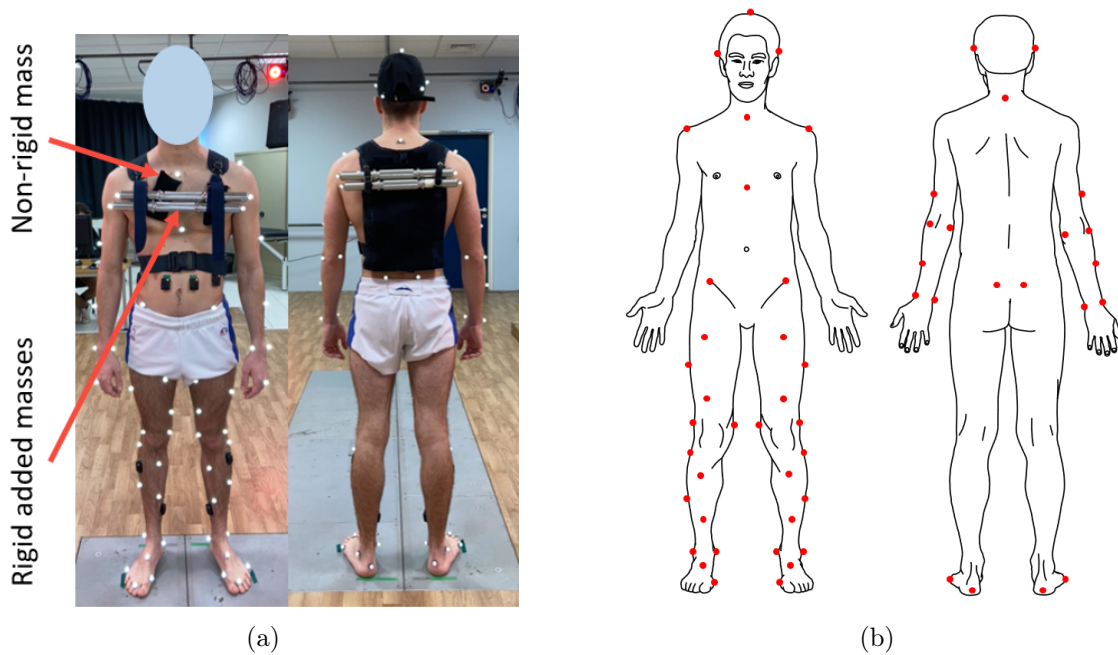


Figure 3.1: (a) Photography of a participants with 13 % added mass to the trunk, on the starting force plates. The four green marks on the force plates indicates the initial positions of the feet. (b) Anterior and posterior view of the markers (red dots) placement. Markers used in this study were placed on the head (5), torso (5) pelvis (4), thigh (2×5), shank (2×5), foot (2×4), upper-arm (2×3) and forearm (2×3).

3.1.4 Data Analysis

In this section, we will describe the data analysis performed for all data in this experiment. Data analysis performed specifically for each study will be described in detail in the corresponding chapter.

3.2. SECOND EXPERIMENT: ANTICIPATION OF CONTACT

3.1.4.1 Kinetic and kinematics

GRF and marker trajectories were filtered using a critically damped zero-phase low-pass filter at 50 and 20 Hz, respectively (Robertson & Dowling, 2003). A virtual force plate was created, as the sum of the filtered GRF of all force plates. A global moment was computed with respect to the origin of this virtual force plate, by adding the moment of each force plate with respect to the origin of the virtual force plate. Finally, the global Centre of Pressure (CoP) was computed in the global reference frame.

Functional movement trials recordings were used to compute joint centres. Hip joint centres were determined according to Halvorsen’s method (Halvorsen, 2003). Knee joint centres were determined as the middle of the femoral condyles, projected onto the axis of flexion (Ehrig et al., 2007). Ankle, elbow, and wrist joint centres were determined as the middle malleoli, humeral epicondyles, radial and ulna styloid processes, respectively. Lumbar, neck and shoulder joint centres were determined using the SCoRe method (Ehrig et al., 2006). Kinematic data were then resampled to 2000 Hz, to have the same timescale as the force plates and avoid approximation of any temporal event.

3.2 Second experiment: Anticipation of contact

3.2.1 Participants

Twenty young healthy adults (characteristics in table 3.2) practising a physical activity including jumps on a weekly basis were recruited for this study. All participants gave informed consent to the protocol in accordance with the institutional guidelines set by the Declaration of Helsinki. Exclusion criteria were: any musculoskeletal injury of the lower-limb during the six months preceding the experiment, any neurological impairment that could affect balance and coordination, and any contraindication to the practice of physical activity. All procedures were approved by the University ethics committee (CER-TP 2022-04-02).

Table 3.2: Participants characteristics for the study on anticipation of contact, with average, standard deviation, minimal and maximal values of females, males, and total participants.

| | Females | Males | Total |
|----------------------------------|---------------------------------|---------------------------------|---------------------------------|
| | n = 10 | n = 10 | n = 20 |
| | average \pm std | average \pm std | average \pm std |
| | [min; max] | [min; max] | [min; max] |
| Age (<i>years</i>) | 22.8 \pm 4.2 [17; 29] | 25.2 \pm 4.0 [17; 34] | 24.0 \pm 4.1 [20; 34] |
| Height (<i>m</i>) | 1.67 \pm 0.04 [1.62; 1.76] | 1.78 \pm 0.07 [1.67; 1.86] | 1.73 \pm 0.08 [1.62; 1.86] |
| Body mass (<i>kg</i>) | 60.9 \pm 4.7 [55; 72] | 69.7 \pm 8.2 [59; 84] | 65.3 \pm 8.1 [55; 84] |
| BMI (<i>kg.m⁻²</i>) | 21.7 \pm 2.4 [19.4; 27.4] | 22.0 \pm 2.2 [18.2; 24.5] | 21.9 \pm 2.3 [18.2; 27.4] |

3.2.2 Protocol

The participants first performed a standing trial designed to scale their anatomical posture to the generic whole-body kinematic chain model (figure 3.4a). They then performed five functional movements bilaterally, rotating each degree of freedom of the hip, knee, shoulder, lumbar and neck to compute joint centres. Finally, participants lied on the back on a massage table, to record the baseline **Electromyography (EMG)** muscle signals.

After a standardised 10-minute warm-up consisting of articular, muscular and plyometrics movements of the lower-limb such as squats, lunges, and hops, the participants performed two dropping tasks: i) drop-landing and ii) drop-jumping from two different drop heights: i) 0.35 m and ii) 0.50 m, randomly presented. Participants performed three trials for each task and drop height. Participants initially stood in an upright standing posture on a rigid elevated platform, with feet apart at approximately shoulder width (figure 3.2). They were instructed to always keep their hands on their hips, and to retrieve an upright standing posture at the end. The participants were instructed to leave the platform with both feet simultaneously, limiting upward jumping, and to land evenly on both feet, with one foot on each force-plate embedded in the ground. For the drop-landing tasks, the participants were instructed to amortise their landing as much as possible. For the drop-jumping task, they were instructed to minimise the ground contact time. The participants familiarised themselves with the tasks, the drop heights, and the instructions before any recording was taken.

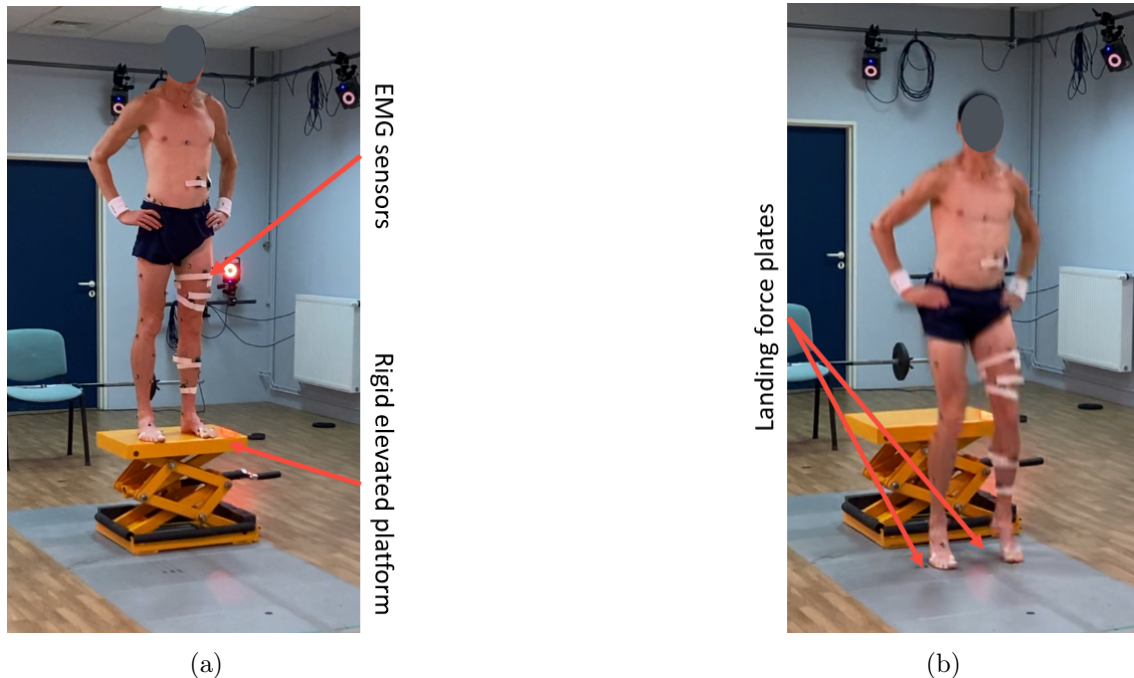


Figure 3.2: (a) Participant in the initial position on the rigid elevated platform. (b) Participant in contact with the two force plates during a drop-jumping task.

At the end of the protocol, the participants performed two passive stretching tests to determine the maximal length of each hamstring muscle length (Retailleau, 2019) (figure 3.3). For both tests, the participant lied on his back and the experimenter manipulated its

3.2. SECOND EXPERIMENT: ANTICIPATION OF CONTACT

degrees of freedom. To determine the maximal length of semitendinosus and semimembranosus, the knee of the participants is held in extension and the experimenter applied a force at the ankle level to induce a maximal hip flexion (figure 3.3a). To determine the maximal length of the biceps femoris long head, the experimenter maximally flexed the hip of the participant, without restriction in knee flexion, and then applied a force at the ankle level to induce a knee extension (figure 3.3b). During both tests, the experimenter checked the absence of hip rotation and abduction. Each test was repeated three times.

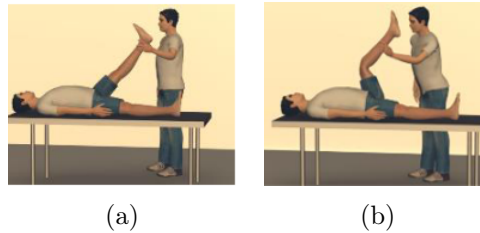


Figure 3.3: The two passive stretching tests used to determine the maximal length of the semitendinosus and semimembranosus (a) and for the biceps femoris long head (b). Images are taken from [Retailleau \(2019\)](#).

3.2.3 Measurements

Nine rectangular surface **EMG** electrodes (Trigno, Delsys, Natick, USA) with a bi-polar parallel bar electrode configuration and an inter-electrode distance of 10 mm were used to record the electrical activity of lower-limb muscles: tibialis anterior, soleus, gastrocnemii medialis and lateralis, vastii medialis and lateralis, rectus femoris, biceps femoris long head, and semitendinosus, (figure 3.4a) at 2000 Hz. Skin was shaved and cleansed with alcohol prior to **EMG** sensor placement. **EMG** sensors were positioned on the muscle belly so that the electrode bars were oriented perpendicular to the underlying muscle fibre direction ([De Luca, 1997](#)). After **EMG** sensors placement, a test muscle contraction was performed to confirm good position and skin-electrode contact. **EMG** sensors were secured with adhesive surface interface strips (Delsys Natick, USA) and double-sided elastic tape. **EMG** sensors were placed only on the dominant lower-limb of each participant, identified as the one used to perform a high jump or a long jump.

The three-dimensional **GRF** and torques were recorded by four force plates (400 × 600 mm, Sensix, Poitiers, France) embedded in the ground and sampled at 2000 Hz: two force plates underneath the elevated platform, and two others in the landing area. The vertical **GRF** under the elevated platform was set to zero when the elevated platform was already in place, to not consider its weight.

Sixty-four reflective markers were placed on the participants' body: 42 on anatomical body landmarks and 22 as technical markers (figure 3.4a), detailed in table 3.4. Their three-dimensional trajectories were recorded by an optoelectronic system composed of 19 cameras (T40, Vicon, Oxford, UK) sampled at 200 Hz. All three measurement systems were synchronised using Vicon Nexus 2.12 (Vicon, Oxford, UK).

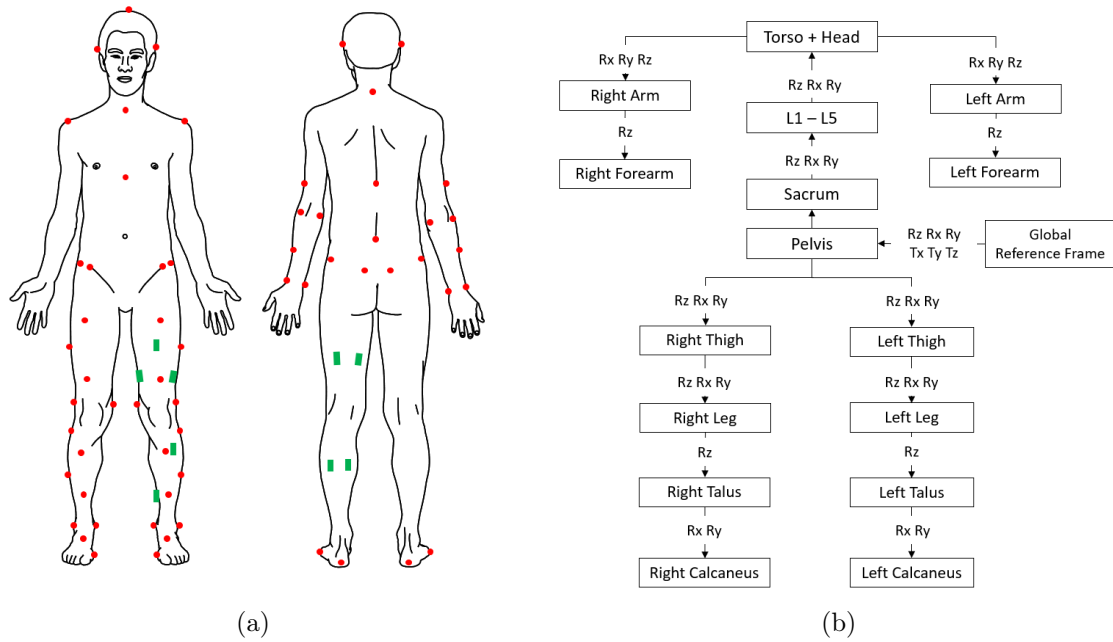


Figure 3.4: (a) Anterior and posterior view of the markers (red dots) placement and EMG sensors (green rectangles). Markers used in this study were placed on the head (5), torso (7) pelvis (8), thigh (2×5), shank (2×5), foot (2×4), upper-arm (2×3) and forearm (2×3). EMG sensors were placed on the dominant lower limb of each participant (see section 3.2). (b) Details of the lower limb kinematic model adapted from [Retailleau & Colould \(2020\)](#) and developed in OpenSim 4.3 ([Delp et al., 2007](#)), with the degrees of freedom allowed between the different segments. Abduction-adduction, internal-external rotation, and flexion-extension are noted Rx, Ry and Rz, respectively. Accordingly, translations are noted Tx, Ty and Tz.

3.2.4 Data Analysis

In this section, we will describe the data analysis performed for all data in this experiment. Data analysis performed specifically for each study will be described in detail in the corresponding chapter.

3.2.4.1 Kinetic and kinematics

To avoid possible undershoot or overshoot of the data around ground contact, GRF and marker trajectories were filtered using a critically damped zero-phase low-pass filter at 50 and 20 Hz, respectively ([Robertson & Dowling, 2003](#)). For each task, take-off from the rigid elevated platform was identified as the first instant when the vertical GRF was lower than 10 N, and ground contact was identified as the first instant when the vertical GRF of the corresponding force plate exceeded 1 N. We used a very small threshold to be sure we detected the first instant of contact. To be able to use such a small threshold, we reset both landing force plates between each trial, when nothing was on the force plates, to eliminate any deviation that could occur with time. For the drop-jumping tasks, the second take-off, after the landing, was identified as the first instant when the vertical GRF was lower than 10 N.

3.2. SECOND EXPERIMENT: ANTICIPATION OF CONTACT

Further analyses focused on the anticipatory phase, which corresponded to the air-time period preceding ground contact. For the drop-jumping task, only the anticipatory period preceding the first ground contact was analysed.

Functional movement trials were used to compute joint centres. Hip joint centres were determined according to Halvorsen’s method (Halvorsen, 2003). Knee joint centres were determined as the middle of the femoral condyles, projected onto the axis of flexion (Ehrig et al., 2007). Ankle, elbow, and wrist joint centres were determined as the middle malleoli, humeral epicondyles, radial and ulna styloid processes, respectively. Lumbar, neck and shoulder joint centres were determined using the SCoRe method (Ehrig et al., 2006). Kinematic data were resampled to 2000 Hz to have the same timescale as the force plates and avoid approximation of any event.

We performed a multi-body kinematic optimisation to reduce the impact of soft-tissue artefacts (Lu & O’Connor, 1999), using a kinematic chain model developed in OpenSim 4.3 (Delp et al., 2007), based on the model developed by (Retailleau & Colloud, 2020). The model consisted of 16 segments articulated by 14 joints and 35 degrees of freedom: the three positions and three orientations of the pelvis, and the 32 joint coordinates figure 3.4b). The anthropometric parameters of the model were scaled for each participant based on the quiet standing trial, using the OpenSim Scaling tool. The Scaling tool scales the segments lengths based on measurement of experimental markers, and then computes the distance between the experimental and the virtual markers over an entire acquisition. In Hicks et al. (2015), they suggested a maximal error between experimental and virtual markers threshold of 0.02 m, and a overall root mean square error threshold of 0.01 m. Here, because we mainly used bony landmarks and joint centres to perform the scaling, we used a maximal error threshold of 0.015 m. Maximal error and root mean square error for each participants are presented in table 3.3.

All marker data were then resampled at 2000 Hz, to have the same timescale as the force plates, and to avoid approximation of the ground contact time.

The foot trajectory was characterised by the trajectory of the midpoint between the first and the fifth metatarsal markers in the global coordinate system, because it is approximately where the centre of pressure is located after ground contact (Gross & Nelson, 1988). From this trajectory, the foot vertical velocity and acceleration were computed using a simple left derivative. The foot was considered to be accelerated upwards relative to a free-falling object when its acceleration was larger (i.e. closer to zero) than the acceleration of gravity, and continued to accelerate until ground contact. The pelvis vertical velocity was computed at the origin of the pelvis segment coordinate system, to represent a free-falling object.

3.2.4.2 Electromyography

The aim of the EMG analyses was to characterise periods of activation of different muscles during the anticipatory period before contact. To do so, we computed EMG envelopes with

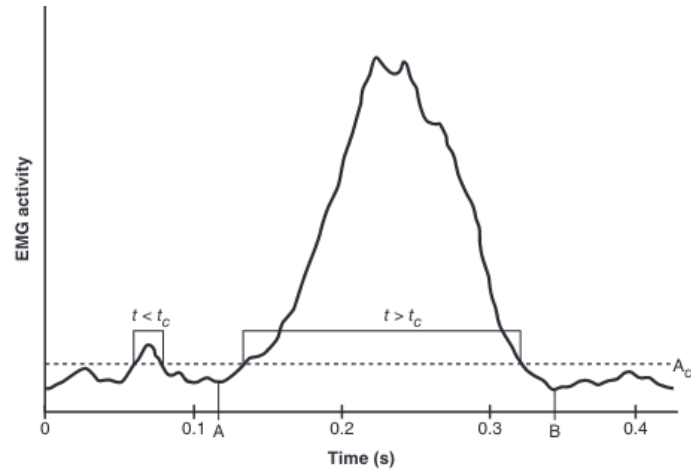
CHAPTER 3. METHODS

a second-order zero-phase low-pass Butterworth filter at 50 Hz, and obtained onsets of muscle activations using a double-threshold method (figure 3.5a: to be considered active, the EMG envelop had to be larger than an activation threshold during at least 25 ms (Hodges & Bui, 1996). The activation threshold of each participant was established as the average plus three standard deviations of the baseline signal recorded when participants were laying on their back. Offsets of muscle activations are less described in the literature. Here, we used the same criteria to characterise muscle offsets during the air time preceding ground contact (Walter, 1984), *i.e.* the EMG envelop had to be smaller than the activation threshold during at least 25 ms. Practically, we first considered each muscle active at take-off. We then computed the first muscle offset, to be sure that this onset is not related to the push-off phase initiating the task. Finally, we also computed the latency of muscle activation, defined as the timing relative to the drop onset (figure 3.5b).

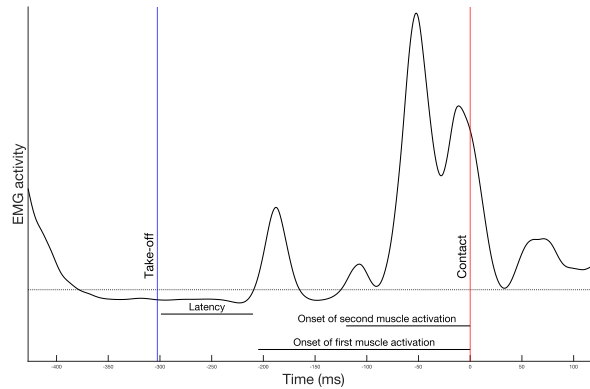
Table 3.3: Root mean square error and maximal error between experimental and virtual markers obtained in OpenSim after Scaling

| Participant | Root mean square error (m) | Maximal error (m) |
|-------------|--------------------------------|-----------------------|
| 1 | 0,0078 | 0,0134 |
| 2 | 0,0075 | 0,0117 |
| 3 | 0,0071 | 0,0116 |
| 4 | 0,0079 | 0,0134 |
| 5 | 0,0073 | 0,0115 |
| 6 | 0,0071 | 0,0119 |
| 7 | 0,0077 | 0,0121 |
| 8 | 0,0068 | 0,0108 |
| 9 | 0,0083 | 0,0132 |
| 10 | 0,0075 | 0,0121 |
| 11 | 0,0066 | 0,0114 |
| 12 | 0,0055 | 0,0106 |
| 13 | 0,0070 | 0,0127 |
| 14 | 0,0065 | 0,0099 |
| 15 | 0,0074 | 0,0110 |
| 16 | 0,0076 | 0,0128 |
| 17 | 0,0068 | 0,0108 |
| 18 | 0,0087 | 0,0135 |
| 19 | 0,0067 | 0,0093 |
| 20 | 0,0079 | 0,0130 |

3.2. SECOND EXPERIMENT: ANTICIPATION OF CONTACT



(a)



(b)

Figure 3.5: (a) Double threshold method used to detect muscle activation. The amplitude of the **EMG** envelop must be larger than the threshold A_C (dotted horizontal line), for a period larger than t_c , the second threshold, from [Walter \(1984\)](#). (b) Example of double activation recorded for a participant during the anticipatory phase preceding contact (vertical line in red) and after take-off (vertical line in blue). Latency represents the duration from take off to the first muscle activation, and onsets of the first and second muscle activation, the time from the first and second activation to contact.

3.3 French summary

3.3.1 Première expérience : Coordination équilibre-mouvement

Treize participants en bonne santé ont été recrutés pour cette étude. Leurs caractéristiques sont présentées dans la table 3.1. Tous les participants ont donné leur consentement pour le protocole en accord avec les recommandations fixées par la Déclaration d’Helsinki. Les critères d’exclusion étaient les suivants : aucune blessure musculo-squelettique au membre inférieur au cours des six derniers mois, aucune déficience neurologique susceptible d’affecter l’équilibre et la coordination, et aucune contre-indication à la pratique d’une activité physique. Toutes les procédures décrites dans la suite ont été approuvées par le comité d’éthique de l’Université (CER-TP-2022-04-22).

Les participants ont d’abord réalisé un essai où ils étaient debout en bougeant le moins possible. Ils ont ensuite réalisé cinq mouvements fonctionnels, entraînant des rotations de chaque degré de liberté des articulations de la hanche, du genou, des épaules, des lombaires et du cou pour calculer les centres articulaires. Ensuite, les participants ont initié la marche avec leur membre inférieur de prédilection et marché jusqu’à une marque située cinq mètres devant eux. Après une période de familiarisation, les positions médio-latérale et antéro-postérieure de leurs pieds étaient marquées au sol pour assurer la répétabilité de l’état initial de la transition durant le protocole. De plus, la position de leur premier pas était également marquée, car cette position a été corrélée avec la vitesse du centre de masse du corps complet lors du premier lever de pied (Bancroft & Day, 2016). Les participants ont ensuite initié la marche dans trois conditions présentées de manière randomisée : une condition contrôle, une condition avec 6 % et une condition avec 13 % de leur masse corporelle rajoutée au niveau du tronc. Les masses additionnelles consistaient en des altères rigides, positionnées au niveau des épaules, et réparties de manière équitable entre l’avant et l’arrière du tronc (figure 3.1a). Des masses non rigides étaient ajoutées pour ajuster à la masse de chaque participant. Les participants ont effectué trois essais pour chaque condition, et se sont familiarisés à la tâche pour chacune des conditions avant de réaliser des essais enregistrés. Les participants ont réalisé d’autres tâches durant le protocole (initiation du pas, changement de direction, marche sur une poutre, dans les trois conditions de masse) qui ne seront pas détaillées dans ce manuscrit.

Les forces et moments de réaction du sol ont été enregistrés par dix plateformes de force (400 × 600 mm, Sensix, Poitiers, France) à 2000 Hz. Les participants ont initié la marche avec un pied sur chaque plateforme, et les huit autres étaient utilisés pour enregistrer les premiers pas. Cinquante-quatre marqueurs réfléchissants étaient positionnés sur le corps des participants : 36 sur des points anatomiques et 18 en tant que marqueurs techniques (figure 3.1b). Des marqueurs additionnels étaient placés sur les extrémités des altères pour quantifier leurs positions et leurs paramètres inertiels. Les dimensions en trois dimensions des marqueurs ont été enregistrées par un système optoélectronique composé de 19 caméras (T40, Vicon, Oxford, UK) à 200 Hz. Les participants étaient également équipés d’électrodes électromyographiques sur les muscles de la jambe et des lombaires,

3.3. FRENCH SUMMARY

qui ne seront pas considérés dans ce manuscrit. Tous les systèmes de mesures étaient synchronisés grâce à Vicon Nexus 2.12 (Vicon, Oxford, UK).

Les données de forces de réaction du sol et les trajectoires des marqueurs ont été filtrées en utilisant un filtre passe-bas à atténuation critique (Robertson & Dowling, 2003) avec une fréquence de coupure de 50 et 20 Hz respectivement. Une plateforme de force virtuelle a été créée comme étant la somme de toutes les plateformes de force filtrées. A partir de cela, un moment de force global a été calculé par rapport à l'origine de la plateforme de force virtuelle, en ajoutant les moments de force de chaque plateforme par rapport à l'origine de la plateforme de force virtuelle. Enfin, la trajectoire du centre des pressions globale a été calculée dans le repère global.

Les mouvements fonctionnels ont permis de calculer les centres articulaires. Les centres articulaires des hanches ont été calculés avec la méthode d'Halvorsen (2003). Les centres articulaires des genoux ont été calculés comme étant le milieu des deux condyles fémoraux, projeté sur l'axe de flexion du genou (Ehrig et al., 2007). Les centres articulaires des chevilles, des coudes et des poignets ont été déterminés comme étant le milieu des malléoles, des épicondyles de l'humérus et des processus styloïdes du radius et de l'ulna, respectivement. Les centres articulaires des lombaires, du cou et des épaules ont été calculés avec la méthode SCoRe (Ehrig et al., 2006). Les données cinématiques ont ensuite été rééchantillonnées à 2000 Hz pour avoir la même échelle temporelle que les plateformes de force et éviter la moindre approximation temporelle.

3.3.2 Deuxième expérience : Anticipation du contact

Vingt participants en bonne santé ont été recrutés pour cette étude. Leurs caractéristiques sont présentées dans la table 3.2. Tous les participants ont donné leur consentement pour le protocole en accord avec les recommandations fixées par la Déclaration d'Helsinki. Les critères d'exclusion étaient les suivants : aucune blessure musculo-squelettique au membre inférieur au cours des six derniers mois, aucune déficience neurologique susceptible d'affecter l'équilibre et la coordination, et aucune contre-indication à la pratique d'une activité physique. Toutes les procédures décrites dans la suite ont été approuvées par le comité d'éthique de l'Université (CER-TP-2022-04-22).

Les participants ont d'abord réalisé un essai où ils étaient debout en bougeant le moins possible pour mettre à l'échelle la chaîne cinématique détaillée ci-après. Ils ont ensuite réalisé cinq mouvements fonctionnels, entraînant des rotations de chaque degré de liberté des articulations de la hanche, du genou, des épaules, des lombaires et du cou pour calculer les centres articulaires. Enfin, les participants ont réalisé un enregistrement allongé sur le dos sur une table de massage, pour enregistrer le signal électromyographique des muscles non-activés.

Après un échauffement standardisé de 10 minutes, les participants ont réalisé deux tâches de réception : un drop-landing et un drop-jumping depuis deux hauteurs : 0.35 et 0.5 m, présenté de manière randomisée. Les participants ont réalisé trois essais de chaque tâche

et depuis chaque hauteur. Les participants débutaient debout sur une plateforme rigide surélevée, avec les pieds à écartement d'épaules (figure 3.2). Ils devaient garder leurs mains sur les hanches durant toute la durée de la tâche et retrouver une posture érigée à la fin de la tâche. Il était demandé aux participants de quitter la plateforme avec les deux pieds simultanés, de limiter l'impulsion vers le haut, et de se réceptionner symétriquement entre les deux pieds, avec un pied sur chaque plateforme au sol. Pour les tâches de drop-landing, les participants devaient amortir le plus possible. Pour les tâches de drop-jumping, les participants devaient minimiser leur temps de contact au sol. Les participants ont pu se familiariser avec les tâches avant les enregistrements. A la fin du protocole, les participants réalisaient deux tests d'étirement passif pour déterminer la longueur maximale de chaque complexe muscle-tendon des ischio-jambiers (Retailleau, 2019) (figure 3.3).

Neuf électrodes électromyographiques (EMG) (Trigno, Delsys, Natick, USA) ont été utilisées pour enregistrer l'activité musculaire des muscles du membre inférieur : tibialis anterior, soleus, gastrocnemii medialis and lateralis, vastii medialis and lateralis, rectus femoris, biceps femoris long head, et semitendinosus, (figure 3.4a) à 2000 Hz.

Les forces et moments de réaction du sol ont été enregistrées par quatre plateformes de force (400 × 600 mm, Sensix, Poitiers, France) à 2000 Hz : deux plateformes étaient positionnées sous la plateforme rigide surélevée, et les deux autres étaient positionnées à l'endroit de la réception. Les plateformes ont été remises à zéro lorsque la plateforme rigide surélevée était positionnée dessus, afin de ne pas considérer sa masse. Soixante-quatre marqueurs étaient placés sur le corps des participants : 42 sur des points anatomiques et 22 en tant que marqueurs techniques (figure 3.4a). Les dimensions en trois dimensions des marqueurs ont été enregistrées par un système optoélectronique composé de 19 caméras (T40, Vicon, Oxford, UK) à 200 Hz. Tous les systèmes de mesure étaient synchronisés grâce à Vicon Nexus 2.12 (Vicon, Oxford, UK).

Pour éviter une variation trop importante des données autour de l'instant de contact avec le sol, les données de forces de réaction du sol et les trajectoires des marqueurs ont été filtrées en utilisant un filtre passe-bas à atténuation critique (Robertson & Dowling, 2003) avec une fréquence de coupure de 50 et 20 Hz respectivement. Pour chaque tâche, le décollage de la plateforme rigide a été identifié comme étant le premier instant à partir duquel la force de réaction verticale était inférieure à 10 N, et l'instant de contact avec le sol a été identifié quand la force verticale de la plateforme de force correspondante était supérieure à 1 N. Pour être capable d'utiliser un si petit seuil, nous avons remis à zéro les plateformes entre chaque essai, lorsque aucune force ne s'appliquait dessus, pour éviter des possibles dérives temporelles. Pour les tâches de drop-jumping, le second décollage, après la réception, était identifié comme étant le premier instant à partir duquel la force de réaction verticale des plateformes de force correspondantes était inférieure à 10 N.

Les mouvements fonctionnels ont permis de calculer les centres articulaires. Les centres articulaires des hanches ont été calculés avec la méthode d'Halvorsen (2003). Les centres articulaires des genoux ont été calculés comme étant le milieu des deux condyles

3.3. FRENCH SUMMARY

fémoraux, projeté sur l'axe de flexion du genou (Ehrig et al., 2007). Les centres articulaires des chevilles, des coudes et des poignets ont été déterminés comme étant le milieu des malléoles, des épicondyles de l'humérus et des processus styloïdes du radius et de l'ulna, respectivement. Les centres articulaires des lombaires, du cou et des épaules ont été calculés avec la méthode SCoRe (Ehrig et al., 2006). Les données cinématiques ont ensuite été rééchantillonnées à 2000 Hz pour avoir la même échelle temporelle que les plateformes de force et éviter la moindre approximation temporelle.

Les données cinématiques ont été traitées à partir d'OpenSim 4.3 (Delp et al., 2007) basé sur un modèle développé par (Retailleau & Colloud, 2020). Le modèle consistait en 16 segments articulés par 14 articulations et 35 degrés de liberté (figure 3.4b). Les paramètres anthropométriques étaient mis à l'échelle pour chaque participant avec la fonction Scaling d'OpenSim.

La trajectoire du pied a été caractérisée par le point au milieu des marqueurs du premier et cinquième métatarse dans le repère global. À partir de cette trajectoire, la vitesse et l'accélération verticale ont été calculées en utilisant la dérivée temporelle. Le pied était considéré accéléré vers le haut par rapport à un objet en chute libre lorsque son accélération était supérieure à celle de la gravité, et continuait à augmenter jusqu'au contact.

Pour détecter les périodes d'activation musculaire, nous avons utilisé la méthode du double seuil de Hodges & Bui (1996). Pour être considéré comme actif, l'enveloppe électromyographique (EMG) doit être supérieure à un seuil d'activation pendant au moins 25 ms (figure 6.1a). Le seuil d'activation de chaque participant a été établi comme étant la moyenne + 3 écarts types du signal lorsqu'ils étaient allongés sur le dos. La manière de détecter la fin d'une activation musculaire est beaucoup moins décrite dans la littérature. Ici, nous avons utilisé les mêmes critères que pour l'activation : l'enveloppe EMG doit être inférieure au seuil pendant au moins 25 ms.

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Table 3.4: Markers locations for each experiment. Names are based on (Wu et al., 2002, 2005; Dumas et al., 2007). Y = Yes, N = No

| Segment | Location | Number of markers | Bilateral | Balance-movement coordination | Anticipation of contact |
|-----------|---|-------------------|-----------|-------------------------------|-------------------------|
| Head | Head Vertex | 1 | N | Y | Y |
| | Sellion | 1 | Y | Y | Y |
| | Occiput | 1 | Y | Y | Y |
| Thorax | Processus Spinosus of the 7 th cervical vertebra | 1 | N | Y | Y |
| | Processus Spinosus of the 10 th thoracic vertebra | 1 | N | N | Y |
| | Processus Spinosus of the 1 th lumbar vertebra | 1 | N | N | Y |
| | Deepest point of Incisura Jugularis | 1 | N | Y | Y |
| | Most caudal point on the sternum | 1 | N | Y | Y |
| | Most lateral point on the lateral edge of the acromial process of scapula | 1 | Y | Y | Y |
| Pelvis | Anterior superior iliac spine | 1 | Y | Y | Y |
| | Posterior superior iliac spine | 1 | Y | Y | Y |
| | Side of the iliac crest | 2 | Y | N | Y |
| Thigh | Epicondylus femoris medialis | 1 | Y | Y | Y |
| | Epicondylus femoris lateralis | 1 | Y | Y | Y |
| | Frontal and medial sides of the thigh | 3 | Y | Y | Y |
| Leg | Tip of the medial malleolus | 1 | Y | Y | Y |
| | Tip of the lateral malleolus | 1 | Y | Y | Y |
| | Fontal and medial sides of the leg | 3 | Y | Y | Y |
| Foot | Posterior point of heel | 1 | Y | Y | Y |
| | Medial point on the head of first metatarsus | 1 | Y | Y | Y |
| | Lateral point on the head of fifth metatarsus | 1 | Y | Y | Y |
| | Anterior point of second toe | 1 | Y | Y | Y |
| | Superior face of the foot | 1 | Y | Y | Y |
| Upper-arm | Most caudal point on lateral epicondyle | 1 | Y | Y | Y |
| | Most caudal point on medial epicondyle | 1 | Y | Y | Y |
| | Lateral face of the upper-arm | 1 | Y | Y | Y |
| Arm | Most caudal-lateral point on the radial styloid | 1 | Y | Y | Y |
| | Most caudal-medial point on the ulnar styloid | 1 | Y | Y | Y |
| | Lateral face of the arm | 1 | Y | Y | Y |

3.3. FRENCH SUMMARY

CHAPTER 4

Balance-movement coordination: Gait initiation

All models are wrong but some models
are useful.

Georges Box

The experiment and part of the data analysis have been realised with the contribution of Alexis Bart, student in 1st year of master degree STAPS at Université de Poitiers.

Part of the results presented here has been presented at the 49th congress of Société de Biomécanique, at Compiègne in October, 2024 (Bechet et al., 2024a).

4.1 Introduction

Gait initiation is a posture to movement transition commonly used in the literature to investigate how the nervous system coordinates balance and movement (Yiou et al., 2017). Gait initiation involves a predictable change of base of support area (*i.e.* from bipedal to unipedal). Because this transition is predictable, a period of mechanical adjustments which has been considered as an anticipatory period precedes the first foot-off fulfilling two mechanical roles: (1) initiate the movement of the whole-body Centre of Mass (CoM), and (2) maintain balance despite the reduced mechanical stability at the end of the anticipatory period. During the anticipatory period of gait initiation, the nervous system seems to purposely create a situation of mechanical instability along the antero-posterior axis, using the mass of the whole-body and gravity to help initiate the forward whole-body movement and the transition between two steady balance states (Brenière et al., 1987; Lepers & Brenière, 1995) (see also section 2.2). However, the mechanical instability generated must be controlled to avoid falls (Cummings & Nevitt, 1989; Robinovitch et al., 2013). Therefore, it appears crucial to understand how balance is regulated during motor transitions to avoid falling situations.

Gait initiation has mainly been investigated through the 'moving the Centre of Pressure (CoP)' mechanism (section 2.2). Stereotyped anticipatory lower-limb muscle activations have been recorded and linked to CoP displacements (Crenna & Frigo, 1991; Brunt et al., 1991; Lepers & Brenière, 1995; Mickelborough et al., 2004). From CoP displacements leading to the first foot-off, two phases have been described to characterise dynamic processes during the anticipatory phase of gait initiation: (1) an *imbalance phase*, with a CoP displacement both backward and towards the future swing lower-limb, and (2) an *unloading phase*, with a lateral CoP displacement towards the stance lower-limb (Crenna et al., 2006). Using a linearised inverted pendulum model (equation (2.3)), the whole-body CoM kinematics has been inferred from these CoP displacements. Along the antero-posterior axis, the backward displacement of the CoP accelerates the whole-body CoM forward, and generates a state of mechanical instability. Along the medio-lateral axis, the whole-body CoM is accelerated towards the stance lower-limb during the imbalance phase, and then decelerated during the unloading phase to avoid a fall toward the stance lower-limb side. In the literature, adjustments along the medio-lateral axis were mainly related to balance maintenance (reviewed Yiou et al. (2017)), whereas adjustments along the antero-posterior axis were rather related to the movement execution and particularly the gait velocity at the end of the first step (Brenière et al., 1987; Lepers & Brenière, 1995), without consideration of balance. However, these studies mainly focused on the relative horizontal distance between the CoP and the projection of the whole-body CoM, and did not infer on the changes of Ground Reaction Forces (GRF) during the anticipatory period of gait initiation (Jian et al., 1993). Second, the 'counter-rotating' mechanism is not considered in the linearised inverted pendulum model (section 2.2.1.1), thus neglecting the contribution of the trunk and the upper-limb segments. Therefore, the contribution of this mechanism in gait initiation remains unclear. If this mechanism is present during gait initiation, it is

also not known if it contributes to the mechanical instability and/or balance maintenance. Thus, total understanding of balance-movement coordination during posture to movement transition is lacking.

Some anticipatory muscle activations that not contribute to CoP displacements have been reported during gait initiation, especially in the trunk muscles (Ceccato et al., 2009; Farinelli et al., 2021). Among the different segments that can modify the counter-rotation of the whole-body, the trunk might play a major role because it has large inertial parameters (mass and inertia tensor) compared to other free-rotating segments such as the upper-limbs. However, the contribution of the trunk segment during gait initiation is not yet fully understood. Computing H_M in this motor task could provide valuable insights and help address this gap in knowledge. In addition, Ceccato et al. (2009); Laudani et al. (2006) have shown a trunk flexion preceding foot-off. These observations should lead to a H_M directed forward around the medio-lateral axis during gait initiation. However, during the anticipatory phase of a stepping task, Begue et al. (2019) showed H_M displayed two distinct phases: H_M is first directed in a forward rotation, and then directed in a backward rotation during the second part of the anticipatory phase. This backward rotation could result from the stepping task, because it is a posture to posture transition, where the upper-body orientation needs to be better controlled to avoid an excessive rotational mechanical instability, rather than a posture to movement transition like gait initiation. The backward rotation could also result from the large inertia of the trunk segment (Begue et al., 2021), but this assumption has not been confirmed yet. In particular, the authors did not provide the time evolution of the contribution of the trunk to H_M (H_M^{Trunk}). Thus, how H_M evolves, and how the different segments contribute to modify H_M , remain to be clarified during gait initiation.

In addition to H_M , its time derivative (\dot{H}_M) is crucial for evaluating the coordination between balance and movement. In equations (2.1) and (2.2), \dot{H}_M is directly linked to the whole-body CoM of a linearised inverted pendulum (Hof, 2007). When \dot{H}_M around the medio-lateral axis is positive, meaning that H_M increases, it accelerates the whole-body CoM forward, and vice-versa. Thus, characterising the time evolution of both H_M and \dot{H}_M should help better infer on balance-movement coordination. Particularly, it would help differentiate the whole-body CoM acceleration due to the backward shift of the CoP, and the acceleration of the whole-body CoM due to variation in H_M . Moreover, characterising the time evolution of the contribution of individual body segments to H_M (H_M^i) would enable to link segment rotations to the whole-body CoM acceleration, and infer on their respective role to balance-movement coordination.

Because motor transitions depend both on the initial and final states (section 2.2.1.2), variations in initial state have been used to better understand the role and the modulation of anticipatory processes. For instance, Vieira et al. (2021) found quicker backward CoP shift when adding 10 % of the body mass at the shoulders level, but no difference when adding mass at the hips level. These results suggest that modifying the mass distribution of the trunk and, by consequence, the whole-body CoM location require adaptations of

4.1. INTRODUCTION

anticipatory processes to execute the task. As a consequence, orientation of the trunk seems crucial for whole-body CoM position due to its large body mass. However, the differences Vieira et al. (2021) found was only at the beginning of the anticipatory phase, probably as a result of additional masses placement. Moreover, they did not standardised the final state of the transition (*i.e.* whole-body CoM velocity or foot placement). Therefore, it is unclear whether the effects they reported or did not reported result from the mass condition or the execution of the task. To accurately infer the anticipatory processes involved during transition from one state to another, both the initial and final states must be consistent.

Using another experimental paradigm, Leteneur et al. (2013) confirmed the importance of the trunk segment contribution during gait initiation. Comparing two groups with the same gait velocity after the first step, they found that participants with a forward inclination of the trunk (forward leaners) had lower hip joint flexion moment than participants with a backward inclination of the trunk (backward leaners). They suggested that forward leaners probably benefit from the mass of the trunk to accelerate their whole-body CoM forward. However, they need to generate a larger lumbar extension joint moment before foot-off, indicating that the trunk inclination should to be limited during motor transition to avoid an excessive increase in mechanical instability. Since the trunk dynamic seems important during gait initiation, its contribution in balance-movement coordination of gait initiation appears crucial to understand. Modifying the mass distribution of the trunk could offer new insights into its contribution to H_M . Adding external masses to the trunk presents an interesting perspective, as it could help isolate and evaluate how changes in trunk mass affect the anticipatory control mechanisms during gait initiation, thereby clarifying the specific role of the trunk in balance-movement coordination.

The general aim of this study is to characterise the role of the counter-rotating mechanism, with a particular focus on the trunk segment, during the anticipatory phase of a posture to movement transition, specifically during gait initiation. We first investigate whether the two phases of the anticipation period identified previously during a stepping task (Begue et al., 2019) are also present during gait initiation. These two phases are identified as follow: (1) when the time derivative of H_M around the medio-lateral axis is negative, and (2) when the time derivative of H_M around the medio-lateral axis is positive. We hypothesise that this new phase delimitation will enable to identify when the whole-body falls forward, and when there are body segments contributing to a counter-rotation. We also hypothesise that the trunk is mainly responsible for the backward H_M . Moreover, to better highlight the role of the trunk, we compare three different trunk mass conditions, and hypothesise that the contribution of the trunk segment to H_M directed forward decreases with added mass, to limit trunk inclination and excessive mechanical instability. Finally, we compare the whole-body CoM acceleration and velocity between experimental results and results from the linearised inverted pendulum model, *i.e.* the 'moving the CoP' mechanism. If the trunk is both rotating backward and responsible for the increase in H_M , like during stepping initiation, we expect the whole-body CoM acceleration and velocity computed from the 'moving the CoP' mechanism to be lower than the ones from the experimental

results, because the counter-rotating mechanism would accelerate the whole-body CoM. If the trunk contribution to H_M is regulated by the added mass, we hypothesise the differences between whole-body CoM acceleration and velocity computed from experimental results and computed from the model to decrease with added mass.

4.2 Methods

Participants, procedure and measurements are described in [Methods \(First experiment: Balance-movement coordination\)](#). Briefly, 13 participants initiated gait from a quiet standing posture and walked for five meters, in three conditions: control, with 6 %, with 13 % of their whole-body mass added to the trunk. The first step length was normalised to ensure the repeatability of gait velocity.

4.2.1 Data Analysis

4.2.1.1 Kinematics and kinetics

Marker trajectories were low pass filtered at 10 Hz. From the filtered markers trajectories, centre of mass, mass, and inertia were computed for 13 segments (pelvis, trunk, head, upper-arms, arms, thighs, legs and feet) according to anthropometric tables from [Dumas et al. \(2007\)](#).

The whole-body CoM position was computed as the weighted sum of all segment positions (equation (4.1)). Whole-body CoM velocity and acceleration were computed as simple and double derivatives of the whole-body CoM position, respectively (See Nomenclature page [xix](#) for definition of all variables). The whole-body CoM acceleration was then low pass filtered using a critically damped zero-phase low-pass filter at 10 Hz ([Robertson & Dowling, 2003](#)).

$$\overrightarrow{OM} = \frac{\sum_{i=1}^n \overrightarrow{OM}_i \cdot m_i}{\sum_{i=1}^n m_i} \quad (4.1)$$

We computed the whole-body CoM acceleration predicted by the 'moving the CoP' mechanism using a linearised inverted pendulum model (equation (4.2)). We fixed the length of the pendulum l to 1. From the whole-body CoM acceleration, we computed the whole-body CoM velocity at each time frame f (equation (4.3)). For the first frame, the whole-body CoM velocity was initiated with the corresponding experimental value.

$$a_{M_x}^{model} = -\frac{(OP_x - OM'_x)FG_y}{m \cdot l} \quad (4.2)$$

$$v_{M_x}^{model}(f) = a_{M_x}^{model}(f)dt + v_{M_x}^{model}(f-1) \quad (4.3)$$

H_M was computed as the sum of the contribution of segment angular momenta (H_M^i)

4.2. METHODS

transferred to the whole-body CoM (equation (4.4)).

$$\overrightarrow{H_M} = \sum_{i=1}^n H_M^i = \sum_{i=1}^n [I_i \cdot \overrightarrow{\omega}_i + (\overrightarrow{OM}_i - \overrightarrow{OM}) \times m_i(\overrightarrow{v_{M}_i} - \overrightarrow{v_M})] \quad (4.4)$$

The number of segments n varied depending on the conditions. For the conditions with 6 % and 13 % body mass added, two and four barbell segments were added. Barbells CoM were estimated as the centre point of markers placed at each extremity (figure 3.1a). Their inertia were estimated with respect to their CoM based from the inertia of a solid cylinder along the z-axis (equation (4.5)).

$$I_b = \begin{bmatrix} m_b(\frac{r_b^2}{4} + \frac{m_b l_b^2}{12}) & 0 & 0 \\ 0 & m_b(\frac{r_b^2}{4} + \frac{m_b l_b^2}{12}) & 0 \\ 0 & 0 & m_b \frac{r_b^2}{2} \end{bmatrix} \quad (4.5)$$

H_M and each H_M^i were normalised by $h_p \cdot m_p \cdot \sqrt{g \cdot h_p}$, with h_p and m_p the height and mass of the participants, and g the gravitational constant (Gomez et al., 2024).

For each segment contribution to H_M (H_M^i), we extracted the instant when the time derivative (\dot{H}_M^i) first became positive and was leading to its maximum during the anticipatory period. This allowed us to determine when the segment started contributing to the backward rotation of the whole-body.

From the segment angular momenta, we computed the coefficient of cancellation κ by dividing the amount of cancelled H_M^i by the total magnitude of H_M (Bennett et al., 2010) (equation (4.6)).

$$\kappa_z = \frac{\sum_{i=1}^n |H_{M_z}^i| - |\sum_{i=1}^n H_{M_z}|}{\sum_{i=1}^n |H_{M_z}^i|} \quad (4.6)$$

The extrapolated centre of mass ($xCoM$) was computed using equation (4.7), with ω_0 the angular eigenfrequency of a pendulum equal to $\sqrt{\frac{g}{(OM_y - OM'_y)}}$.

$$\overrightarrow{xCoM} = \overrightarrow{OM} + \frac{1}{\omega_0} \cdot \overrightarrow{v_M} \quad (4.7)$$

The CoP was computed in the global reference frame. Antero-posterior CoP, CoM and xCoM positions were normalised by the length of the base of support, defined as the distance between the calcaneous and the second toe tip markers position during the first frame of the quiet standing period.

4.2.1.2 Temporal analysis

The anticipatory period of gait initiation started from the first instant when whole-body CoM velocity exceeded the average + 3 standard deviation measured during quiet standing, either in the forward direction or directed laterally towards the stance foot (Begue et al., 2021), and ended at the first foot-off, *i.e.* when the vertical GRF under the swing foot was lower than 10 N. We then divided the anticipatory period into two phases using two methods. First, we divided phases based on the CoP trajectory as it is classically done in the literature (Crenna et al., 2006): the *imbalance phase* starts at the beginning of the anticipatory phase, and ends when the CoP is the most directed towards the swing lower-limb; and the *unloading phase* starts at the end of the imbalance phase, and ends at the end of the anticipatory period. Second, we divided phases based on H_M temporal evolution: a first phase from the start of the anticipatory period to the first instant the time derivative of H_M (\dot{H}_M) became positive, and a second phase during the remaining of the anticipatory period (figure 4.1). We normalised the two phases based on (\dot{H}_M) independently, and concatenated them, taking their relative duration into account, to create a time vector from 0 to 100 %.

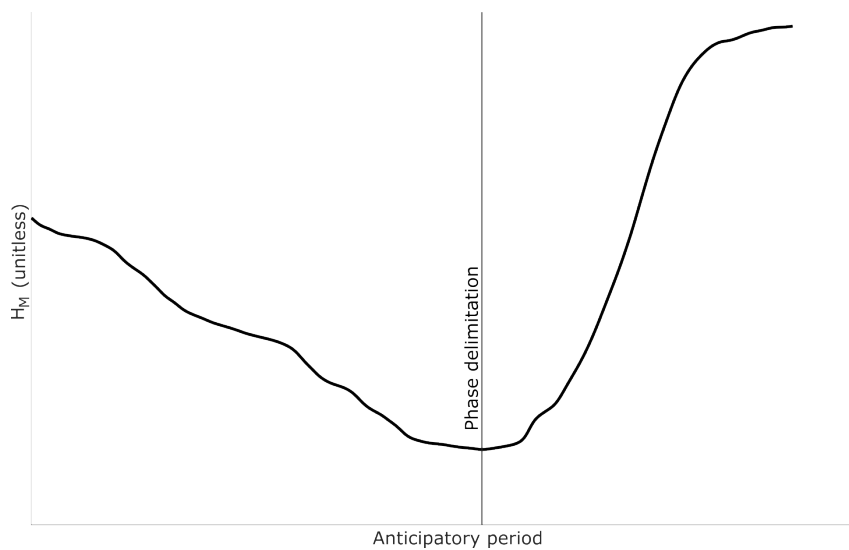


Figure 4.1: Example a typical trial, with H_M around the medio-lateral axis represented, and the phase delimitation, defined the first time the time derivative of H_M (\dot{H}_M) became positive, and a second phase during the remaining of the anticipatory period, thus when H_M increases.

4.2.1.3 Trials considered

We chose to analyse only one trial per condition per participant. For each participant, the three selected trials (one per mass condition) were chosen so that the difference in whole-body CoM velocity at first foot-off was minimised between the trials. This choice was made to improve the repeatability between the gait initiation trials because step length has been correlated with whole-body CoM velocity at first foot-off (Bancroft & Day, 2016).

4.3. RESULTS

4.2.2 Statistical analyses

Statistical analyses were performed using Matlab (MathWorks, version 2021b). We tested the normality of the discrete data using a Shapiro-Wilk test. Because the null hypothesis was rejected for multiple variables, we then performed non-parametric tests. First, we tested the effect of the mass condition on the initial state (*i.e.* whole-body CoM and CoP position at the beginning of the anticipatory period) and final state (*i.e.* whole-body CoM velocity at foot-off) using a Friedman test.

Next, we tested the effect of the mass condition on the entire anticipatory period duration, as well as on the duration of the imbalance and unloading phases and on the duration of the two new phases we defined based on \dot{H}_M , using a Friedman test. We tested whether the two methods of dividing phases result in different phases duration using a Wilcoxon signed rank test, regardless of the mass condition. Then, we tested the effect of the mass condition on the onset of segment backward contribution, using a Friedman test.

For each continuous data, we tested the effect of the mass with a non-parametric [Statistical Parametric Mapping \(SPM\)](#) during the total anticipatory period ([Nichols & Holmes, 2002](#); [Pataky, 2010](#)). When we found a significant effect, we compared the three conditions non-parametric post-hoc tests. Finally, we compared H_M^{Trunk} and $H_M^{Trunk+additionalMasses}$ around the medio-lateral axis with a non-parametric comparison between paired values using non-parametric [SPM](#).

4.3 Results

4.3.1 Centre of pressure and whole-body centre of mass

The time evolution of the antero-posterior CoP, whole-body CoM, xCoM, and whole-body CoM velocity are presented in figure 4.2a. First, there was no difference in both the initial and final states across the three different mass conditions (table 4.1 and figure 4.2a). As classically defined in the AP direction, the CoP first exhibited a backward shift until the end of the imbalance phase, then moved forward before exhibiting a second backward shift until foot-off. The [SPM](#) analysis revealed that the backward CoP shift was lower in the two conditions with added mass compared to the control condition, both from 40 to 51 % of the anticipatory period. There was no difference between mass conditions for the whole-body CoM, xCoM and whole-body CoM velocity curves. These three variables continuously increased from the beginning of the anticipatory period to foot-off. Around 80 % of the anticipatory period, the projection of the xCoM on the ground exited the forward limit of the base of support.

4.3.2 Phases of anticipation

We found no effect of the added mass on the total duration of anticipatory processes, and neither on the duration of each of the two phases, both for phases usually described in the literature or the two phases we characterised based on the change of sign of \dot{H}_M

Table 4.1: Comparison of initial state (whole-body CoM and CoP positions at the beginning of the anticipatory period), final state (whole-body CoM velocity at foot-off), and durations of anticipatory period and phases between the three different mass conditions.

| | | Control | 6 % added mass | 13 % added mass | <i>p</i> value |
|-------------------------------------|--|----------------------|----------------------|----------------------|-------------------|
| | | median [Q1; Q3] | median [Q1; Q3] | median [Q1; Q3] | |
| Initial state | CoP position (<i>normalised</i>) | 40.6 [32.6, 43.8] | 37.6 [35.7, 44.2] | 35.6 [33.4, 42.2] | 0.93 |
| | Whole-body CoM position (<i>normalised</i>) | 41.9 [37.4, 45.9] | 41.3 [37.8, 45.4] | 43.8 [38.1, 47.7] | 0.23 |
| Final state | Whole-body CoM velocity (<i>m.s</i> ⁻¹) | 0.35 [0.30, 0.39] | 0.34 [0.29, 0.40] | 0.36 [0.29, 0.38] | 0.58 |
| Durations of anticipatory phases | Anticipatory period duration (<i>ms</i>) | 597 [478, 664] | 636 [551, 750] | 610 [544, 716] | 0.12 |
| | Imbalance duration (<i>ms</i>) | 295 [247, 337] | 282 [260, 338] | 228 [203, 333] | 0.50 |
| | Unloading duration (<i>ms</i>) | 308 [225, 333] | 303 [272, 448] | 345 [278, 349] | 0.13 |
| | Negative \dot{H}_M duration (<i>ms</i>) | 366 [334, 393] | 406 [347, 466] | 349 [301, 444] | 0.37 |
| | Positive \dot{H}_M duration (<i>ms</i>) | 194 [174, 285] | 253 [182, 284] | 250 [229, 261] | 0.40 |

(table 4.1). We found that the first phase we computed based on the change of sign of \dot{H}_M was significantly longer than the imbalance phase (median [first, third quartile], 373 [325, 405] and 275 [228, 336] ms, respectively, $p < 0.001$) (figure 4.2b). On average, this first phase ended at 60 % of the anticipatory period, and the imbalance period at 47 % of the anticipatory period.

4.3.3 Whole-body angular momentum and segment contribution to whole-body angular momentum

H_M and the coefficient of cancellation κ for each condition are presented in figure 4.2b. SPM analysis revealed no effect of the condition for these two parameters. H_M was around zero during the first 20 % of the anticipatory period, and then directed forward until the change of sign of \dot{H}_M . During this period, the coefficient of cancellation κ decreased and was close to zero. In particular, κ was close to zero and constant during the time period between the end of the imbalance phase and when the sign of \dot{H}_M changes. During the second phase, when \dot{H}_M increased, both H_M and κ increased until the end of the anticipatory period, *i.e.* the foot-off. Particularly, the variability in κ decreases at the end of the anticipatory period. These curves were similar for each participant, despite some differences in timings.

4.3. RESULTS

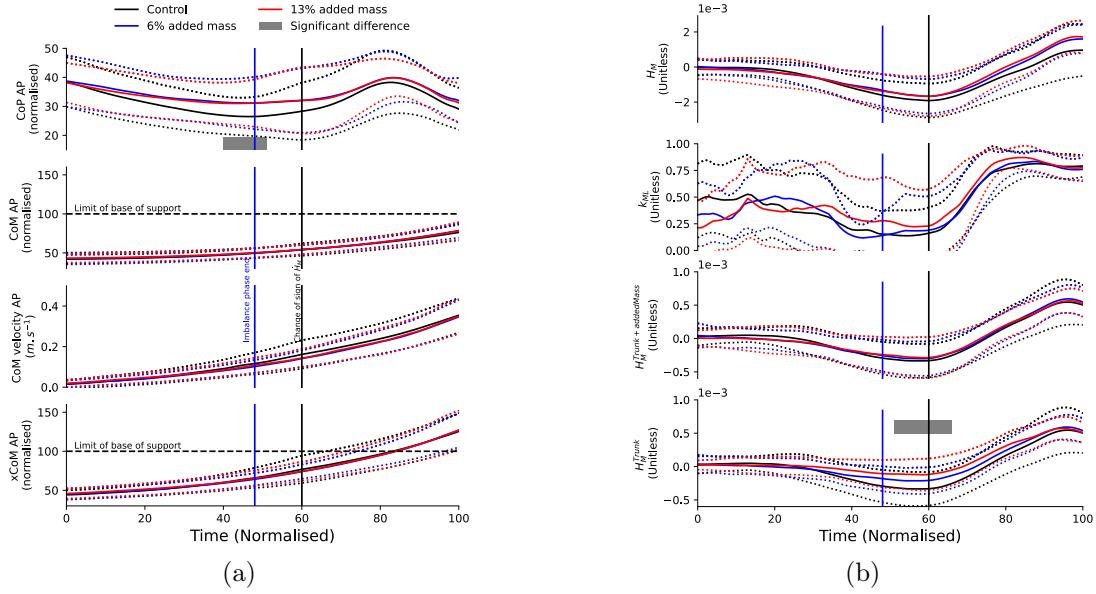


Figure 4.2: Average (continuous lines) and standard deviation (dotted lines) of main continuous variables computed during the anticipatory phase of gait initiation, from 0 %, the onset of the movement, to 100 %, the first foot-off, in the control (black), 6 % (blue) and 13 % (red) added mass to the trunk conditions. Black vertical lines represent the time when the sign of \dot{H}_M changes. Blue vertical lines represent the averaged end of the imbalance phase. Grey rectangles represent the statistical differences computed using SPM. (a) Antero-posterior CoP, whole-body CoM, whole-body CoM velocity and extrapolated centre of mass (from top to bottom) (b) H_M , κ coefficient, H_M^{Trunk} with additional masses, H_M^{Trunk} without the additional masses (from top to bottom), all around the medio-lateral axis.

Segment contributions to H_M (H_M^i) are presented in figure 4.3. With additional masses compared to the control condition, SPM analyses revealed an increase in H_M^{trunk} (*i.e.* closer to zero) from 51 to 66 % of the anticipatory period, an increase in the swing thigh contribution from 89 to 100 %, a decrease in the pelvis contribution from 67 to 100 %, and a decrease in the stance thigh contribution from 92 to 100 %. All post hoc tests were not significant. Finally, we found no influence of the added masses to H_M^{trunk} (figure 4.2b).

Four body segments were identified to have a clear change in the time rate change of H_M^i (\dot{H}_M^i) (figure 4.3): the trunk and the three segments of the swing lower-limb. The first segment to exhibit a counter rotation was the swing thigh that started at 45.2 % [40.9, 52.2] (median [first quartile, third quartile]), 48.5 % [43.4, 55.9] and 44.8 % [36.4, 56.1] of the anticipatory period, respectively for the control, 6 % and 13 % added mass conditions, with no difference between the three conditions ($p = 0.92$). Following was the swing leg that started counter rotating at 50.1 % [44.7, 55.7], 52.5 % [45.3, 53.5] and 54.8 % [46.6, 56.6], respectively for the control, 6 % and 13 % added mass conditions, with no difference between the three conditions ($p = 0.79$). After that, the trunk segment started the counter rotation at 58.9 % [57.2, 60.0], 58.10 % [53.1, 59.1] and 58.8 % [55.5, 60.0], respectively for the control, 6 % and 13 % added mass conditions, without difference between the three conditions ($p = 0.07$). Finally, the swing foot started the counter rotation at 82.1 % [72.6,

85.6], 77.3 % [70.9, 83.0] and 81.7 % [76.4, 85.2], respectively for the control, 6% and 13 % added mass conditions, without difference between the three conditions ($p = 0.79$). For the pelvis and the head segments, a clear change of sign of \dot{H}_M^i was not present in every participant, and thus is not presented in figure 4.3.

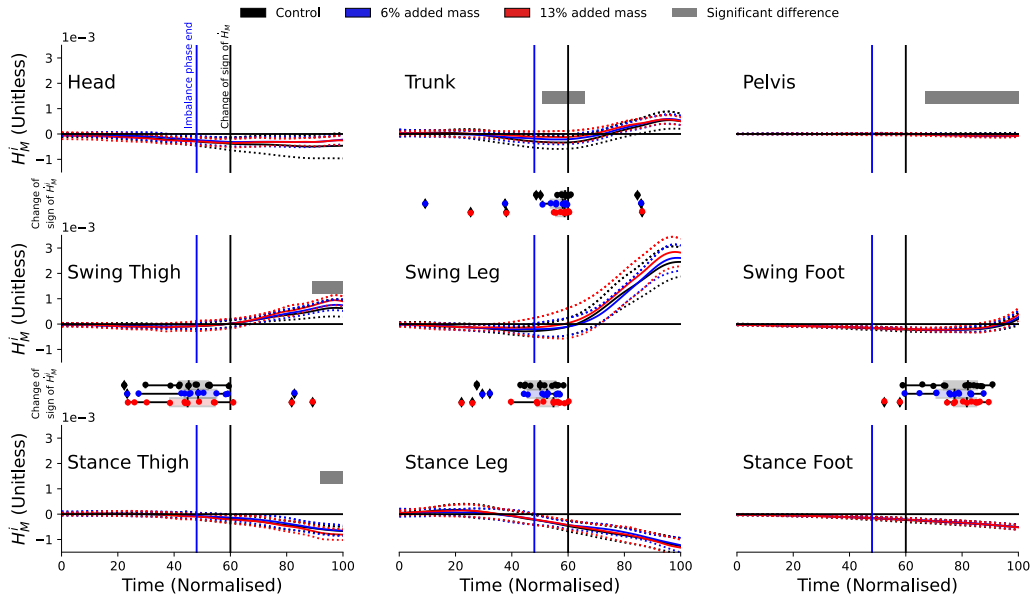


Figure 4.3: Average (continuous lines) and standard deviation (dotted lines) of the segment contribution to H_M around the medio-lateral axis during the anticipatory phase of gait initiation, from 0 %, the onset of the movement, to 100 %, the first foot-off, in the control (black), with 6 % (blue) and 13 % (red) added mass to the trunk conditions. Black vertical lines represent the time when the sign of \dot{H}_M changes. Blue vertical lines represent the averaged end of the imbalance phase. Horizontal lines represent the null contribution of the given segment. Grey rectangles represent the statistical differences computed using SPM. Horizontal boxplots represents the instants when the sign of \dot{H}_M^i changes, with individual values indicated by the points. We only presented segments for which the change of sign was observed in all participants.

4.3.4 Comparison between experimental and modelled whole-body CoM kinematics

Figure 4.4 presents the whole-body CoM accelerations and velocities computed for both the experimental data and the inverted pendulum model, in the three mass conditions. Experimental whole-body CoM acceleration was larger than the whole-body CoM acceleration computed with the model during the second phase, *i.e.* when \dot{H}_M is positive, from 57 to 100 %, 67 to 96 % and 78 to 92 % of the anticipatory period for the control, 6 % and 13 % added mass conditions, respectively. Experimental whole-body CoM velocity was also larger than the whole-body CoM velocity computed with the model at the beginning and at the end of the anticipatory period, from 0 to 100 %, from 4 to 10 % then from 85 to 100 %, and from 4 to 7 % then from 95 to 97 % for the control, 6 % and 13 % added mass conditions, respectively.

4.4. DISCUSSION

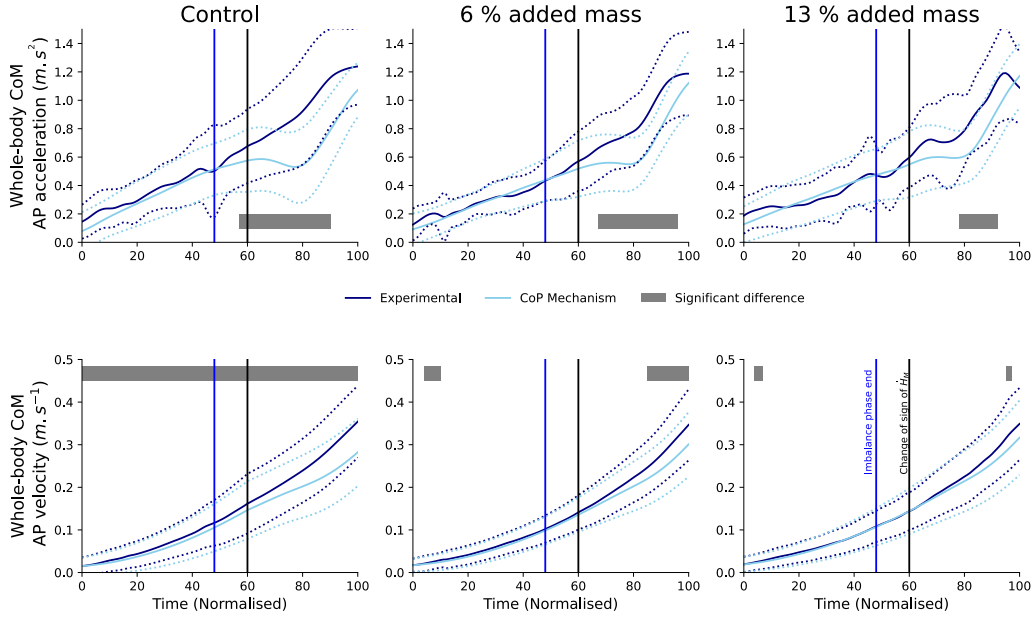


Figure 4.4: Average (continuous lines) and standard deviation (dotted lines) of the whole-body CoM acceleration (upper panel) and velocity (lower panel) computed with experimental data (dark blue) and an inverted pendulum model (light blue) during the anticipatory period of gait initiation. Duration goes from 0 %, the onset of the movement, to 100 %, the first foot-off. Panels display results in the control (left), with 6 % (middle) and 13 % (right) added mass conditions. Black vertical lines represent the time when the sign of \dot{H}_M changes. Blue vertical lines represent the averaged end of the imbalance phase. Grey rectangles represent the statistical differences computed using SPM.

4.4 Discussion

The aim of this study was to characterise the role of the counter-rotating mechanism during the anticipatory period of a posture to movement transition: gait initiation. We quantified H_M during the anticipatory phase, and divided this period into two phases based on \dot{H}_M . During the first phase, the whole-body rotated forward, with the contribution of almost every segments (figures 4.2b and 4.3). During the second phase, both the trunk and the swing lower-limb contributed to rotate the whole-body backward, probably to limit the rotational mechanical instability generated during the first phase. When adding mass to the trunk, the trunk contribution to H_M (H_M^{trunk}) decreased, suggesting that (1) inertial parameters are integrated by internal models, and (2) the whole-body dynamic is adjusted by the nervous system to perform the same movement. Finally, the differences between whole-body CoM acceleration and velocity computed with experimental data and with a model representing the CoP mechanism decreased, further suggesting that the trunk counter-rotation decreases when it weights more. As a result, the whole-body seems to act more like a simple inverted pendulum when masses are added and more like a double inverted pendulum in the control condition.

4.4.1 Protocol validation

One of our objectives was to clarify the contribution of the trunk during gait initiation, by comparing three trunk mass conditions. To infer on the role of the trunk and limiting confounding factors, we added masses symmetrically between the front and the back of our participants' trunk. As a result, the initial state of the transition, characterised by the antero-posterior CoP and whole-body CoM position during the quiet standing posture, did not differ between conditions (table 4.1). Moreover, contrary to the literature (Azuma et al., 2007; Caderby et al., 2017; Vieira et al., 2021), we specifically instructed our participants to reproduce the same step length during the three conditions, because step length has been correlated with whole-body CoM velocity at first foot-off (Bancroft & Day, 2016), and should help harmonise anticipatory processes between conditions. For each participants, we analysed the most similar trials in term of whole-body CoM velocity at foot-off to ensure that we compared identical tasks. Hence, we did not have difference for the final state (*i.e.* whole-body CoM velocity at first foot-off) between the three mass conditions (table 4.1). The absence of differences in the initial and final states between conditions with different masses added to the trunk segment confirms that the same motor transition was performed across conditions, reducing the confounding factors that could be present in our subsequent analyses.

4.4.2 Two phases of anticipation during gait initiation

The first aim of this study was to identify whether the two phases of anticipation identified during a stepping task (Begue et al., 2019) were also present during gait initiation. We found that these two phases were also present during gait initiation. The first phase is characterised by a decrease in H_M around the medio-lateral axis (*i.e.* a negative \dot{H}_M) (figure 4.2b), contributing to accelerate the whole-body CoM backward. This first phase is also characterised by a low coefficient of cancellation κ (figure 4.2b), meaning that the majority of segment angular momenta are generated forward. This phase is longer than the imbalance phase described in the literature (Crenna et al., 2006), suggesting that the phase of required rotational mechanical instability lasts longer than the period characterised by the first backward CoP shift alone. At the end of this first phase, the CoP has already begun to shift forward, but not by a large magnitude. During this time, the whole-body continued to rotate forward, without any regulation, because of the absence of segment counter rotation characterised by a low coefficient of cancellation κ until the end of the first phase (figure 4.2b).

The second phase we quantified is characterised by an increase in H_M around the medio-lateral axis (*i.e.* a positive \dot{H}_M), contributing to accelerate the whole-body CoM forward (equation (2.1)). This second phase goes along with a large increase in κ , showing that segment rotations cancel each other out (figure 4.2b). Moreover, the standard deviation of κ decreased during this second phase until foot-off, suggesting that the strategy of counter-rotating segments is used similarly by all participants during this phase. The backward oriented rotation of H_M has already been described during a stepping task (Begue et al.,

4.4. DISCUSSION

2021), a posture to posture transition, where the use of the counter rotating mechanism could have contributed to better control the upper-body orientation in anticipation for the final state. Like in the stepping task, we quantified an increase in H_M during the end of gait initiation, that cannot be related to an anticipation of the final state because participants walked on for 5 meters. We can thus suggest that the counter rotation we observed illustrates a regulation mechanism enabling to limit the whole-body forward rotation and the rotational mechanical instability generated during the first phase, *i.e.* when \dot{H}_M is negative. This suggests that posture to movement transitions are not only a period of required instability, with a free fall of the whole-body as suggested by the throw and catch model (Bancroft & Day, 2016). Even if the body is indeed falling during the first phase, characterised by the low coefficient of cancellation κ , trunk adjustments are present during the remaining of the anticipatory period of gait initiation. This balance regulation during the second phase of the anticipatory period aligns with results of Tisserand et al. (2018), where the vestibular influence on balance increases again at the end of the anticipatory period. It remains to be confirmed that (1) the timing coincides with our phases delimitation and/or, (2) if it exists for other sensory input modalities such and visual or proprioceptive information.

Contrary to our hypothesis, the change of sign of \dot{H}_M did not mainly resulted from the trunk segment. The swing thigh and swing leg first contributed to generate the backward H_M , and were then followed by contributions of the trunk and the swing foot (4.3). An initial backward contribution of the swing lower-limb makes sense because it corresponds to the swing hip flexion required to initiate gait. The increase in $H_M^{SwingThigh}$ and $H_M^{SwingLeg}$ even preceded the increase in H_M , reducing the absolute value of \dot{H}_M . Once \dot{H}_M was near zero, the trunk also started to contribute to increase H_M (figure 4.3). The contribution of the trunk to the increase in H_M at the end of the first phase aligns with muscle activations recorded in the erector spinae during this time period (Ceccato et al., 2009; Farinelli et al., 2021), to produce extension joint moment at the lumbar level. Contrary to the swing lower-limb, the backward contribution of the trunk does not seem necessary to perform the task. Yet, it appears important that the trunk and head remain vertical, because the head is the only segment equipped with the three sensory organs determinant for balance (Pozzo et al., 1990). Our results on the role of the trunk segment enable to interpret in the context of reaction to unexpected perturbations. Indeed, the trunk kinematics was suggested as a key determinant to the ability to avoid fall (Grabiner et al., 2008). Due to its large inertia, the trunk forward acceleration may need to be reduced, to facilitate the maintenance of its vertical position during the upcoming gait movement. Indeed, excessive trunk forward inclination would require large muscle activations to counter the combined effects of the trunk mass and gravity.

4.4.3 Adjustments with added mass

Adding mass to the trunk had limited effect on the dependent variables. The global variables such as whole-body CoM position, velocity (figure 4.2a) or H_M (figure 4.2b) did not change between conditions. Despite absence of significant differences between

conditions, that may be due to insufficient increase in added masses, we still got evidences that the coordination responsible for the whole-body movements may have been adapted to the mass. Indeed, the antero-posterior **CoP** trajectory was influenced by the added mass (figure 4.2a).

The first parameter impacted by additional masses was the antero-posterior **CoP** trajectory (figure 4.2a). According to the inverted pendulum model, when we added mass to the trunk, the weight applied to the whole-body **CoM** increased, accentuating the resulted whole-body **CoM** acceleration (equation (2.3)) with an identical backward **CoP** shift. We observed a slightly reduced **CoP** shift during this first phase in the two added mass conditions compared to the control condition, without any change in whole-body **CoM** velocity. This suggests that the added mass was integrated in the internal models by the nervous system, because it was used to accelerate the whole-body **CoM** forward and initiate the transition. The change in **CoP** backward shift contrasts with the results of [Vieira et al. \(2021\)](#) who found a more backward **CoP** at the very beginning of the anticipatory period, but not a reduced **CoP** shift during the remaining of the anticipatory period. This difference may come from the imposition of a given step length in our study, that they did not do.

Second, the mass condition also impacted the difference between the whole-body **CoM** acceleration and velocity computed with experimental data and from the linearised inverted pendulum model (figure 4.4). The whole-body **CoM** acceleration computed experimentally was larger than when computed from the model during the second phase. This difference can be explained by whole-body **CoM** acceleration resulting from the counter-rotating mechanism (figure 4.2b). During the second phase, the increase in H_M accelerated the whole-body **CoM** forward, completing the 'moving the **CoP**' mechanism. The fact that we observed significant differences between the whole-body **CoM** acceleration computed with experimental data and from the 'moving the **CoP**' mechanism suggests that we cannot omit the counter-rotating mechanism during the anticipatory phase of gait initiation when evaluating the whole-body **CoM** kinematics. These differences also suggest that only shifting the **CoP** relative whole-body **CoM** is not enough to accelerate the whole-body **CoM** sufficiently.

The decrease in differences between whole-body **CoM** acceleration and velocity computed experimentally and mathematically in the conditions with the added mass suggests that when more mass is present, the mass is used to accelerate the whole-body **CoM**, through an increase in F_{G_y} (figure 4.4).

Such adaptations to accelerate the whole-body **CoM** forward have already been described in another context: participants with a backward inclination of the trunk during gait initiation exhibited a larger hip joint flexion moment during the second phase of gait initiation ([Leteneur et al., 2013](#)). Collectively, our results and results from [Leteneur et al. \(2013\)](#) suggest that the mechanical instability generated during the anticipatory period of gait initiation does not only result from the **CoP** mechanism and the use of gravity, but is also adapted to the constraints of the task by modulating hip and/or lumbar muscle

4.5. CONCLUSION

activations and joint moments. Thus, the first phase of the anticipatory period seems to be characterised by a double-pendulum behaviour (the lower-limbs and the trunk), with the trunk increasing the rotational mechanical instability. During the second phase, the counter-rotating mechanism of the trunk seems to control this instability and helps keeping the upper-body vertical. The dissociation between the two parts of the double-pendulum may be modulated according to the mass added to the trunk: the more mass is added to the trunk, the less the double-pendulum is dissociated, and looks like a simple pendulum.

The last parameter impacted by additional masses was the contribution of the trunk alone (*i.e.* without the added mass), which significantly decreased when adding mass (figure 4.2b), suggesting that the modification of the mass was integrated by the nervous system. This small difference in the use of the trunk segment would probably not have been detected using only kinematic measurements because trunk kinematics is very small (3° in the sagittal plane) during gait initiation and gait (Thorstensson et al., 1982, 1984; Ceccato et al., 2009). The large inertial parameters of the trunk make such small adjustments important for the whole-body dynamics. The large importance of the trunk our study suggests, along with the small kinematic changes during the task, may confirm the importance of timed muscles activations from erector spinae and abdominii muscles during gait initiation (Ceccato et al., 2009; Farinelli et al., 2021), to control the trunk dynamics and balance during the transition. However, more detailed analyses, such as musculoskeletal modelling to link muscle activations to variation in H_M (Neptune & McGowan, 2011, 2016) and in H_M^{Trunk} , are required to better link these anticipatory muscle activations to the trunk dynamics.

4.5 Conclusion

In this study, we characterised the counter-rotating mechanism during the anticipatory period of a posture to movement transition: gait initiation. First, we divided the anticipatory period in two new phases, based on \dot{H}_M , instead of the two phases classically divided based on the CoP trajectory. This new delimitation enabled to show that the mechanical instability is generated for longer than the imbalance phase classically defined in the literature using only the CoP trajectory, characterised by the whole-body CoM acceleration continuing to increase. During the second phase, the swing lower-limb and the trunk segments contributed to initiate a backward rotation of the whole-body, probably to limit the rotational mechanical instability generated during the first phase. We also used three mass conditions to better highlight the role of the trunk. When adding mass to the trunk, its contribution to H_M is adapted, so that H_M remains constant, suggesting that the inertial parameters are considered by internal models to maintain H_M constant. Moreover, it also suggested that the counter-rotating mechanism regulates balance during the second phase of a posture to movement transitions. Altogether, these results suggest an important role of the trunk segment for balance-movement coordination during the anticipatory period of gait initiation: generating and then regulating the rotational mechanical instability. This contribution is dissociated from the lower-limbs, suggesting the whole-body behaves more

CHAPTER 4. BALANCE-MOVEMENT COORDINATION: GAIT INITIATION

like a double-inverted pendulum model (at least around the medio-lateral axis) rather than a simple inverted-pendulum model.

4.6 French summary

4.6.1 Introduction

L'initiation à la marche est une transition entre une posture et un mouvement largement utilisée dans la littérature pour étudier comment le système nerveux coordonne l'équilibre et le mouvement. Puisque la transition est volontaire, des activations musculaires anticipées ont été enregistrées et ont deux rôles mécaniques : (1) initier le mouvement du centre de masse du corps complet, et (2) maintenir l'équilibre malgré la réduction de la stabilité à la fin de la période d'anticipation. Le système nerveux crée donc une phase d'instabilité mécanique suivant l'axe antéro-postérieur afin d'initier la transition (Brenière et al., 1987; Lepers & Brenière, 1995) (voir aussi chapitre 2.2). Cependant, cette instabilité doit être contrôlée afin d'éviter les chutes (Cummings & Nevitt, 1989; Robinovitch et al., 2013).

L'initiation à la marche a été principalement étudiée via le mécanisme du déplacement du centre des pressions, modulé via des activations anticipées des muscles du membre inférieur (Crenna & Frigo, 1991; Brunt et al., 1991; Lepers & Brenière, 1995; Mickelborough et al., 2004). A partir du déplacement du centre des pressions, deux phases ont été décrites dans la littérature : une phase de déséquilibre, avec un déplacement du centre de pressions vers l'arrière et vers le futur pied oscillant, et une phase de déchargement avec un déplacement latéral du centre des pressions vers le pied d'appui (Crenna et al., 2006). Cependant, ce modèle ne prend en compte ni l'intensité des forces de réaction du sol, ni le mécanisme de contre-rotation, rendant incomplète notre compréhension de l'initiation à la marche.

Des activations musculaires anticipées qui ne contribuent pas au déplacement du centre des pressions ont été enregistrées, notamment au niveau du tronc (Ceccato et al., 2009; Farinelli et al., 2021). Le tronc pourrait en effet avoir un rôle important dans la contre-rotation étant donné ces paramètres inertiels importants. Calculer la quantité de mouvement angulaire du corps complet (H_M) et la contribution du tronc (H_{MTrunk}) pourraient apporter des informations quant au rôle du tronc dans l'initiation à la marche. Durant une tâche d'initiation du pas, H_M autour de l'axe médio-latéral montrait deux phases successives : il est d'abord dirigé vers l'avant, puis vers l'arrière durant la période anticipatoire. En plus de la valeur de H_M , sa dérivé (\dot{H}_M) est importante pour évaluer la coordination entre l'équilibre et le mouvement. En effet, \dot{H}_M est directement relié à l'accélération du centre de masse du corps complet. Caractériser l'évolution temporelle de H_M et de (\dot{H}_M) pourrait donc permettre de différencier l'accélération du centre de masse du corps complet lié au mécanisme du déplacement du centre des pressions et l'accélération due à la contre-rotation.

Le but de cette étude est de caractériser le rôle de la contre-rotation durant l'initiation à la marche, avec un intérêt particulier pour le rôle du tronc. Nous avons utilisé trois conditions de masses différentes pour inférer sur le rôle du tronc, pour savoir s'il participe à l'augmentation ou à la régulation de l'instabilité mécanique.

4.6.2 Méthode

La méthode générale est décrite en section 3.1. 13 participants ont initié la marche dans trois conditions : contrôle, avec 6 % et avec 13 % de leur masse rajoutée au tronc. La cinématique du corps complet a été calculée expérimentalement à partir des données de marqueurs, et via le modèle du pendule inverse (equation (4.2) et 4.3). Nous avons également calculé H_M et \dot{H}_M , ainsi que la contribution des segments H_M^i et \dot{H}_M^i .

Nous avons divisé la période d'anticipation de deux manières différentes. Premièrement, nous avons fait la division habituellement faite dans la littérature, à partir du centre des pressions (Crenna et al., 2006). Deuxièmement, nous avons fait la division basée sur l'évolution temporelle de H_M et de \dot{H}_M : une première phase du début de la période jusqu'au premier instant où \dot{H}_M devient positive, et une deuxième phase jusqu'à la fin de la période (figure 4.1).

4.6.3 Résultats

Nous avons trouvé des durées de phases différentes selon la manière de calculer, avec une première phase basée sur l'évolution temporelle de H_M plus importante que la phase d'instabilité.

En ajoutant des masses, nous avons trouvé un moindre déplacement vers l'arrière du centre des pressions. En revanche, la position ou la vitesse du centre de masse du corps complet n'ont pas été modifiées par l'ajout de masse au tronc. Nous avons observé des différences au niveau des accélérations et vitesses du centre de masse du corps complet, entre les valeurs expérimentales et les valeurs obtenues par le modèle du pendule inverse. Ces différences sont moins importantes dans les conditions où de la masse a été ajoutée au tronc.

4.6.4 Discussion

Les phases que nous avons quantifiées basées sur l'évolution temporelle de H_M montrent que le corps complet tourne vers l'avant durant la première phase, et vers l'arrière durant la deuxième. Nous avons également montré que la phase où le corps tourne vers l'avant est plus longue que la phase d'instabilité décrite dans la littérature. C'est-à-dire que, lorsque le centre des pressions a fini de reculer, le corps complet continue de tourner vers l'avant. Cela suggère également que lors de la phase habituellement nommée déchargement, l'instabilité mécanique en rotation continue d'augmenter puisque le mécanisme de contre-rotation n'a pas encore débuté. La deuxième phase basée sur l'évolution temporelle de H_M est caractérisée par une augmentation de H_M autour de l'axe médio-latéral, contribuant à accélérer le centre de masse du corps complet vers l'avant. Nous pouvons suggérer que cette contre-rotation permet de limiter l'instabilité mécanique de rotation produite durant la première phase, tout en contribuant à l'accélération du centre de masse du corps complet. Cela suggère également que l'initiation à la marche n'est pas uniquement une période d'instabilité mécanique, où le corps tombe vers l'avant pour initier le mouvement, mais que des ajustements sont présents pour éviter une instabilité en rotation excessive

4.6. FRENCH SUMMARY

qui serait difficilement rattrapable. La contre-rotation du corps complet est initiée par les trois segments du membre inférieur qui va osciller (cuisse, jambe et pied), ainsi que par le tronc. La contre-rotation du tronc est cohérente avec les activations musculaires anticipées enregistrées au niveau des muscles des lombaires (Ceccato et al., 2009; Farinelli et al., 2021). La contre-rotation du tronc pourrait permettre, en plus de gérer l'état d'instabilité, de garder le tronc et la tête à la verticale durant la totalité de la transition motrice.

L'ajout de masse n'a pas eu d'effet sur les variables liées au centre de masse du corps complet ou à H_M . Malgré tout, la coordination responsable du mouvement du corps complet est adaptée à l'ajout de masse. En effet, la trajectoire antéro-postérieure du centre des pressions est modifiée avec l'ajout de masse, avec un recul plus faible lorsque la masse augmente. Selon le modèle du pendule inverse, lorsque la masse du tronc augmente, cela se traduit par une augmentation de l'accélération du corps complet si le recul du centre des pressions est identique. La réduction de ce recul, sans modification de la vitesse du centre de masse du corps complet, nous indique que les masses ajoutées au tronc ont été prises en compte par le système nerveux au moment d'exécuter la transition.

Ensuite, la condition de masse a eu un effet sur la différence entre la vitesse et l'accélération du centre de masse du corps complet expérimental et provenant du modèle du pendule inverse. Nous avons montré que l'accélération du centre de masse du corps complet ne considère pas la force de réaction du sol antéro-postérieur, qui est générée suite à l'accélération initiale du centre de masse du corps complet. La diminution de différences entre les valeurs expérimentales et modélisées indique que lorsque nous ajoutons de la masse au tronc (ou plus généralement en haut du corps), cette masse est utilisée pour accélérer le centre de masse. A l'inverse, lorsque la masse n'est pas présente, le déplacement seul du centre des pressions n'est pas suffisant pour accélérer suffisamment le centre de masse du corps complet, et la génération d'une force de réaction antéro-postérieure est nécessaire. Ainsi, la première phase de la période anticipatoire semble être caractérisée par un comportement en double pendule (les membres inférieurs et le tronc), avec le tronc qui augmente l'instabilité mécanique. Durant la deuxième phase, le mécanisme de contre rotation permet de contrôler cette instabilité et de garder le haut du corps à la verticale. La dissociation entre les deux parties du double pendule semble être modulée avec la masse ajoutée au tronc : plus il y a de masse ajoutée au tronc, moins le double pendule est marqué, et ressemble d'avantage à un simple pendule.

Anticipation of contact: Kinematics anticipation before contact

One believes things because one has
been conditioned to believe them

Aldous Huxley (Brave new world)

The experiment and part of the data analysis have been realised with the contribution of Dylan Dupuis Longati, student in 2nd year of master degree STAPS at Université de Saint Etienne.

Part of this chapter has been published in *Human Movement Science* (Bechet et al., 2024b).

Part of the results presented here has been presented at the 18th international symposium on CMBBE in Paris (Bechet et al., 2023b) and at the 48th congress of Société de Biomécanique in Grenoble (Bechet et al., 2023c).

5.1 Introduction

Drop-landing tasks (drop-landing and drop-jumping) have been largely used to study how humans anticipate contact with the ground, because they can accurately predict the instant of contact, and program anticipatory muscle activations depending on this predicted instant of contact. Moreover, the change in linear momentum can be modified by modulating the drop height and/or the task to perform, and is easy to quantify, making drop-landing tasks appropriate to identify anticipatory muscle activations and the subsequent *favourable conditions* to cope with gravity during contact with the ground.

As mentioned in section 2.3 (chapter 2), the consequences of anticipatory muscle activations on biomechanical output seem to be well understood *during* ground contact period: to prepare accelerating the whole-body upward; but it remains largely unclear whether they have kinematic consequences *before* ground contact (chapter 2). Some evidence suggest that anticipatory kinematic adjustments may exist before contact. From figure 2 presented in Devita & Skelly (1992) and figure 6 presented in Horita et al. (2002), the hip and knee joints flex during the last 100 ms ground contact, but this result was not further discussed. Yu et al. (2006) negatively correlated hip and knee angular velocity at ground contact time with the peak of vertical **Ground Reaction Forces (GRF)**, suggesting that these anticipatory kinematic adjustments may bring *favourable conditions* to the landing task. These observations of joint angular velocity *at* ground contact also suggests that hip and knee joints start flexing before ground contact. However, when analysing these results, one can observe that flexion angular velocity was not present in every participant at ground contact, and that some participants even had extension angular velocity. Nevertheless, the two correlations described by Yu et al. (2006) might indicate that hip and knee angular velocity is a biomechanical solution used by the nervous system to protect the skeletal system when large **GRF** are expected. However, a complete understanding of the *favourable conditions* brought by these possible adjustments is lacking. Thus, the main aim of this chapter is to **characterise anticipatory kinematic adjustments during the air-time phase preceding ground contact during different drop-landing tasks**: (1) a movement to posture transition (a drop-landing task) and (2) a movement to movement transition (a drop-jumping task) We quantified the onset time of lower-limb joint flexions to determine whether they arise from ground contact or from anticipatory muscle activations, as well as the time evolution of joint angles and angular velocities before ground contact to determine if they arise come from anticipatory muscle activations.

To test how anticipatory kinematic adjustments contribute to create *favourable conditions* to the movement execution, we compared drop-landing and drop-jumping tasks from the same drop height. Because larger joint angles are reached at ground contact during drop-jumping compared to drop-landing (Mache et al., 2013; Hovey et al., 2021), we hypothesise that participants would start flexing joints earlier during drop-jumping. Next, we compared anticipatory kinematic adjustments between two drop heights, independently for the two tasks. Because the literature reports an absence of difference in **Electromyography (EMG)** onset with increase in drop height (Santello & McDonagh, 1998; Arampatzis et al., 2001),

we expected to find no difference in anticipatory joints flexions onsets between the two drop heights but an increase in joint angles and angular velocities with the increase in drop height, to cope with the larger increase in GRF at contact. This increase may be more attenuated during drop-jumping compared to drop-landing, because the task requires larger production of GRF. Finally, we also computed the foot kinematics to determine the impact of anticipated lower-limb joints rotations at the end of the kinematic chain.

5.2 Methods

Results from this study were obtained using Protocol 2. Participants, procedure, measurements and generic data analysis are described in [Methods](#) (section 3.2). Briefly, participants performed drop-landing and drop-jumping tasks from 0.35 and 0.5 m, when they were instructed to amortise as much as possible and to minimise ground contact time, respectively.

5.2.1 Data Analysis

5.2.1.1 Trials considered

For each participant, only the best trial of each task was analysed, and only the dependent variables from the dominant lower limb were extracted from that best trial. For the drop-landing, the best trial was the trial with the smallest vertical GRF peak. For the drop-jumping, the best trial was the trial with the shortest ground contact time.

5.2.1.2 Kinematics

Lower-limb segment coordinate systems were computed based on ISB recommendations ([Wu et al., 2002](#)), using a custom script (Matlab, MathWorks, version 2021b). They were used to compute lower-limb joint angles, which correspond to the Euler angles between the proximal and distal coordinate systems, following a Z (mediolateral axis) - X (antero-posterior axis) - Y (longitudinal axis) sequence. Angular velocities were then obtained by computing a simple left derivative of the joint angles to avoid any effect due to ground contact. The onset of joint flexion was determined as the first instant when the angular velocity was positive and continued to increase until ground contact.

Three comparisons were made in this study. First, we compared drop-landing and drop-jumping tasks from 0.35 m to assess whether anticipatory kinematic adjustments exist and differ to characterise potential *favourable conditions* to protect the skeletal system, relative to the task to perform. We chose to analyse the 0.35 m drop height because our participants are probably more used to land from 0.35 than 0.5 m. Maximal counter movement jump height from professional male athletes averages 0.5 m ([Haugen et al., 2020](#)), but our participants might not have this level. Moreover, in their daily practice, they probably do not performed their maximal jump height each time. Thus, we hypothesised they were more used to land from 0.35 m. Also, it requires more muscular strength to perform a drop-jumping task from 0.5 m than from 0.35 m ([Beattie et al., 2017](#)), making

5.3. RESULTS

drop-jumping from 0.5 m a specific task requiring specific abilities to be mastered. Next, we tested the effect of drop-height on these anticipatory kinematic adjustments. For this purpose, we compared drop-landing tasks from 0.35 and 0.5 m, and drop-jumping tasks from 0.35 and 0.5 m, independently.

5.2.2 Statistical Analysis

Statistical analyses were performed using Matlab (MathWorks, version 2021b). Normality of the data was tested using a Shapiro-Wilk test. The null hypothesis was rejected for most variables. Therefore, only non-parametric tests were used. For all three comparisons, we used a Wilcoxon signed rank test for each dependant variable. Moreover, for each condition, we compared the foot and pelvis vertical velocities at ground contact, we used a Wilcoxon signed rank test to assess whether the foot kinematics were modified by lower-limb kinematic adjustments during the air-time phase. For all tests, the significance threshold was set at 5%.

5.3 Results

We found a systematic (i.e. for each participant and each task) hip and knee flexion starting before ground contact (figures 5.1 to 5.3). In contrast, no clear ankle dorsiflexion was observed before ground contact in all tasks.

For all participants and during all tasks, the vertical acceleration of the foot became larger (i.e. closer to zero) than the acceleration of gravity before ground contact (figure 5.4). Consequently, the foot vertical velocity was larger than the pelvis vertical velocity at ground contact in every tasks (table 5.1).

Table 5.1: Comparison between pelvis and foot vertical velocity at ground contact for drop-landing and drop-jumping for each drop height. Negative values for vertical velocities indicate a downward velocity.

| | | Pelvis | Foot | <i>p</i> value |
|--------------|--------|------------------------------|------------------------------|----------------|
| | | median [Q1; Q3] | median [Q1; Q3] | |
| | | (<i>m.s</i> ⁻¹) | (<i>m.s</i> ⁻¹) | |
| Drop-landing | 0.35 m | -2.38 [-2.47, -2.28] | -2.09 [-2.17, -1.91] | < 0.01 |
| | 0.5 m | -3.03 [-3.10, -2.89] | -2.55 [-2.66, -2.46] | < 0.01 |
| Drop-jumping | 0.35 m | -2.41 [-2.44, -2.32] | -2.11 [-2.18, -1.95] | < 0.01 |
| | 0.5 m | -2.93 [-3.05, -2.96] | -2.53 [-2.70, -2.41] | < 0.01 |

5.3.1 Comparison of tasks, drop-landing and drop-jumping from 0.35 m

Joint kinematics and linear motion of the foot are presented in figure 5.1 and in figure 5.4a, respectively. We found no difference in timing of hip ($p = 0.90$) and knee ($p = 0.70$) flexion. At ground contact, there was no difference in both the hip flexion ($p = 0.35$) and ankle dorsiflexion ($p = 0.16$) angles between the two tasks, whereas the knee was significantly more flexed in drop-jumping compared to drop-landing ($p = 0.012$). For every joint, there was no difference in angular velocity at ground contact ($p = 0.26$, $p = 0.55$ and $p = 0.76$

for the hip, knee, and ankle joints, respectively). Moreover, there was no difference in the onset of foot upward acceleration and foot vertical acceleration at ground contact ($p = 0.68$ and $p = 0.99$, respectively).

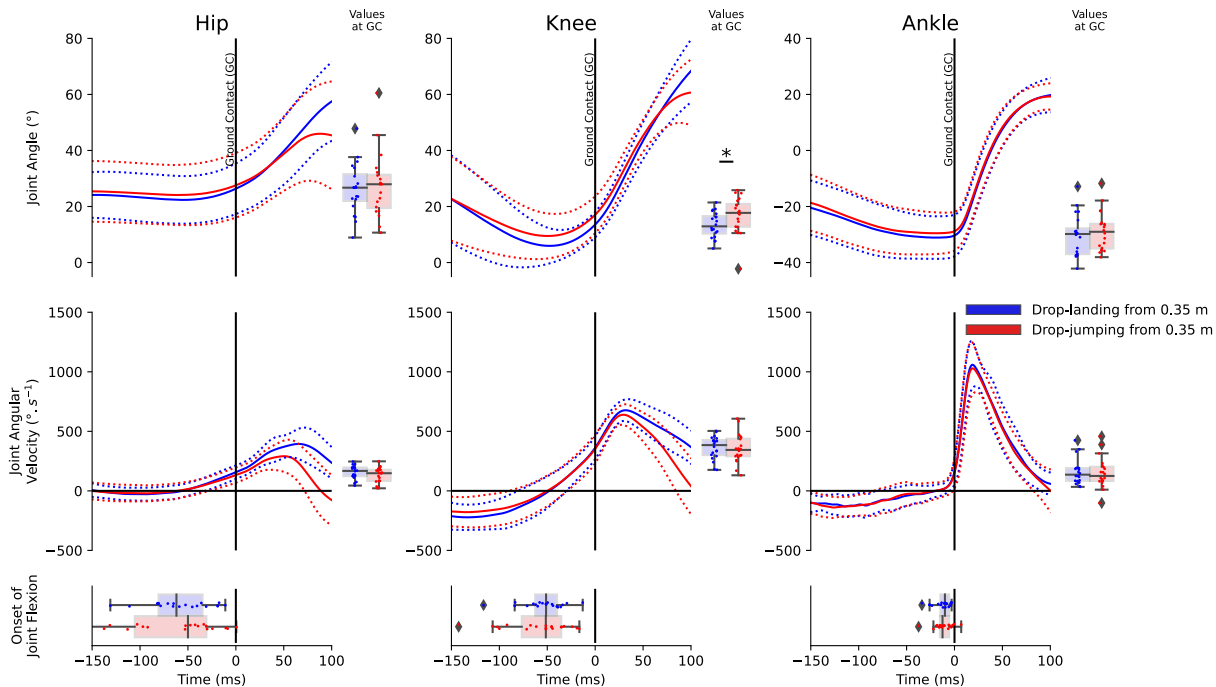


Figure 5.1: Sagittal kinematic results in the two landing tasks (drop-landing in blue, drop-jumping in red) for the three lower-limb joints: hip (left), knee (middle), and ankle (right) during the [-150 to +100 ms] time interval. Thick lines represent results averaged across all participants ($n = 20$), and dotted lines represent one standard deviation from the mean. The first row presents the joint angles (in $^{\circ}$), the second row presents the joint angular velocities (in $^{\circ} \cdot s^{-1}$), and the third row presents the onset of joint flexion (in ms), corresponding to the first instant when the angular velocity was positive with individual values. Each vertical boxplot on the right side of each graph presents results at ground contact in the two landing tasks, with individual values (joint angles for the first row, joint angular velocities for the second row). A star indicates a significant difference between the two landing tasks.

5.3.2 Height effect, drop-landing from 0.35 and 0.5 m

Joint kinematics and linear motion of the foot for this comparison are presented in figure 5.2 and in figure 5.4b, respectively. We did not find difference in timing of hip flexion ($p = 0.26$), but we found earlier knee flexion during drop-landing from 0.5 m compared to 0.35 m ($p = 0.006$). At ground contact, hip and knee joints were more flexed during drop-landing from 0.5 m compared to 0.35 m ($p = 0.007$ and $p < 0.001$, respectively), but we found no difference in ankle dorsiflexion ($p = 0.74$). Joint angular velocity at ground contact tended to be larger for the hip ($p = 0.052$), and was larger for the knee ($p < 0.01$) during drop-landing from 0.5 m compared to 0.35 m. There was no difference for ankle angular velocity at ground contact ($p = 0.33$). The foot started to be accelerated upward earlier during drop-landing from 0.5 m compared to 0.35 m ($p = 0.026$), but there was no difference of foot vertical acceleration at ground contact ($p = 0.15$).

5.4. DISCUSSION

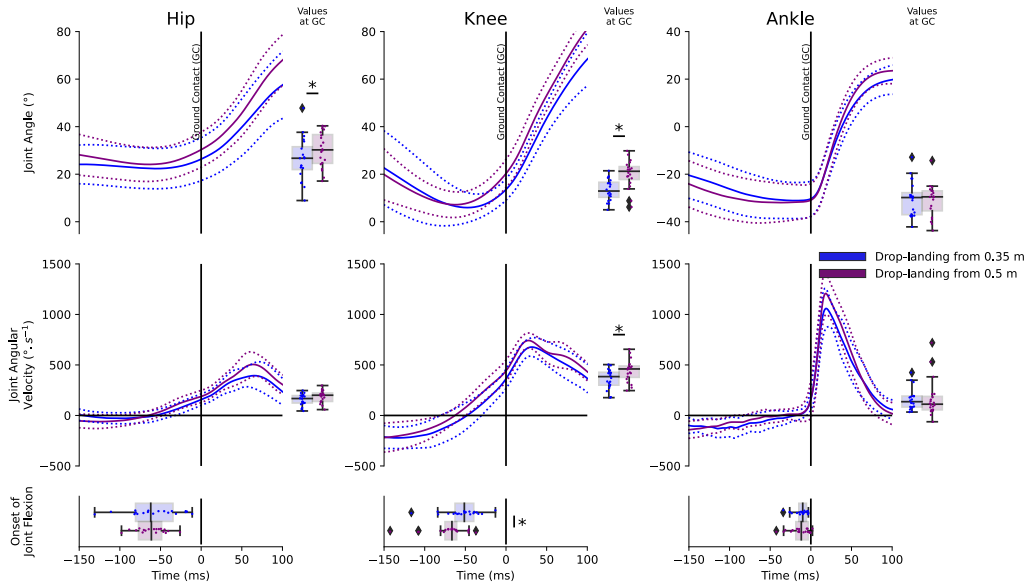


Figure 5.2: Drop height effect during drop-landing. Caption are the same as figure 5.1, with drop-landing from 0.35 m still in blue and drop-landing from 0.50 m in purple.

5.3.3 Height effect, drop-jumping from 0.35 and 0.5 m

Joint kinematics and linear motion of the foot for this comparison are presented in figure 5.3 and in figure 5.4c, respectively. We found no difference in timing of hip ($p = 0.48$) and knee ($p = 0.88$) flexion. At ground contact, there was no difference in flexion angle for every joint ($p = 0.37$, $p = 0.25$ and $p = 0.08$ for hip, knee and ankle joint flexion, respectively). For the hip and ankle joint, there was no difference in angular velocity at ground contact ($p = 0.97$ and $p = 0.60$, respectively), but there was larger knee angular velocity when drop-jumping from 0.5 m compared to 0.35 m ($p = 0.0045$). An earlier foot upward acceleration when drop-jumping from 0.5 m compared to 0.35 m came close to significance threshold ($p = 0.059$), but there was no difference in foot vertical acceleration at ground contact ($p = 0.12$).

5.4 Discussion

Our objective was to characterise the kinematic consequences of anticipatory muscle activations before ground contact during different landing tasks: a transition from a drop movement to a standing posture (drop-landing), and a transition from a drop movement to a jump (drop-jumping), to determine whether anticipatory muscle activations are adapted to cope with gravity, to the movement to perform, or both. Analysis of the temporal evolution of lower-limb joint angles revealed that anticipatory muscle activations have anticipatory kinematic consequences starting during the air-time phase, because hip and knee joint flexions were initiated before ground contact for all participants and in both tasks. This suggests that these anticipatory joint flexions are not adapted to the dynamic constraints of the movement. Consecutive to these flexions, the foot started to be accelerated upward before ground contact. The systematicity of these results among all participants, despite different objectives between the tasks or the drop heights, suggests that these an-

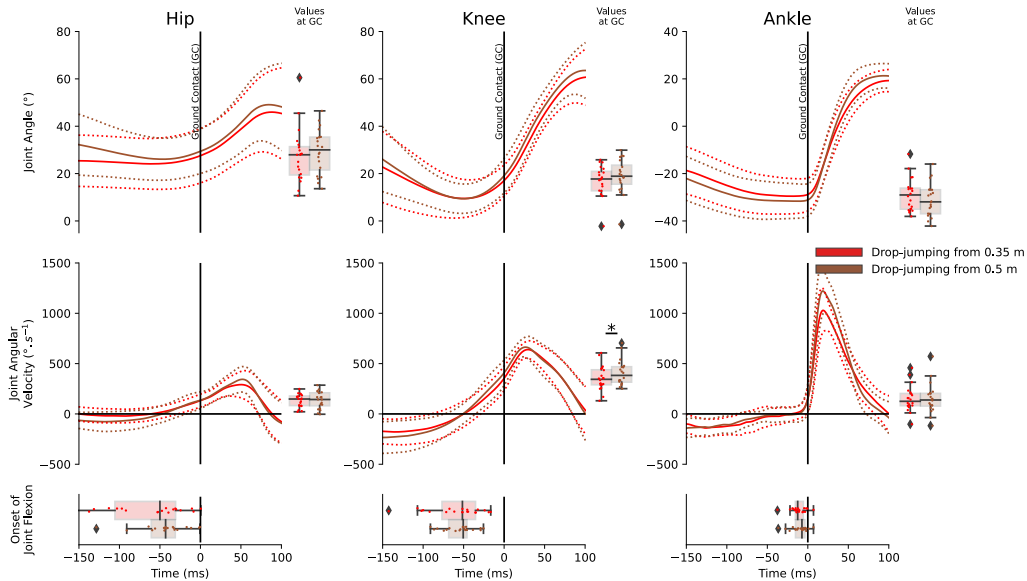


Figure 5.3: Drop height effect during drop-jumping. Caption are the same as figure 5.1, with drop-jumping from 0.35 m still in red and drop-jumping from 0.50 m in orange.

ticipatory joint flexions are a common strategy used by the nervous system to provide *favourable conditions* to cope with gravity, regardless of the landing task.

5.4.1 General pattern of anticipatory kinematic adjustments

Our results showed that the hip and knee joints started flexing systematically before ground contact (figures 5.1 to 5.3) for all participants, in both landing tasks and from both drop heights. Such anticipatory joint flexions can also be observed in Devita & Skelly (1992); Horita et al. (2002), but they did not discuss this result. These anticipatory hip and knee flexions started after onsets of muscle activation (presented in chapter 6). The onsets of muscle activations we found were similar to those described in previous studies (Ambegaonkar et al., 2011; Arampatzis et al., 2001; Santello & McDonagh, 1998), but these authors did not report anticipatory joint flexion either. Although a direct relationship between EMG and joint rotations cannot be made, the joint rotations we observed here are likely to result from the anticipatory muscle activations. In light of the available evidence, it seems reasonable to suggest that the actions of the rectus femoris (and the iliopsoas that we could not record) are responsible for hip flexion, while biceps femoris long head, and semitendinosus are responsible for knee flexion. However, this remains a hypothesis that is yet to be confirmed.

Our results showed that the lower-limb configuration of flexed hip and knee joints at ground contact are achieved through joint flexions initiated shortly before ground contact (figures 5.1 to 5.3). By anticipating joint flexions that would have been induced by ground contact, the hip and knee joints displayed no distinct change of angular velocity shortly after ground contact, contrary to the ankle joint. This anticipated increase of angular velocity for the hip and knee joints should help in reducing the magnitude of GRF. Indeed, by limiting any abrupt change in joint angle and angular velocity, the upward acceleration

5.4. DISCUSSION

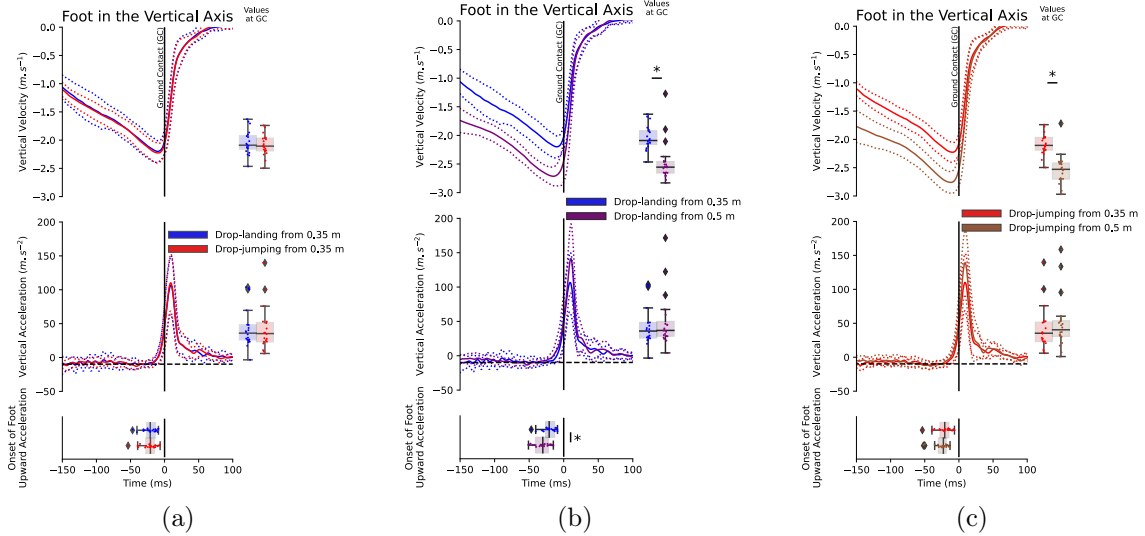


Figure 5.4: Foot vertical kinematic results in the two landing tasks (drop-landing in blue and drop-jumping in red) from 0.35 m (a); in drop-landing from 0.35 and 0.5 m (b); and in drop-jumping from 0.35 and 0.5 m (c) during the [-150 to +100 ms] time interval. Thick lines represent mean results across all participants ($n = 20$), while dotted lines represent one standard deviation from the mean. The first row presents the foot vertical velocity (in $m.s^{-1}$), the second row presents the foot vertical acceleration (in $m.s^{-2}$), and the third row presents the onset of foot upward acceleration (in ms), corresponding to the first instant when the foot acceleration was larger than the acceleration of gravity, represented by the horizontal dotted line in the second row, with individual values. Each vertical boxplot on the right side of each graph represents results at ground contact in the two landing tasks, with individual values (vertical velocity for the first row, vertical acceleration for the second row).

of the whole-body centre of mass is reduced and, according the Newton's second law, less GRF should be produced. Contrary to the study of Yu et al. (2006), our participants always landed with flexion angular velocity at ground contact, for both the knee and hip joints. This result suggests that presence of angular velocity is important in minimising the magnitude of GRF, generating *favourable conditions* in complement to the flexed-joint configurations previously described in the literature (Devita & Skelly, 1992; Podraza & White, 2010; Wakabayashi et al., 2021). These anticipatory joint flexions may contribute to protect the skeletal system by avoiding any joint extension movements that could lead to joint injury and/or imbalance during contact. The absence of difference between landing tasks is contrary to the findings of Horita et al. (2002), which suggested that knee angular velocity at ground contact is related to drop-jumping performance. Along with the systematicity of these anticipatory joint flexions among our results, and the absence of difference between drop-landing and drop-jumping tasks (figure 5.1), suggest that these flexions are an invariant component of the landing context selected by the nervous system to cope with gravity, regardless of the upcoming movement to perform. Such protective strategy depending on the predicted impact has already been suggested, with anticipatory muscle activations adjusted close to contact time, despite different initial conditions (Galindo et al., 2009).

Due to the multi-body structure of the human skeletal system, any kinematic adjustments influence the position and orientation of the segment located at the end of the open kinematic chain, the foot, in our study. Despite no noticeable change in the ankle angle before ground contact (figures 5.1 to 5.3), an upward acceleration of the foot started before ground contact in both tasks and for all participants (figure 5.4), leading to a larger vertical velocity for the foot, compared to the pelvis. The larger vertical velocity of the foot reduces the velocity differential between the foot and the ground at ground contact (table 5.1). Simultaneous to the flexing hip joint we recorded (figures 5.1 to 5.3), the flexing knee joint accelerates the foot downward. Thus, the hip flexion mainly contributes to the upward foot acceleration and counteracts the downward effect of the knee flexion. The combined hip and knee flexions leading to an upward acceleration of the foot, regardless of the landing task (figure 5.4), reduce the upward foot acceleration that will be required during contact. This biomechanical solution seems efficient to limit the impact GRF during the beginning of ground contact.

The anticipatory joint rotations we quantified seem to complement the stiffening role of anticipatory muscle activations extensively described in the literature. In particular, ankle dorsiflexion was induced only by ground contact (figures 5.1 to 5.3), confirming that the ankle muscles were anticipatorily co-contracted to increase ankle joint stiffness (Santello & McDonagh, 1998). This result is consistent with previous studies, which suggested that landing with a plantarflexed ankle joint enables landing on the forefoot, using a large ankle range of motion after ground contact to amortise (Gross & Nelson, 1988; Santello, 2005). Given the results we have presented here, the anticipatory hip and knee joint kinematic behaviours can also be interpreted as stiffening in preparation for ground contact. Indeed, maximal angular velocities occurred shortly after ground contact in both joints (figure 5.1), and could not be the result of a stretch reflex (Jones & Watt, 1971b), indicating that muscle activations contributing to limit joint excursions are voluntarily-initiated (Zuur et al., 2010). Based on this interpretation, we suggest that the anticipatory muscle activations need to be precisely timed and coordinated according to the expected instant of ground contact: early activations enable the initiation of joint flexions, while latter activations stiffen joints to limit angular velocities shortly after ground contact, without causing an abrupt change of angular velocity. Thus, we suggest anticipatory muscle activations have two complementary consequences, joint flexing and stiffening, that seems to serve the same purpose of coping with gravity to protect the skeletal system.

5.4.2 Strategy modulations

In the previous section, we suggested that anticipatory kinematic adjustments enable to generate *favourable conditions* to cope with gravity and limit the magnitude of GRF. Given the increase of whole-body velocity at ground contact when increasing drop height, we expected that these adjustments would be exacerbated when drop height increases, particularly during drop-landing.

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5.4.2.1 Drop-landing

Our results support our hypothesis for drop-landing, with larger hip and knee flexion angles at contact when the drop height increases (figure 5.2). Since it was suggested that landing with larger hip and knee flexion angles at contact would decrease the peak of GRF (Devita & Skelly, 1992; Podraza & White, 2010; Wakabayashi et al., 2021), employing the same strategy when landing from increasing height, and therefore when facing larger GRF, seems an appropriate strategy. However, there is no consensus in the literature: some studies found no difference in hip and knee joint flexion angle at contact between different drop heights (McNitt-Gray, 1991; Yeow et al., 2009a), whereas more recent studies reported an increase in knee joint flexion angle at contact with increase in drop height (Helm et al., 2020) and gravity (Waldvogel et al., 2023). In our study, we specifically instructed our participants to amortise as much as possible. Devita & Skelly (1992) showed that when focusing on reducing GRF while landing, participants exhibited larger knee flexion at ground contact than when participants landed stiffly. Therefore, differences in hip and knee joint flexion angles may come from a different execution of the landing task between our study and the literature. For instance, McNitt-Gray (1991) studied gymnasts that are used to land with more extended lower-limbs to meet judges criteria. Therefore, we can suggest that the objectives of the task are integrated to modulate the strategy and to perform anticipatory kinematics adjustments adapted to the movement execution.

In addition to larger joint flexion angles at contact, we found larger joint angular velocities in the hip (although not significant but very close to threshold, $p = 0.052$) and in the knee joints at ground contact when increasing the drop height (figure 5.2). Yu et al. (2006) suggested a negative correlation between the hip and knee flexion angular velocity at ground contact and the peak vertical GRF. Similarly to joint angles at ground contact, the increase in joint angular velocity when increasing drop height appears to be an appropriate strategy to cope with larger GRF at contact, and may confirm that flexing joints in anticipation of contact is a strategy used to cope with gravity and protect the skeletal system. Moreover, when increasing drop height, McNitt-Gray (1991) described an increase in the maximum joint angular velocity during ground contact increases (see also figure 5.2). The larger joint angular velocities at ground contact may be a strategy to reach larger joint angular velocities later during contact, without a large change in angular velocity during the early contact period, to reduce joint moments when experiencing large GRF.

The largest knee angle and angular velocity at ground contact during drop-landing from 0.5 m is achieved because of an earlier onset of the knee joint flexion, compared to the 0.35 m height (figure 5.2). This confirms that estimation of the instant of ground contact by the nervous system is crucial for safe landing, because the anticipatory kinematic adjustments seem to be timed relative to this instant. By anticipating the onset of knee flexion, there is no requirement to increase joint angular acceleration to be able to reach a larger joint angular velocity and joint angle at ground contact. Therefore, because joint angular acceleration may not be different between two drop height conditions, muscle activation amplitudes required to initiate these flexions may not differ, resulting in an efficient

strategy (*i.e.* in term of energy) to cope with gravity.

5.4.2.2 Drop-jumping

Constraints differ between drop-jumping and drop-landing. Larger whole-body **Centre of Mass (CoM)** acceleration is required during drop-jumping compared to during drop-landing. Moreover, in our study, we instructed participants to minimise ground contact time, increasing the required the magnitude of whole-body **CoM** acceleration. Therefore, there is a trade off between **GRF** minimisation to protect the skeletal system, and **GRF** production to quickly accelerate the whole-body **CoM** upward and perform the upcoming jump.

Contrary to the drop-landing task, we found no difference in joint angles at ground contact between the two drop-jumping heights (figure 5.3). This absence of difference between the two heights indicates that the nervous system does not modulate the strategy to cope with gravity. Because of the trade off between **GRF** minimisation to protect the skeletal system and **GRF** production for movement execution, the system cannot increase the **GRF** production while increasing the protection of the skeletal system. However, the presence of anticipatory kinematic adjustments during drop-jumping from both drop heights indicates that the system always uses adjustments to protect the skeletal system, even if these adjustments are not adapted to the drop height. This trade-off comes from the two different muscle functions: rotating joint and increasing stiffness to use stretch-shortening cycle (Fukutani et al., 2021). By favouring one function, it limits the use of the other function. Here, we can suggest that the system always rotates lower-limb joints, even if the goal of the movement is to perform a drop-jumping, therefore limiting the use of the stretch-shortening cycle.

In summary, adaptations to increasing drop heights differ between drop-landing and drop-jumping tasks. During drop-landing, participants increased joint angles and joint angular velocities at ground contact, probably to take account of the increase in whole-body velocity and consecutive **GRF** to deal with drop height, which is consistent with the hypothesis that these adaptations prepare the skeletal system to face large **GRF**. During drop-jumping, these adaptations were not present because large **GRF** must also be produced during ground contact to accelerate the whole-body **CoM** even further than during drop-landing. These results clearly suggest that the nervous system integrates both the drop height and the objective of the task when programming motor commands dedicated to create *favourable conditions* to protect the skeletal system. Nevertheless, it appears that the system always implements the protective strategy, regardless of the objectives of the task.

5.4.3 General implications of anticipatory kinematic adjustments preceding ground contact

In this study, we used landing contexts to investigate how humans anticipate the consequences of gravity and/or the consequences of the motor task. The systematicity of the anticipatory kinematic adjustments we recorded across landing tasks, together with

5.4. DISCUSSION

their precise timing relative to ground contact, and the fact that they were recorded in experienced athletes, reflect automaticity (i.e. the ability to perform actions with little to no conscious attention) (Shiffrin & Schneider, 1977). Because these adjustments are programmed depending on the expected instant of ground contact, our findings are relevant for sports-injury prevention. Future studies should assess the underlying mechanisms mobilised by an athlete to accurately predict ground contact, especially when the athlete is disturbed during the air-time phase, when injuries such as anterior cruciate ligament ruptures frequently occur (Krosshaug et al., 2007).

Since gravity is a ubiquitous external force, these automatic anticipatory kinematic adjustments may look similar in other types of movement. For instance, similar observations have been reported during walking in different contexts. Indeed, the vertical velocity of the foot decreases before ground contact during unperturbed flat gait, and this is notably due to the knee flexion preceding heel-strike (Winter, 1992). During a step-down task, when the change in linear momentum increases, the knee flexion angle at ground contact was reported to be larger than during flat gait (Müller et al., 2014), supporting that lower-limb joint flexion that accelerates the foot upward before ground contact is an efficient biomechanical solution adopted by humans when downward vertical velocity increases. Thus, our findings encourage future research to continue studying how humans cope with gravity, and to clarify whether these anticipatory kinematics adjustments are part of a universal strategy to protect the skeletal system from injuries.

5.4.4 Perspectives on anticipatory kinematic adjustments

Here, we made several assumptions on the possible roles of the anticipatory kinematic adjustments before ground contact during landing contexts based on our results and the literature, yet we were not able to establish a clear cause-effect relationship. For example, Yu et al. (2006) proposed an inverse relationship between hip and knee angular velocity at ground contact and the peak of GRF experienced during contact. Here, we found systematic anticipatory flexions, but we were not able to establish such relationships, probably because we gave specific instructions to our participants, limiting the variety of peak GRF and joint angular velocities experienced during tasks. Similarly, experiment with cheating tasks (McDonagh & Duncan, 2002; Helm et al., 2020) used to fool the predictive ability of the system would help testing our hypotheses, by investigating the differences of behaviour when prediction of ground contact is correct and when it is fooled. Our model predicts that:

- if real ground contact occurs before the predicted ground contact instant, joint flexions would only be initiated, or not initiated yet (depending on the difference between real and predicted ground contact instants).
- if real ground contact occurs after the predicted ground contact instant, joint flexions would be initiated accordingly before the expected ground contact, and this flexion would be stopped shortly after, corresponding to the maximum flexion angular velocity visible, when we suggest that the stiffening role occurs. If the real ground

contact occurs long after the predicted ground contact, we expect that the absence of stretch reflex indicates the nervous system of the absence of contact (McDonagh & Duncan, 2002), and the nervous system may stop the joint flexion to avoid too much joint flexion during the forthcoming contact.

In both cases, it should result in larger peak GRF, if our hypotheses are correct, because *favourable conditions*, *i.e.* the joint angle, angular velocity, and foot linear velocity, would not be met.

Moreover, it remains unknown whether foot kinematics are also adapted to the constraints of the task, such as drop height. Vertical foot acceleration at ground contact was very similar between drop-landing and drop-jumping from 0.35 m ($p = 0.99$, figure 5.4a). However, they started to differ (although not significantly) when increasing drop height for both drop-landing and drop-jumping ($p = 0.15$ and $p = 0.12$, respectively, figures 5.4b and 5.4c), with earlier, and tendency for earlier foot upward acceleration during drop-landing and drop-jumping with increasing height, respectively. In our study, we had only two drop heights separated by 0.15 m and we can wonder if significant differences may be found if we increase the difference of drop height, or if there is a correlation between vertical foot acceleration at contact and drop height.

Finally, our results suggested that the system always implement anticipatory processes to protect the skeletal system and cope with gravity, even when drop-jumping. However, it remains partially unknown what anticipatory processes enable to perform a drop-jumping task. It is accepted that larger amplitudes of anticipatory muscle activations are required for drop-jumping compared to drop-landing (Dyhr-Poulsen et al., 1991; Leukel et al., 2011; Waldvogel et al., 2023), but less is known about joint configurations required for efficient drop-jumping. In agreement with the literature (Hovey et al., 2021; Mache et al., 2013; Waldvogel et al., 2023), we found larger knee flexion angle at ground contact during drop-jumping compared to drop-landing (figure 5.1), that may be a *favourable condition* for drop-jumping. Moreover, in another study, participants were not able to switch from drop-landing to drop-jumping when instructed to change task 50 ms before ground contact, and were unable to switch 31 % of the time when instructed to change task 110 ms before contact (Leukel et al., 2011). This confirms that particular *favourable conditions* are required for drop-jumping, and adjustments of knee flexion before ground contact may be one of them. It is also possible that the instructions were not integrated quickly enough. Since anticipatory muscle activations are generally programmed in a feedforward way, this short time available to switch between tasks appears to short to modify these muscles activations.

5.4.5 Conclusion

Our results show that anticipatory muscle activations used by humans have systematic and invariant kinematic consequences during the air-time phase: they contribute to initiate the hip and knee joints flexion before ground contact. Together with the stiffening function described in previous studies, these anticipatory joint flexions also contribute to prepare and protect the skeletal system for the landing task. These adjustments are exacerbated

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when drop height increases, providing additional evidence of their importance. As a direct consequence of these anticipatory kinematic adjustments, the foot is accelerated upward to decrease its upcoming deceleration due to ground contact. Because these anticipatory kinematic adjustments were systematic and invariant, this suggests that this is an efficient biomechanical solution selected by the nervous system to provide *favourable conditions* for coping with gravity.

5.5 French summary

5.5.1 Introduction

Les conséquences biomécaniques des activations musculaires anticipées semblent être bien comprises durant la période de contact : préparer à accélérer le corps complet vers le haut ; mais restent largement inexplorées avant l'instant de contact avec le sol.

Quelques éléments suggèrent que des ajustements cinématiques du membre inférieur existent avant le contact au niveau de la hanche et du genou, mais n'ont pas été interprétés.

Yu et al. (2006) a négativement corrélé la vitesse angulaire de flexion lors du contact avec la force de réaction verticale, suggérant que ces ajustements cinématiques pourraient apporter des conditions favorables pour préparer la réception, afin de protéger le système squelettique lorsque la force de réaction du sol est importante. L'objectif de ce chapitre est de caractériser les ajustements cinématiques anticipés durant la phase de vol précédant le contact avec le sol durant deux tâches impliquant une réception : une transition entre un mouvement et une posture (drop-landing) et une transition entre deux mouvements (drop-jumping). Nous avons quantifié l'instant d'apparition des flexions des différentes articulations du membre inférieur pour déterminer si elles résultent du contact avec le sol ou des activations musculaires anticipées. Nous avons également caractérisé l'évolution temporelle des angles et vitesses angulaires des articulations en flexion avant l'instant de contact.

5.5.2 Méthode

Les résultats de cette étude proviennent du protocole 2. Brièvement, les participants ont réalisé des réceptions (drop-landing) et des drop-jump depuis 0.35 et 0.5 m. Il leur était demandé d'amortir le plus possible (minimiser la force de réaction du sol verticale) et de minimiser le temps de contact au sol, respectivement pour les deux tâches. Dans ce chapitre, nous avons calculé les angles de flexion des articulations du membre inférieur, ainsi que l'instant du début de flexion de chaque articulation, défini comme étant le premier instant à partir duquel la vitesse angulaire (la dérivée temporelle de la vitesse) était positive et continuait à augmenter jusqu'à l'instant du contact.

Trois comparaisons ont été réalisées dans ce chapitre. Premièrement, nous avons comparé le drop-landing et le drop-jumping depuis 0.35 m pour voir si les ajustements dépendent de la tâche. Ensuite, nous avons testé l'effet de la hauteur sur les ajustements cinématiques anticipés, en comparant le drop-landing à 0.35 et à 0.5 m, et le drop-jumping à 0.35 et à 0.5 m, de manière indépendante.

5.5.3 Résultats

Nous avons trouvé une flexion systématique (pour chaque participant et chaque tâche) de la hanche et du genou avant l'instant de contact avec le sol. En revanche, une dorsiflexion anticipée n'a pas été observée. Pour tous les participants et lors des deux tâches,

5.5. FRENCH SUMMARY

l'accélération verticale du pied était plus importante (plus proche de zéro) que l'accélération de la gravité avant l'instant de contact avec le sol.

Au niveau de la comparaison entre les tâches, nous n'avons pas trouvé de différence sur l'instant de début de flexion pour la hanche ou le genou. A l'instant du contact, le genou était légèrement plus fléchi en drop-jumping comparé au drop-landing ($p = 0.012$), et aucune différence n'a été trouvée pour la hanche et la cheville.

Pour l'effet de la hauteur de chute en drop-landing, nous avons trouvé une flexion du genou plus anticipée à 0.5 comparé à 0.35 m ($p = 0.006$). A l'instant du contact, la hanche et le genou étaient plus fléchis durant le drop-landing à 0.5 comparé à 0.35 m. La vitesse angulaire à l'instant du contact flirtait avec la significativité ($p = 0.052$) et pourrait être plus importante pour la hanche, et était plus importante pour le genou ($p < 0.01$) durant le drop-landing à 0.5 comparé à 0.35 m. Enfin, le pied commençait à être accéléré vers le haut plus tôt en drop-landing à 0.5 comparé à 0.35 m.

Pour l'effet de la hauteur de chute en drop-jumping, nous avons trouvé une vitesse de flexion angulaire du genou plus importante au contact en drop-jumping à 0.5 comparé à 0.35 m ($p = 0.0045$). De plus, le pied était accéléré vers le haut plus tôt en drop-jumping 0.5 comparé à 0.35 m.

5.5.4 Discussion

L'analyse de l'évolution temporelle des angles de flexion des articulations du membre inférieur a montré que les activations musculaires anticipées ont des conséquences cinématiques qui débutent durant la phase de vol. En effet, la hanche et le genou commencent à se fléchir avant le contact au sol pour tous les participants, et durant toutes les tâches. Cela suggère que les flexions anticipées ne sont pas adaptées aux contraintes dynamiques du mouvement (drop-landing contre drop-jumping). Consécutivement à ces flexions, le pied commençait à être accéléré vers le haut avant le contact avec le sol. La systématisme des résultats à travers les participants et malgré les différents objectifs induits par la tâche suggère que ces ajustements cinématiques anticipés sont une stratégie commune utilisée par le système nerveux pour apporter des *conditions favorables* afin de faire face à la gravité, indépendamment de la tâche.

Les flexions anticipées de la hanche et du genou que nous décrivons débutent après que les muscles du membre inférieur soient activés (présentés dans le chapitre 6). Les instants d'activation que nous avons trouvés sont cohérents avec ceux décrits dans des études précédentes (Ambegaonkar et al., 2011; Arampatzis et al., 2001; Santello & McDonagh, 1998), mais ils n'avaient pas décrit de flexion anticipée des articulations.

Nos résultats montrent que la configuration articulaire avec la hanche et le genou fléchis au contact est permise grâce à une flexion initiée avant le contact. En anticipant la flexion de ces deux articulations, qui aurait sinon été induite par le contact avec le sol, la hanche et le genou ne montrent pas de changement net de vitesse angulaire dû au contact, contrairement à la cheville. L'augmentation progressive et anticipée de la vitesse de flexion angulaire de

la hanche et du genou pourrait limiter l'intensité de la force de réaction du sol au début du contact au sol. En effet, en évitant un changement net de flexion et de vitesse angulaire, l'accélération instantanée du corps vers le haut est réduite et, selon la 2nd loi de Newton, la quantité de force de réaction du sol à produire est moins importante. L'absence de différence entre les deux tâches (drop-landing et drop-jumping), est contraire aux résultats de Horita et al. (2002), qui suggéraient que la vitesse angulaire du genou à l'instant du contact était associée à la performance en drop-jumping. L'absence de différence que nous avons observée, en plus de la systématisme des flexions chez nos participants et dans les deux tâches, suggèrent au contraire que ces flexions sont un invariant de la tâche de réception pour faire face à la gravité, quel que soit l'objectif de la tâche. Une stratégie protective du contact avait été suggérée par Galindo et al. (2009), avec la description d'ajustements musculaires anticipés juste avant l'instant de contact, malgré différentes conditions expérimentales.

En raison de la structure multi-corps du corps humain, chaque ajustement articulaire influence la position de l'effecteur en bout de chaîne, le pied dans notre cas. Malgré l'absence d'ajustements au niveau de la cheville avant le contact, le pied était accéléré vers le haut avant le contact avec le sol, durant toutes les conditions et chez tous les participants, entraînant une vitesse verticale du pied à l'instant du contact plus importante que celle du pelvis. Cette vitesse verticale du pied permet de réduire la différence de vitesse entre le pied et le sol à l'instant du contact, et réduit l'accélération vers le haut requise pour arrêter le pied, ce qui semble être une solution biomécanique efficace pour limiter la production de forces de réaction du sol au début de la phase de contact avec le sol.

Les flexions anticipées que nous décrivons complètent le rôle d'augmentation de la raideur déjà décrit dans la littérature. En particulier, la dorsiflexion de la cheville était seulement induite par le contact avec le sol, et confirme que les muscles de la cheville sont co-contractés de manière anticipée pour augmenter la raideur de la cheville. Nos résultats permettent aussi de suggérer qu'une augmentation de la raideur est présente au niveau de la hanche et du genou. En effet, la vitesse angulaire maximale intervient rapidement après le contact au sol, et ne semble pas pouvoir provenir d'une activation réflexe (Jones & Watt, 1971b), indiquant alors que les activations musculaires anticipées permettent également de limiter la rotation après l'impact. Sur la base de cette interprétation, nous suggérons que les activations musculaires anticipées doivent être programmées et coordonnées de manière précise avec l'instant de contact prédit : les activations les plus précoces permettent l'initiation des flexions, alors que les activations les plus tardives augmentent la rigidité des articulations afin de limiter la vitesse angulaire de flexion pendant le contact. Nous suggérons alors que les activations musculaires anticipées ont deux conséquences complémentaires : l'initiation des rotations et la rigidification, qui semblent servir le même rôle de faire face à la gravité et de protéger le système squelettique.

En augmentant la hauteur de chute, les résultats diffèrent selon la tâche. Durant le drop-landing, les participants augmentent la flexion et la vitesse angulaire au contact de la hanche et du genou, probablement pour prendre en compte l'accélération plus importante

5.5. FRENCH SUMMARY

qui va devoir être produite lors du contact. Cela suggère donc que les ajustements sont adaptés en fonction de la vitesse du corps complet à la réception. Pendant le drop-jumping, ces adaptations ne sont pas présentes parce qu'une importante force de réaction verticale doit être produite pour effectuer le mouvement. Ces résultats suggèrent alors que le système nerveux prend en compte aussi bien la hauteur de chute que la tâche à réaliser au moment de programmer les activations musculaires anticipées et de générer les *conditions favorables* à la réalisation du mouvement.

CHAPTER 6

Anticipation of contact: Two anticipation phases

Life is essentially an endless series of problems. The solution to one problem is merely the creation of another.

Mark Manson (The subtle art of not giving a f*ck)

Part of the data analysis and the rationale of this chapter have been realised with the contribution of Adrien Péneaud, student in 1st year of master degree STAPS at Université de Poitiers.

6.1 Introduction

The prediction by the central nervous system of perturbations resulting from voluntarily-initiated movements results in programmed anticipatory muscle activations (*i.e.* starting before the perturbation) which provide *favourable conditions* to cope with these perturbations. These anticipatory muscle activations are made possible by a forward model, predicting a future state of the whole-body based on the initial state and a copy of the motor commands. In case of an expected external perturbation, a prior experience of the perturbation is required to provide adequate anticipatory muscle activations. Because gravity constantly accelerates our whole-body downward, humans have learnt to anticipate its consequence, and adapt their muscle activations to the intended task, both in term of timing and magnitude (White et al., 2020).

In landing contexts, muscles are activated before contact to prepare accelerating the whole-body upward (Jones & Watt (1971b); Santello (2005), see also section 2.3). These anticipatory muscle activations provide different *favourable conditions* for landing. First, it has largely been suggested that these anticipatory muscle activations increase lower-limb stiffness, and thus limit joint excursion and whole-body Centre of Mass (CoM) vertical displacement at the beginning of ground contact (Jones & Watt, 1971b; Butler et al., 2003; DeMers et al., 2017). Second, we showed that anticipatory muscle activations before ground contact have also kinematic consequences: they initiate hip and knee joint flexion before contact, thus limiting the change in joint angular velocity due to ground contact, contributing to protect the skeletal system (chapter 5).

During drop-landing and drop-jumping from 0.2 to 0.6 m, anticipatory muscle activations have been recorded during the last 150 ms preceding ground contact (Arampatzis et al., 2001; Ambegaonkar et al., 2011), with a theoretical air-time (*i.e.* the time from take-off of an elevated platform to ground contact) between 202 ms and 349 ms. Authors did not characterised the possible muscle activation periods existing between the time from take-off to the identified anticipatory muscle activation onsets. In this respect, Greenwood & Hopkins (1976b) recorded a first burst of muscle activation just after dropping. In their experiment, participants were suspended, tied in a harness, and release unexpectedly. Thus, they characterised the first burst as a startle reaction, that did not provide any further *favourable condition* for the landing task. When landing on hands (simulating a forward fall), the same startle reaction has been identified (Borrelli et al., 2020). However, the startle reaction may not be the only reason they recorded anticipatory muscle activations. Indeed, during this task, rapid upper-limb orientation was also recorded (Borrelli et al., 2020), and should result from anticipatory muscle activations, in addition to gravity which plays a major role to direct upper-limbs vertically. Yet, early anticipatory muscle activations could also serve the orientation of upper or lower-limb drop-landing tasks.

The aim of the chapter is to explore the possible presence of an anticipatory muscle activation period before the one already described in the literature, and the possible role of earlier anticipatory muscle activations. Based on the literature, we hypothesise that

a period of muscle activation would be present before the one already described if some lower-limb adjustments are required. Also, we computed the timing of the onsets of this earlier anticipatory muscle activation period, and hypothesised that their onset would not be time-locked to take-off, because this is not a startle reaction.

6.2 Methods

Participants, procedure and measurements are described in [Methods \(Second experiment: Anticipation of contact\)](#).

6.2.1 Data Analysis

6.2.1.1 Electromyography

[Electromyography \(EMG\)](#) envelopes were computed with a zero-phase second-order zero-phase low-pass Butterworth filter at 50 Hz, and onsets of muscle activations using a double-threshold method ([Hodges & Bui, 1996](#)). To be considered active, the [EMG](#) envelop had thus to be larger than an activation threshold during at least 25 ms (figure 6.1a). The activation threshold of each participant was established as the average plus three standard deviations of the baseline signal recorded when participants were laying on their back. Offsets of muscle activations are less described in the literature. Here, we used the same criteria to characterise muscle offsets during the air-time preceding ground contact ([Walter, 1984](#)), i.e. the [EMG](#) envelop had to be smaller than the activation threshold during at least 25 ms. Practically, we first considered each muscle active at take-off. We first computed the first muscle offset, and computed muscle onsets and offset, to be sure that the first muscle onset we computed was not related to the push-off phase initiating the task.

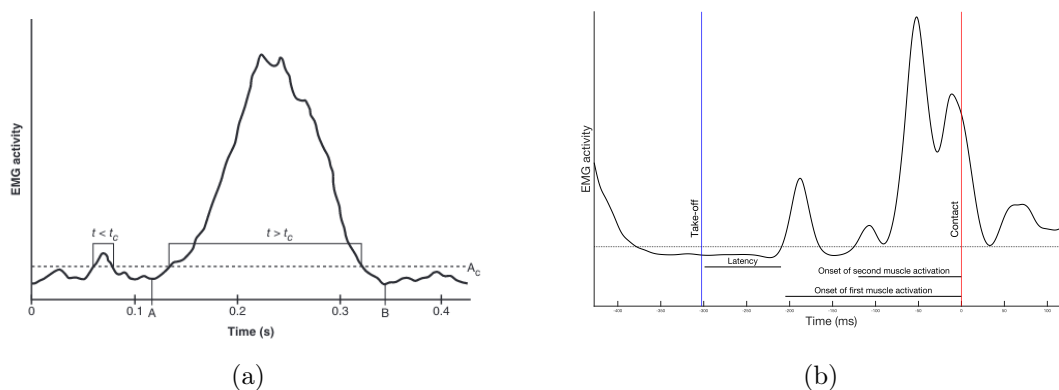


Figure 6.1: (a) Double threshold method to detect muscle activation. The duration of [EMG](#) envelop must be larger than the duration threshold (dotted horizontal line), for a period larger than t_c , the second threshold, from [Walter \(1984\)](#). (b) Example of double activation recorded for a participant during the anticipatory phase preceding contact (vertical line in red) and after take-off (vertical line in blue). Latency represents the duration from take off to the first muscle activation. Onsets of the first and second muscle activation are the time from the first and second activation to contact.

In this chapter, we did not differentiate landing tasks (*i.e.* drop-jumping and drop-landing),

6.3. RESULTS

but we consider all trials together (four trials per participants -two drop heights and two task per drop-height-, twenty participants, for a total of 80 trials). For each muscle we recorded the EMG signals, we then computed the percentage of trials with two anticipatory muscle activation periods during the anticipatory phase (*the air-time phase*). For each muscle, we then divided trials into two groups: one group presenting two anticipatory muscle activation periods during the anticipatory phase, and one group with one anticipatory muscle activation period during the anticipatory phase. The sample size for each group varied between muscles (see Results section). Finally, for all trials with two anticipatory muscle activation periods, we computed the latency of the first anticipatory muscle activation, defined as the time between the take-off and the onset of the first anticipatory muscle activation (figure 6.1b).

6.2.2 Kinematics

Lower-limb flexion joint angles were calculated (section 5.2.1.2). We computed both the time evolution of joint angles and the onset of joint flexion during the anticipatory period.

6.2.3 Statistical Analysis

Statistical analyses were performed using Matlab (MathWorks, version 2021b). As specified in chapter 5, most variables were not normally distributed, therefore only non-parametric tests were used. We performed a Wilcoxon signed rank test to compare latency of the first muscle activation period (when present) between the two drop heights (0.35 and 0.5 m), to determine whether muscles activations are timed according to the onset of the drop or according to the expected contact time. Next, we performed Wilcoxon signed rank tests to compare onsets of hip and knee joint flexion between trials with two anticipatory muscle activation periods and with one anticipatory muscle activation period, independently for each muscle. When onsets of joint flexion were different between trials with and without two anticipatory muscle activation periods, we performed a non parametric Statistical Parametric Mapping (SPM) to compare joint angle and joint angular velocity curves (Pataky, 2010).

6.3 Results

6.3.1 Characterisation of two muscle activation periods

Two periods of anticipatory muscle activation were found for every lower-limb muscle in some trials (table 6.1). For trials with two anticipatory muscle activation periods, the latency of the first activation period is presented for each lower-limb muscle investigated in table 6.2. A longer latency was found in the 0.5 m drop height compared to the 0.35 m drop height for gastronemius medialis and rectus femoris, whereas no difference was found for all other the muscles. A representation of the two anticipatory muscle activation periods with their timing and duration is presented in figure 6.4).

Table 6.1: Total and percentage trials with two muscle activation periods for both the drop-landing and drop-jumping tasks, and from the two drop heights.

| | Trials with two activation periods | Percentage of trial with two activation periods | | |
|-------------------------|--|---|----------------|---------------|
| | | Total | Drop 0.35 m | Drop 0.5 m |
| Tibialis anterior | 55 | 68.75 | 67.5 | 70 |
| Soleus | 26 | 32.5 | 32.5 | 32.5 |
| Biceps femoris | 52 | 65 | 70 | 67.5 |
| Gastrocnemius medialis | 36 | 45 | 50 | 40 |
| Gastrocnemius lateralis | 43 | 53.75 | 52.5 | 55 |
| Semitendinous | 52 | 65 | 65 | 65 |
| Vastus medialis | 50 | 62.5 | 65 | 60 |
| Vastus lateralis | 54 | 67.5 | 67.5 | 67.5 |
| Rectus femoris | 52 | 65 | 65 | 65 |

6.3.2 Difference between groups of trials

When comparing lower-limb kinematics in trials with and without two anticipatory muscle activation periods, we found later onsets of hip and knee flexion in trials who displayed two anticipatory muscle activation periods in the soleus ($p = 0.019$ and $p = 0.022$ for the hip and knee, respectively), and we found an earlier onset of knee flexion in trials who displayed two anticipatory muscle activation periods in the rectus femoris ($p < 0.001$) (figure 6.3). For all others muscles, there was no difference in onset of hip and knee flexion between groups of trials.

Compared to the trials with only one anticipatory muscle activation period in the soleus, trials with two anticipatory muscle activation periods had a larger knee joint flexion at the onset of the air-time phase (from 234 to 202 ms before ground contact), and a larger extension angular velocity in the knee from 165 to 109 ms before contact, and in the hip from 129 to 99 ms before ground contact (figure 6.2).

Compared to the trials with only one anticipatory muscle activation period in the rectus femoris, trials with two anticipatory muscle activation periods has a lower hip flexion angle from 192 ms before ground contact to 3.5 ms after ground contact, a lower knee flexion angle from 173 to 51 ms before ground contact, and a larger knee flexion angular velocity from 78 to 26 ms before ground contact (figure 6.3).

6.4 Discussion

Our goals were to explore the possible presence of an anticipatory muscle activation period between take-of and the one already described in the literature, and explore the possible role of earlier anticipatory muscle activations. Here, we found two anticipatory muscle activation periods in all muscles investigated, but not in all trials. For two of the muscles investigated, the presence or the absence of two anticipatory muscle activation periods led to differences in onsets of joint flexion and in the anticipatory kinematics adjustments, and

6.4. DISCUSSION

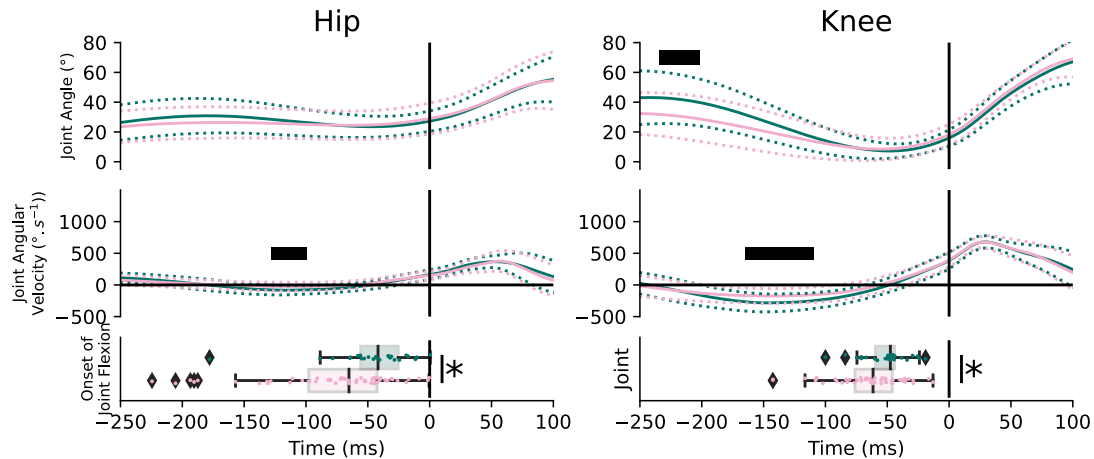


Figure 6.2: Hip and knee joint flexion angles, angular velocities and onset of flexion for trials with one (pink) and two (green) activation periods in the soleus. Thick lines represent mean results across participants, while dotted lines represent one standard deviation from the mean. Points in the bottom graphs represent each individual values. Black rectangles represent periods of significant difference between the two groups based on the non-parametric *SPM*. Because there was no difference between groups for ankle angle, angular velocity, and onset of ankle flexion, we chose not to represent ankle kinematic results.

to differences in joint angles and angular velocity during the anticipatory phase. Combined with the fact that these activations seem not to be startle reactions, these two anticipatory muscle activation periods may serve the role of adjusting the lower-limb kinematics before initiating joint rotations we previously described (chapter 5), but need to be confirmed in future studies.

6.4.1 Presence of two periods of muscle activation

Contrary to previous studies (Santello & McDonagh, 1998; Arampatzis et al., 2001; Ambe-
gaonkar et al., 2011), we quantified -and found- the presence of two anticipatory muscle ac-
tivation periods in all muscles investigated, but not in all trials during voluntarily-initiated
drop-landings tasks (table 6.1). It appears that the majority of the literature only searched
for one anticipatory muscle activation period before ground contact, and did not charac-
terise possible muscle activations between take-off and the anticipatory muscle activation
leading to ground contact. During involuntarily-initiated landing tasks, Greenwood &
Hopkins (1976b,a) quantified two anticipatory muscle activation periods in the soleus, tib-
ialis anterior, hamstrings and quadriceps muscles before ground contact. They qualified
the first activation period as a startle reaction because the activation period was timed
relative to the release instant, and was not present during voluntarily-initiated falls. Before
explaining why we obtained different results from their studies, we must determine if the
first activation period we recorded can be characterised as a startle reaction. The startle re-
action recorded by Greenwood & Hopkins (1976b) is supposed to be triggered by vestibular
contribution, through the detection of a distinct and large change in whole-body vertical
acceleration. During voluntarily-initiated movements, the reafference principle suggests
that the nervous system is able to differentiate between the sensory information due to the

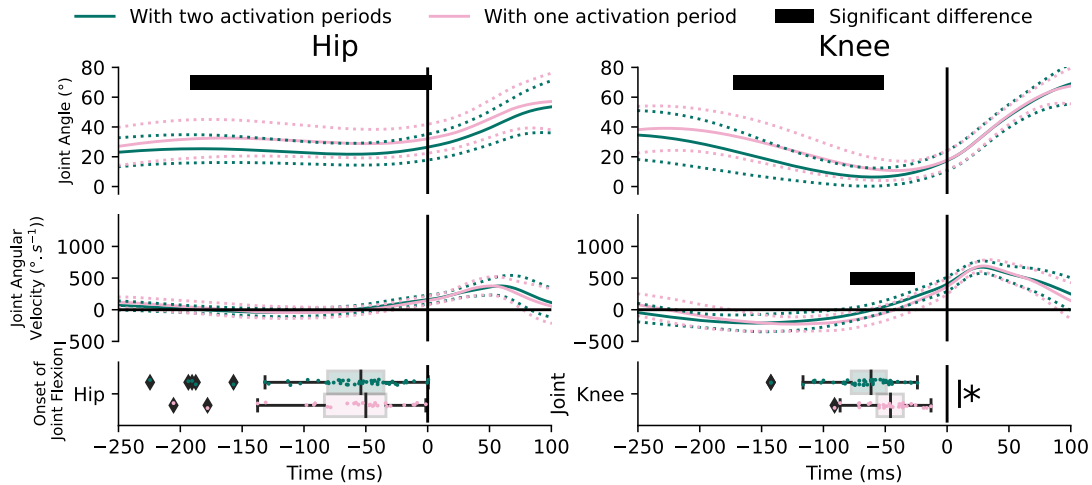


Figure 6.3: Hip and knee joint flexion angles, angular velocities and onset of flexion for trials with one (pink) and two (green) activation periods in the rectus femoris. Thick lines represent mean results across participants, while dotted lines represent one standard deviation from the mean. Points in the bottom graphs represent each individual values. Black rectangles represent periods of significant difference between the two groups based on the non-parametric *SPM*. Because there was no difference between groups for ankle angle, angular velocity, and onset of ankle flexion, we chose not to represent ankle kinematic results.

voluntary movement and the sensory information due to perturbation from external environment (von Holst & Mittelstaedt, 1971). Applied to voluntarily-initiated drop-landing tasks, the change in whole-body vertical acceleration is expected, and therefore not considered as a perturbation by the nervous system. Thus, as suggested by Greenwood & Hopkins (1976b), it is unlikely that startle reactions occur during voluntarily-initiated falls.

When looking at muscle latencies (table 6.2), two additional arguments may confirm that these anticipatory muscle activations are not startle reactions. First, latencies in our studies are smaller than the one reported during externally-initiated falls in the tibialis anterior and the gastrocnemius (Sanders et al., 2015). Second, we found differences in muscle latencies for two muscles between drop-heights, suggesting that these muscle activation onsets are not timed according to the take-off time. These two arguments may suggest that these anticipatory muscle activations are programmed in a feedforward way, and released at a predicted time after take-off.

6.4.2 Potential roles of these activations

Similarly to chapter 5, we must look at lower-limb joint kinematic as consequences of muscular activations to investigate possible roles of the first muscle activation period we observed. In our study, participants performed both extension and flexion of hip and knee joints during the air-time period preceding ground contact (figures 6.2 and 6.3). The link between muscle activations and kinematics is difficult to make for a pluri-articular system, notably because of the presence of dynamic coupling (Hollerbach & Flash, 1982; Zajac &

6.4. DISCUSSION

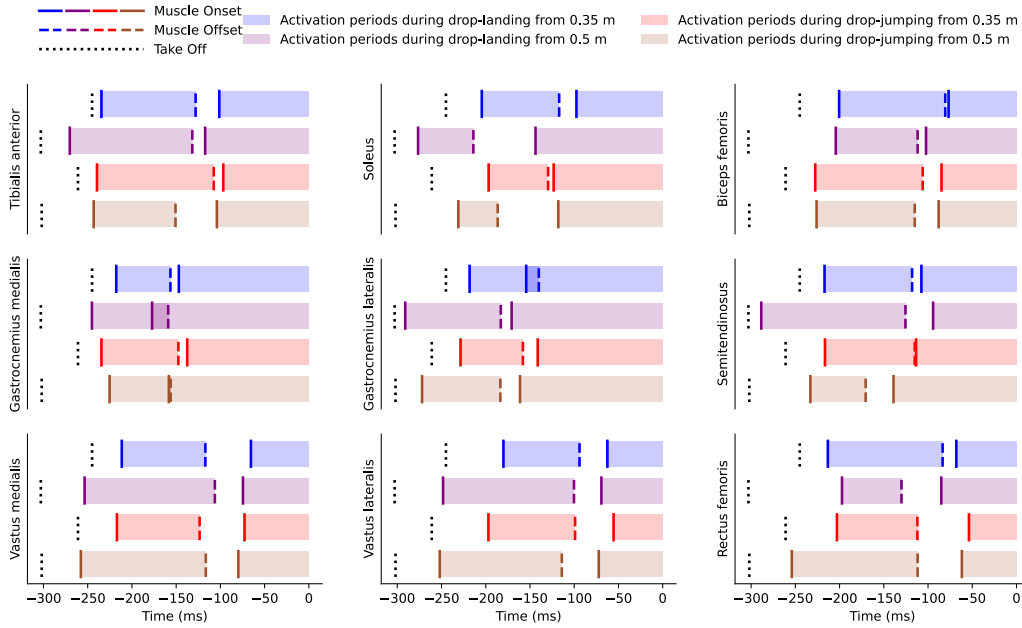


Figure 6.4: Graphical representation of the two muscle activation periods. Black dots represent the median time when participants left the elevate platform. Vertical lines represent the median onset of muscle activations (when present), and dotted vertical lines the median offset of the first muscle activation period (when present).

Gordon, 1989), the motion of one segment affecting the motion of another segment due to induced forces. Here, we compared anticipatory kinematic adjustments between trials with and without the first muscle activation period. We focused on two muscles, the soleus and the rectus femoris, because we found a significant difference in onset of hip and/or knee flexion between trials with and without two anticipatory muscle activations periods for these muscles (figures 6.2 and 6.3).

We found differences in knee angle, knee angular velocity and hip angular velocity between trials with and without first anticipatory activation period in the soleus (figure 6.2). Whereas a direct link between soleus activation and hip and knee kinematics is not obvious, motion of one joint can be influenced by muscles not crossing this joint due to dynamic coupling (Zajac & Gordon, 1989; Yamaguchi & Zajac, 1990). For instance, during walking, knee kinematics in early swing phase are influenced not only by muscles that cross the knee, but also by moments generated at other joints, such as the ankle (Anderson et al., 2004; Arnold et al., 2007). In particular, plantarflexors (including soleus) of the swing lower-limb were demonstrated to accelerate the knee toward extension during the swing phase of gait (Anderson et al., 2004; Arnold et al., 2007). In their study, ankle moment changed knee flexion by a fine margin, mostly because the largest contribution of knee flexion comes from stance lower-limb muscles, acting directly on the pelvis (Arnold et al., 2007). However, in absence of contact with the ground, as in our study, muscles activations necessarily plays an important role to control lower-limb joints, in addition to gravity (Anderson et al., 2004). Thus, the fact that plantarflexors would help extending the knee joints is consistent with our findings. Trials with a first anticipatory activation period in the soleus had the knee more flexed during the beginning of the air-time phase, and then exhibited a larger

Table 6.2: Latency of each muscle first activation period (when present), for each drop height. Q1 = first quartile, Q3 = third quartile. Bold rows indicate a significant difference between the two drop heights for the corresponding muscle.

| | Drop 0.35 m | Drop 0.5 m | <i>p</i> value |
|-------------------------------|------------------------------------|-------------------------------------|----------------|
| | median | median | |
| | [Q1; Q3] | [Q1; Q3] | |
| Tibialis anterior | 13.0 [4.5; 26.0] | 18.8 [4.5; 104.1] | 0.20 |
| Soleus | 12.0 [10.0; 84.5] | 23.5 [7.0; 29.5] | 0.98 |
| Biceps femoris | 32.8 [11.3; 96.6] | 68.5 [24.0; 124.8] | 0.16 |
| Gastrocnemius medialis | 17.8 [0.38; 53.6] | 88.0 [45.5; 106.8] | 0.01 |
| Gastrocnemius lateralis | 7.0 [2.5; 54.5] | 9.3 [0.1; 75.1] | 0.86 |
| Semitendinous | 32.5 [4.3; 68.6] | 34.0 [0.4; 84.2] | 0.92 |
| Vastus medialis | 36.0 [11.5; 62.6] | 48.5 [5.4; 93.3] | 0.45 |
| Vastus lateralis | 52.5 [17.3; 84.0] | 60.5 [32.5; 97.5] | 0.45 |
| Rectus femoris | 50.8 [20.3; 88.5] | 77.8 [61.6, 118.9] | 0.03 |

knee extension angular velocity to reach an extended knee position similar to the other group before flexing again the knee joint (figure 6.2), as described in chapter 5.

We also found differences in hip and knee angles, as well as knee angular velocity between trials with and without two anticipatory activation periods in the rectus femoris (figure 6.3). Rectus femoris is a bi-articular muscle, being both a hip flexor and a knee extensor. During swing phase of gait, rectus femoris mainly acts as a knee extensor (Arnold et al., 2007). Likewise, we found that trials with two anticipatory activation periods in the rectus femoris exhibited a more extended knee during a large part of the air-time period preceding ground contact. After that, the knee started to flex earlier than in trials with one anticipatory activation period in the rectus femoris, to reach the same knee joint angle and angular velocity at ground contact figure 6.3.

In both cases, the kinematic adjustments consecutive to soleus or rectus femoris first activation period seem to place the knee in an extended position, similar to the trials without only one activation period. This extended knee position seems required to reach a given knee joint angle at ground contact with a given angular velocity. Therefore, based on our results, we can suggest that activating the soleus and/or the rectus femoris during the air-time phase is part of a strategy used to reach this first knee joint configuration during the air-time period preceding ground contact. If these muscle activations enable such kinematic adjustments, it may partly explain why Greenwood & Hopkins (1976b) did not find similar muscle activations during voluntarily-initiated falls. In their experiments, par-

6.4. DISCUSSION

ticipants were suspended, tied in a harness. Their lower-limbs were thus already extended during the air-time period. In contrast, our participants initiated a drop from a rigid elevated platform. Our participants probably had flexed knee joints just after the voluntary drop initiation (figures 6.2 and 6.3), and had to adjust their lower-limb kinematics to reach the knee extended position required to initiate the flexing motion at ground contact.

6.4.3 Limits

Here, we compared trials with and without two muscle activation periods to infer on their role in anticipation of contact. There are multiple limits to this work. First, the study of **EMG** signals often results in large variance among different participants. In particular, both the cut-off frequency and the thresholds selected to obtain the envelop and the onset of muscular activations can introduce variabilities (Hodges & Bui, 1996). Nevertheless, threshold methods, as the one we used, remain the most used method in the research literature (Carvalho et al., 2023), with the advantages that results can be verified visually. Moreover, our results of the anticipatory muscle activation just before ground contact were consistent with previous studies (Santello & McDonagh, 1998; Arampatzis et al., 2001; Ambegaonkar et al., 2011). Second, we computed muscle offset based on the same criteria than muscle onset, but we can imagine characterising a decrease in muscle activation as a strategy controlled by the nervous system. Indeed, in some situations, a muscle offset could not be detected because the minimum time the **EMG** signal has to be under the threshold was not respected, in particular when air-time duration is low. However, the **EMG** signal significantly decreased during this time interval, and would indicate muscle relaxation. We suggest that using high density **EMG** would help in having more quantitative information about muscle activity during the anticipatory phase of drop-landing (Del Vecchio et al., 2020). Third, estimation of muscle force (and thus muscle action) based on **EMG** is not straightforward (Dick et al., 2024). In particular, muscle force depends on muscle state (muscle and fibres length and variation of lengths, level of activation, passive properties of the muscle tendon unit), and the onset of muscle force depends on the electromechanical delay, which is muscle and task dependent. In addition, and in accordance with our previous point, characterisation of force offset remains unexplored, making it difficult to describe a sequence of muscle force production during a given period of time. To overcome these limitations and further test the assumptions we presented here, (Dick et al., 2024) proposed that using electromyography in combination with muscle models would be a promising approach to better characterise the muscle force produced during a task (Sartori et al., 2012), and **EMG** in combination to musculoskeletal models would help to better characterise the recorded kinematics. Indeed, these musculoskeletal simulations completed by induced acceleration analyses, such as in (Anderson et al., 2004; Arnold et al., 2007) for the swing phase of gait, would enable elaborating cause-effect relationships between muscle activations and joint angle changes, to complete our understanding of the biomechanical adjustments performed during the air-time period preceding ground contact.

6.4.4 Perspectives

Here, we did not compare the two tasks (drop-landing and drop-jumping). Similar to results presented in chapter 5, we can expect different strategies and anticipatory phases between these two tasks. Indeed, Leukel et al. (2011) found that participants were not able to switch from a drop-landing to a drop-jumping task if instructed too late during the air-time period preceding ground contact. Although they argued that a lack of muscle stiffness could be responsible for this incapacity to switch between tasks, our results suggest that it can also be the joint configuration before contact: it is possible that participants were not able to match the joint configuration required to perform the anticipatory kinematic adjustments before ground contact. In particular, we recorded a larger knee flexion angle at ground contact during drop-jumping compared to drop-landing from the same-height, without any difference in joint flexion timing or angular velocity (figure 5.1). Therefore, the knee must be less extended to perform a drop-jumping task, and this reduced extension must be both predicted and anticipated during the air-time period to enable the proper realisation of the task.

6.4.5 General implication of two anticipation periods

The presence of two anticipatory muscle activation periods have implications for general anticipation, and not only for drop landing tasks. In chapter 5, we proposed that initiating hip and knee joint flexion before ground contact limits the change in joint angular velocity due to contact. We thus proposed that landing with 1) flexed joint positions and 2) flexion angular velocity at contact time represent *favourable conditions* to protect the skeletal system. To satisfy these two conditions, extended joints are required during air-time, so that a flexing motion can be initiated to reach a given value of joint flexion, with angular velocity. Therefore, as it is the case in our experiment, if hip and knee joints are already flexed during the air-time period, and participants want to contact the ground with flexed joints and flexing angular velocity, they must start by extending their joints, to be in a configuration enabling them to perform these anticipated flexing motions. Therefore, during the simple task of drop-landing, the *favourable condition* at contact (*i.e.* flexed joints and flexion angular velocities) requires its own *favourable condition* (*i.e.* extended lower-limbs that enable to reach the flexed joints with adapted flexion angular velocities) to be attained. By contributing to slightly extend the hip and knee joints in the first instants of the air-time period, the first anticipatory muscle activation period we described in this chapter may contribute to generate these *favourable conditions* for landing, when voluntarily dropping from a box.

6.5 Conclusion

Our results show the existence of an anticipatory muscle activation period before the one already described in the literature during the air-time phase preceding ground contact of drop-landing tasks. Due to the latency of this anticipatory muscle activation, it appears not to be a startle reaction, contrary to externally-induced landing tasks described in the

6.5. CONCLUSION

literature. When comparing trials with and without two anticipatory muscle activation periods, we found differences in onsets of hip and knee joints flexion, angles and angular velocities during air-time, suggesting that this first anticipatory muscle activation period would adjust the lower-limb orientation. Finally, a specific lower-limb kinematic configuration seems to be required before initiating the lower-limb joint flexions we described in chapter 5, and may result from this anticipatory muscle activation period.

6.6 French summary

6.6.1 Introduction

Dans des contextes de réception, les muscles sont activés avant de toucher le sol pour préparer à accélérer le corps complet vers le haut. Ces activations musculaires anticipées apportent différentes *conditions favorables* à la réception. Premièrement, il a largement été suggéré que ces activations musculaires anticipées permettent de rigidifier les articulations du membre inférieur, et ainsi limiter les amplitudes articulaires et le déplacement vertical du centre de masse du corps complet durant le contact. Deuxièmement, nous avons montré que ces activations musculaires anticipées ont également des conséquences cinématiques : elles permettent d’initier la flexion de la hanche et du genou avant le contact au sol, limitant ainsi la variation de vitesse angulaire à cause du contact, protégeant ainsi le système squelettique (chapitre 5).

Durant des tâches de réceptions de 0.2 à 0.6 m, les activations musculaires anticipées ont été enregistrées durant les 150 ms précédant le contact. Cependant, le temps théorique de vol est entre 202 et 349 ms, et les auteurs n’ont pas caractérisé les autres activations musculaires entre le début de la chute et le début des activations musculaires déjà identifiées. Pourtant, [Greenwood & Hopkins \(1976b\)](#) ont enregistré une première période d’activation musculaire juste après le début de la chute. Durant leur expérience, les participants étaient maintenus par un harnais, et relâchés de manière soudaine et imprévisible. Ils ont donc caractérisé la première période d’activation comme étant une réaction de sursaut, qui n’apporterait pas de *condition favorable* à la tâche. Durant des réceptions sur les mains (en simulant une chute vers l’avant), cette même réaction de sursaut a été enregistrée ([Borrelli et al., 2020](#)). Cependant, lors de cette tâche, une orientation rapide du membre supérieur est également visible, et pourrait provenir de la première période d’activation musculaire, en plus de la gravité qui joue un rôle majeur pour diriger les membres supérieurs de manière verticale vers le bas. Ainsi, la première période d’activation musculaire pourrait servir à l’orientation des membres supérieur et inférieur durant des tâches de réception. Le but de ce chapitre est d’explorer la possible présence de différentes périodes d’activation musculaires anticipées.

6.6.2 Méthode

Pour détecter les périodes d’activation musculaires, nous avons utilisé la méthode du double seuil de [Hodges & Bui \(1996\)](#). Pour être considéré comme actif, l’enveloppe électromyographique (EMG) doit être supérieure à un seuil d’activation pendant au moins 25 ms (figure 6.1a). Le seuil d’activation de chaque participant a été établi comme étant la moyenne + 3 écarts types du signal lorsqu’ils étaient allongés sur le dos. La manière de détecter la fin d’une activation musculaire est beaucoup moins décrite dans la littérature. Ici, nous avons utilisé les mêmes critères que pour l’activation : l’enveloppe EMG doit être inférieure au seuil pendant au moins 25 ms.

Dans ce chapitre, nous n’avons pas différencié les tâches, et nous avons considéré tous les essais réalisés par tous les participants. Pour chaque muscle étudié, nous avons calculé le

6.6. FRENCH SUMMARY

pourcentage d'essai où deux périodes d'activation étaient présentes. Pour chaque muscle, nous avons séparé les essais en deux groupes : un groupe avec les essais contenant deux périodes d'anticipation, un groupe avec les essais contenant une seule période d'activation. Le nombre d'essais dans chaque groupe varie donc selon les muscles. Nous avons comparé les variables cinématiques (évolutions temporelles des angles et vitesses angulaires et début de flexion des articulations du membre inférieur) entre les deux groupes. Enfin, pour les essais avec deux périodes d'activation, nous avons calculé la latence (le temps entre le début de la chute et la première activation).

6.6.3 Résultats

Nous avons trouvé deux périodes d'activation musculaire pour chaque muscle étudié. Leur occurrence est présentée table 6.1. Pour ces activations, les latences sont présentes table 6.2. Nous avons trouvé une latence plus importante lors des chutes de 0.5 comparés à 0.35 m. pour le *gastrocnemius* médial et le *rectus femoris*, et aucune différence n'a été trouvée pour les autres muscles.

Lorsque nous avons comparé la cinématique du membre inférieur entre les essais avec et sans deux périodes d'activation musculaire, nous avons trouvé une initiation de flexion de la hanche et du genou plus tardive dans les essais avec deux périodes d'activation du *soleus* ($p = 0.019$ et 0.022 , respectivement), et une initiation de flexion du genou plus précoce dans les essais avec deux périodes d'activation du *rectus femoris* ($p < 0.01$).

Les essais avec deux périodes d'activation du *soleus* montrent une flexion du genou plus importante 234 à 202 ms avant le contact, et une plus grande vitesse angulaire d'extension du genou 165 à 109 ms et de la hanche 129 à 99 ms avant le contact. Les essais avec deux périodes d'activation du *rectus femoris* montrent une flexion de hanche plus faible de 192 ms avant le contact à 3.5 ms après le contact, une plus faible flexion de genou de 173 à 51 ms avant le contact, et une vitesse angulaire d'extension du genou plus importante de 78 à 26 ms avant le contact.

6.6.4 Discussion

Nous avons trouvé deux périodes d'activation musculaires anticipées pour tous les muscles étudiés, mais pas pour tous les essais. Pour deux des muscles étudiés, la présence ou non de la première période d'activation a mené à des différences d'instant de début de flexion de la hanche et du genou, et à des différences d'angles et de vitesses angulaires durant la phase de vol (la phase d'anticipation). Etant donné que les sauts réalisés dans notre expérience sont des mouvements volontairement initiés, il apparaît peu probable que la première période d'activation enregistrée soit une réaction de sursaut. En effet, le principe de réafférence suggère que le système nerveux est capable de différencier les informations sensorielles qui proviennent d'un mouvement volontaire des informations sensorielles qui proviennent d'une perturbation extérieure (von Holst & Mittelstaedt, 1971). Ici, le changement d'accélération du centre de masse du corps complet lors de la chute est initié volontairement, et ne devrait donc pas provoquer de réaction de sursaut. De plus, les latences que nous avons enregistrées

dans cette étude sont plus faibles que les latences enregistrées lors de réaction de sursaut, pour les mêmes muscles étudiés (Sanders et al., 2015). De plus, nous avons trouvé des différences de latences entre les sauts depuis deux hauteurs différentes, suggérant que la première activation n'intervient pas à un temps fixe après le début de la chute.

De la même manière que dans le chapitre 5, nous avons regardé la cinématique du membre inférieur pour caractériser les conséquences de cette première période d'activation musculaire. Dans notre étude, les participants ont réalisé une extension puis une flexion de la hanche et du genou durant la phase de vol précédant l'instant de contact. Le lien entre les activations musculaires et la cinématique est difficile à réaliser pour les systèmes multi-corps, notamment à cause de la présence de couples d'interaction (Zajac & Gordon, 1989), le mouvement d'un segment qui influence les segments adjacents.

Nous avons trouvé des différences au niveau des angles de flexion et des vitesses angulaires de la hanche et du genou entre les essais avec et sans deux périodes d'activation musculaire. Premièrement, les essais avec deux périodes d'activation du soleus montrent une articulation du genou plus fléchie au début de la période d'anticipation, puis montrent une vitesse angulaire en extension plus importante. Un lien indirect entre l'action des fléchisseurs plantaires et l'extension du genou avait déjà été suggéré pendant la phase d'oscillation de la marche (Anderson et al., 2004; Arnold et al., 2007). Deuxièmement, les essais avec deux périodes d'activation du rectus femoris montrent une articulation du genou plus en extension au début de la période d'anticipation, puis commencent à fléchir le genou de manière plus précoce avec le même angle de flexion et la même vitesse angulaire en flexion à l'instant du contact.

Dans les deux cas, les ajustements cinématiques suite à la première période d'activation musculaire semblent mener à une extension du genou, pour arriver à un angle similaire aux essais qui n'ont pas la première période d'activation. Cette position semble nécessaire pour pouvoir ensuite initier une flexion et toucher le sol avec un certain angle et une certaine vitesse angulaire. Nous pouvons suggérer, sur la base de nos résultats, que la première activation du soleus et du rectus femoris fait partie d'une stratégie pour atteindre cette première configuration des articulations du membre inférieur.

6.6. FRENCH SUMMARY

CHAPTER 7

Anticipation of contact: Kinematics of bi-articular muscle tendon units

Where all men think alike, no one thinks very much.

Walter Lippman

Part of the results presented here have been presented at the 28th Annual Congress of the European College of Sport Science in Paris (Bechet et al., 2023a).

7.1 Introduction

Anterior Cruciate Ligament (ACL) rupture is dramatic injury that affects individuals both in daily life and in athletic activities, with an incidence up to 39 injuries per 100,000 people (Singh, 2018). ACL rupture has significant detrimental consequences for humans: it is a important emotional trauma (Padaki et al., 2018), only 65 % of the athletes recover their pre-operation level (Gobbi & Francisco, 2006), and 35 % of injured humans will suffer from knee osteoarthritis 10 years after the injury (Lie et al., 2019). Despite extensive research on ACL ruptures across various sports activities, no definitive cause has been identified (Beaulieu et al., 2023), and the number of ACL injuries continues to increase, particularly among adolescents (Kooy et al., 2023). Since an ACL rupture occurs when the mechanical load on the knee exceeds the ligament’s capacity, it is crucial to understand the situations that increase the mechanical stress on the ACL. This knowledge is essential for developing more effective prevention strategies. The majority of the ACL rupture mechanisms were deduced from posteriori video analyses of injuries (Carlson et al., 2016). Thus, it was long hypothesised that ACL rupture occur following a unique traumatic event. However, evidences from in vitro studies suggested that ACL ruptures can occur following ligament fatigue (Lipps et al., 2013; Wojtys et al., 2016). The accumulation of damage from repetitive strain reduces both the ligament’s strength and the threshold of mechanical load required for an ACL rupture. Therefore, we must identify how it is possible to limit the daily exposition of ACL strain to reduce the risk of injury.

Significant ACL strain and ruptures are typically observed during movements that involve a rapid deceleration, such as landing from a jump or a quick change of direction (Shimokochi & Shultz, 2008). During these movements that involve large **Ground Reaction Forces (GRF)**, three-dimensional movements of the leg relative to the thigh —namely anterior translation, internal rotation, and abduction— can increase ACL strain and rupture (Krosshaug et al., 2007; Koga et al., 2010; Beaulieu et al., 2023). In vitro apparatus were developed to be able to quantify how these movements influence the mechanical load of the ACL (Withrow et al., 2006). Using this apparatus, it was suggested that, the combination of anterior translation and internal rotation puts more strain on the ACL than the combination of anterior translation and abduction during jump landings (Oh et al., 2012). Therefore, gaining a deeper understanding of the mechanisms that limit knee internal rotation is essential for developing more effective prevention strategies.

Another key factor in reducing ACL strain during dynamic movements is the force generated by the hamstrings, which counteracts the pull of the quadriceps muscle, as reviewed in Maniar et al. (2022). Quadriceps muscle force is required to decelerate knee flexion during ground contact, but provokes the anterior translation of the leg relative to the leg (Demorat et al., 2004; Victor et al., 2010). Hamstrings muscle force limit the anterior translation of the leg, thus increasing knee joint stability (Baratta et al., 1988; Victor et al., 2010). Still using in vitro studies, it was suggested that hamstrings contraction reduces the knee internal rotation and the ACL strain during quasi-static (Li et al., 1999; MacWilliams et al., 1999) and landing situations (Withrow et al., 2008). Given that a

muscle can produce larger magnitude of force during an eccentric contraction (Westing et al., 1991), Withrow et al. (2008) suggested that ACL strain can be reduced by an eccentric hamstrings activation during landing tasks. They suggested that increasing hip flexion during ground contact could lengthen the hamstrings Muscle Tendon Units (MTU), and potentially reducing ACL strain. However, this hypothesis has not been confirmed experimentally. Additionally, while they did not test for statistical significance, the study indicated that knee internal rotation might be lower when the hamstrings are activated eccentrically compared to isometrically (Withrow et al., 2008). In chapter 5, we showed that humans initiate hip and knee joint flexions before ground contact during drop-landing tasks. Anticipatory hip flexion could prepare the hamstring muscles to lengthen, thereby limiting the knee internal rotation and reducing ACL strain during ground contact. In other words, some motor strategies could help reduce the risk of ACL rupture during daily life and sport activities.

The results regarding the role of hamstrings should be interpreted with caution when considering knee joint stability in the transverse plane because each hamstring muscle affects knee internal rotation differently. The medial hamstrings, the *Temi Tendinosus (ST)* and *SSemi Membranous (SM)*, act as knee internal rotators, while the lateral hamstrings, the biceps femoris short head (BFSH) and *Biceps Femoris Long Head (BFLH)*, act as knee external rotators (Rajagopal et al., 2016). Their functional roles can be assessed by analysing their respective moment arms, indicating the efficiency of each muscle in generating the motion of interest (Sherman et al., 2013). Accordingly, both in vitro (Guelich et al., 2016; Victor et al., 2010) and in silico studies (Maniar et al., 2020) suggested that the force generated by the lateral hamstring (BFLH and BFSH) reduces knee internal rotation, while the force generated by the medial hamstrings (ST and SM) increases it. The force production of each hamstring muscle can be an important factor to reduce the ACL strain during landing. In their review, Maniar et al. (2022) showed that the moment arm of each hamstring muscle depends on the knee flexion angle (see their figure 3). However, the moment arm of a bi-articular muscle depends on all degrees of freedom of the spanned joints: here the three rotations at the knee, and the three rotations at the hip. Therefore, the ratio of moment arms between the knee internal and external rotators could influence the knee rotation during ground contact. How these moment arms, and by extension the force produced, are modulated by all degrees of freedom remain unknown. Because of the importance to control the knee rotation to reduce the ACL strain during landing tasks, quantifying the modulation of moment arms seems important to better understand the importance of each hamstrings muscle to limit knee internal rotation and ACL strain.

The general aim of the study is to characterise anticipatory MTU kinematics of hamstrings, to then infer whether they contribute to protect ACL. First, we computed MTU lengths of each bi-articular hamstrings muscle during both the anticipatory phase and the beginning of the ground contact, to determine if humans use eccentric contractions to increase the force production, as suggested by Withrow et al. (2008). We hypothesise that (1) all three bi-articular hamstrings muscles are more lengthened by hip flexion than the are

7.2. METHODS

shortened by knee flexion; and (2) increased lengthening of the hamstring muscles results in reduced knee internal rotation. Additionally, we computed the ACL length and assume greater hamstring lengthening results in less the ACL elongation during contact, in line with the hypothesis of [Withrow et al. \(2008\)](#). Furthermore, we compute the knee internal rotation moment arm of each hamstring muscle during both the anticipatory phase and the beginning of the ground contact. We hypothesise that a larger moment arm for the BFLH compared to the medial hamstrings will result in reduced knee internal rotation and less change in ACL length during ground contact.

7.2 Methods

Participants, procedure and measurements used in this chapter were described in [Methods \(Second experiment: Anticipation of contact\)](#). Here, we analysed data only extracted from the 0.35 m drop-landing task. Contrary to chapter 5, we analysed all trials performed by all participants to obtain a larger dataset and capture a variety of knee joint angles, particularly with respect to knee external and internal rotations.

7.2.1 Data analysis

From musculoskeletal models scaled for each participants (section 3.2), MTU lengths and muscle moment arms of the BFLH, ST and SM were computed from the personalised musculoskeletal model using the “Analyze” tool from OpenSim. Absolute length of each muscle (expressed in %) were normalised using the maximal lengths we recorded during passive stretching tests (figure 3.3) using equation (7.1), where $L_{MTU}(test)$ is the instantaneous MTU length, $L_{MTU}(max)$ is the maximal MTU length obtained from passive stretching tests and $L_{MTU}(nominal)$ the MTU length when the participant performed in quiet standing trial.

$$L_{MTU}(normalised) = \frac{L_{MTU}(test) - L_{MTU}(nominal)}{L_{MTU}(max) - L_{MTU}(nominal)} \cdot 100 \quad (7.1)$$

Variation in MTU length δL_{MTU} due to variation of one degree of freedom angle can be calculated using the moment arm integration method (equation (7.2)) ([An et al., 1984](#); [Hoy et al., 1990](#)), with r_k the moment arm of the MTU with respect to the joint degree of freedom k , $\delta\Theta_k$ the angle variation of joint degree of freedom k , and d the number of degrees of freedom for the given joint (See Nomenclature page [xix](#) for definition of all variables).

$$\delta L_{MTU} = \sum_{k=1}^d r_k \cdot \delta\Theta_k \quad (7.2)$$

For each bi-articular MTU, the variation in MTU length is the sum of the contribution from each degree of freedom of each joint the MTU crosses (equation (7.3)), with j the number of joints crossed by the MTU.

$$\delta L_{MTU} = \sum_{i=1}^j \sum_{k=1}^j r_{k_i} \cdot \delta \Theta_{k_i} \quad (7.3)$$

We computed a ratio of knee external rotation moment arm by dividing the external moment arm of the **BFLH** by the absolute value of the internal rotation moment arm of the **ST** and **SM**. Because the **SM** has a larger moment arm than the **ST**, we used the value of **SM** for this ratio calculation against the **BFLH**. (equation (7.4)). A ratio greater than 1 indicates that the external moment arm of the **BFLH** is greater than the internal moment arm of the **SM**, while a ratio less than 1 indicates that the external moment arm of the **BFLH** is smaller than the internal moment of the **SM**.

$$ratio = \frac{r_{externalRotation_{knee}(BFLH)}}{|r_{internalRotation_{knee}(SM)}|} \quad (7.4)$$

We computed the **ACL** length based on [Pillet et al. \(2016\)](#) data. At each time frame, we placed endpoints of the **ACL** on the thigh and leg segment coordinate systems. **ACL** length was then estimated from the Euclidean distance between both endpoints, and expressed as a percentage, with 100 % representing the **ACL** length of when participants stood in anatomical reference position.

7.2.2 Statistical Analysis

Statistical analyses were performed using Matlab (MathWorks, version 2021b). The normality of each dependent variable was checked using a Shapiro-Wilk test. For all variables, the null hypothesis was not rejected, so we used only parametric correlation tests. We tested the correlation between hamstrings **MTU** length changes and the knee internal rotation during the first 50 ms of ground contact, according to the hypothesis of [Withrow et al. \(2008\)](#). We also tested the correlation between hamstrings **MTU** length changes and **ACL** length change during the same time interval to quantify the effect directly on the **ACL**. Then, we tested the correlation between the ratio of external moment arm at the time of ground contact and the knee internal rotation amplitude during the first 50 ms of ground contact, according to our last hypothesis. We also tested the correlation between the ratio of external moment arm at the time of ground contact with the **ACL** length change during the first 50 ms of ground contact, to quantify the effect directly on the **ACL**. For all above correlations, selected the first 50 ms of ground contact because the maximum **ACL** strain occurs during this time interval ([Withrow et al., 2008](#)), when the **GRF** is the largest.

7.3 Results

Among the 60 trials recorded, 5 were excluded from analysis because of markers occlusion, marker loss during the trial, or inappropriate ground contact time detection.

We found that all three bi-articular hamstrings **MTU** lengthened during a part of the

7.3. RESULTS

anticipatory period of drop-landing task, from the beginning of the period to approximately 75 ms before ground contact on average figure 7.1. During the beginning of ground contact, we found that all three MTU shortened, due to a larger contribution of the knee compared to the contribution of the hip (see the fourth subplot in figure 7.1). BFLH shortened less than the SM and ST, and lengthened from 40 ms after ground contact. The knee internal rotation, when present, slightly lengthened the BFLH during the landing phase (figure 7.1).

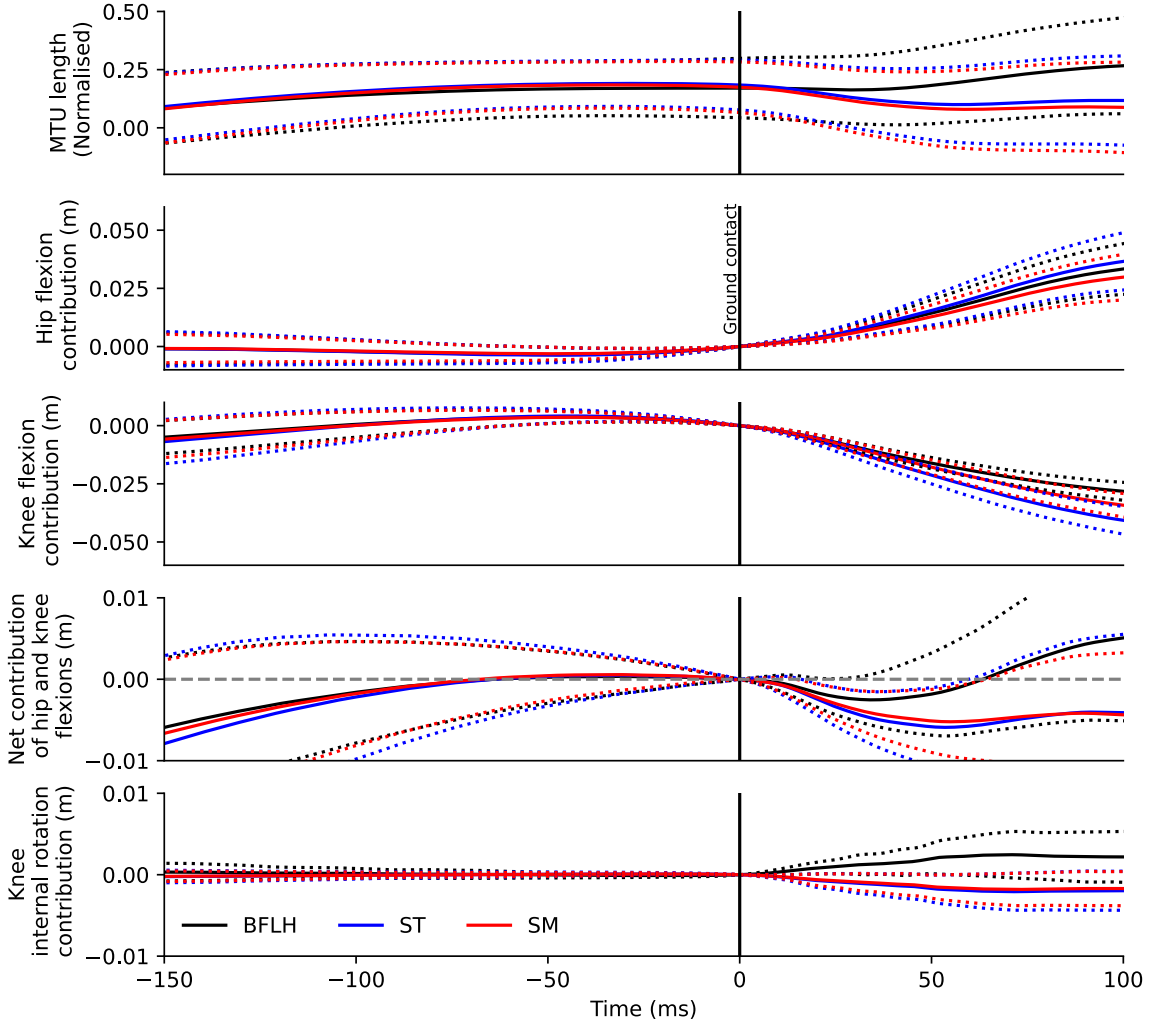


Figure 7.1: MTU change in length (δL_{MTU}) for the BFLH, the ST and SM during the [-150:100] ms time interval. From top to bottom: MTU change in length (%). MTU change in length (m) due to the hip ($r_{flexion_{hip}} \cdot d\theta_{flexion_{hip}}$) and knee flexions ($r_{flexion_{knee}} \cdot d\theta_{flexion_{knee}}$), respectively. MTU change in length resulting for the combination of the hip and knee flexions. MTU change in length due to the knee internal rotation ($r_{internalRotation_{knee}} \cdot d\theta_{internalRotation_{knee}}$). The vertical lines present the ground contact time.

When testing the correlation between MTU change in length and knee internal rotation during the first 50 ms of ground contact, we found no correlation ($p = 0.3$) for BFLH and weak negative correlations ($p < 0.01$, $r^2 = 0.19$ and $r^2 = 0.20$) for ST and SM, respectively (figure 7.2). When testing the correlation between MTU length changes and ACL length change during the first 50 ms of ground contact, we found no correlation ($p = 0.29$) for BFLH and very weak negative correlations for ST and SM ($p = 0.02$, $r^2 = 0.09$ and $p =$

0.04, $r^2 = 0.07$, respectively) (figure 7.2).

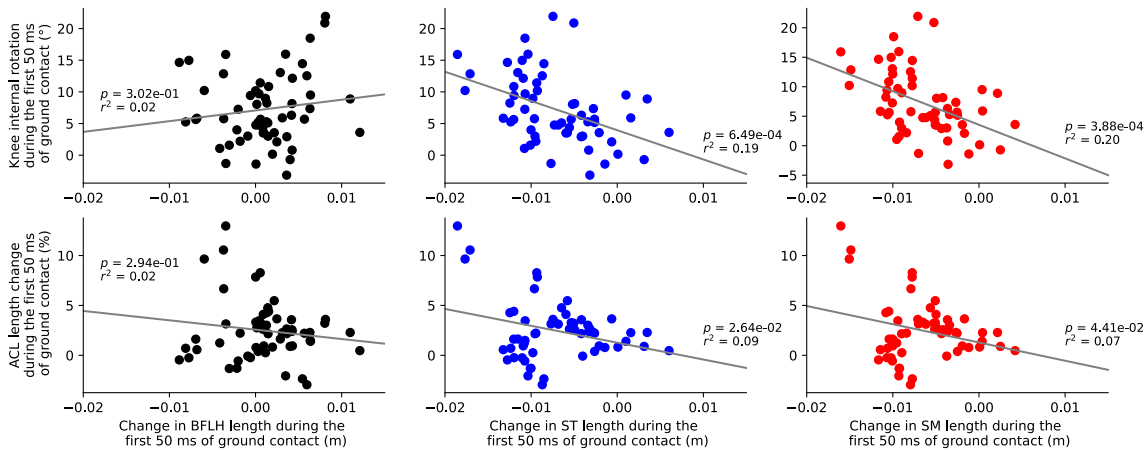


Figure 7.2: Change in length during the 50 ms of ground contact. First row: knee internal rotation ($^{\circ}$) with respect to MTU change in length (m) for the BFLH in black, the ST in blue and SM in red during the first 50 ms of ground contact. Second row: ACL change in length (%) with respect to MTU change in length (m) for the BFLH in black, ST in blue and SM in red during the first 50 ms of ground contact.

Figure 7.3a presents an example of the time evolution of the moment arms for the three hamstring muscles for the three trials of one typical, representative, participant during the anticipatory phase up to 50 ms after ground contact. The external rotation moment arm of the BFLH increased during the anticipatory phase, and increased more than the internal rotation moment arm of both ST and SM during ground contact. We found a negative correlation between the ratio of external moment arms at ground contact and the knee internal rotation during the first 50 ms of ground contact ($p < 0.01$, $r^2 = 0.43$), representing a moderate correlation (figure 7.3b). However, the correlation was not present between the ratio of external moment arms at ground contact and the ACL length change during the first 50 ms of ground contact ($p = 0.18$).

7.4 Discussion

The aim of the study was to characterise MTU kinematics of hamstrings muscles during both the anticipatory phase and the beginning of ground contact, to then infer whether they contribute to limit the knee internal rotation and the ACL change in length, to ultimately protect the ACL. We first found that the bi-articular hamstrings did not lengthen just before ground contact, but even shortened at the beginning of ground contact. This occurs even though it has been suggested that eccentric activation of the hamstrings would reduce the strain on the ACL (Withrow et al., 2008). Moreover, we found that the less the shortening of the ST and SM muscles, the less the knee internal rotation at the beginning of ground contact. Second, we described changes in external rotation of moment arms of hamstrings muscles, and found that the configuration of these moment arms at ground contact influence the knee internal rotation during the beginning of ground contact. Based on these results, it appears that anticipatory kinematic adjustments modify the force capabilities of bi-articular MTU around the knee joint, generating favourable conditions to

7.4. DISCUSSION

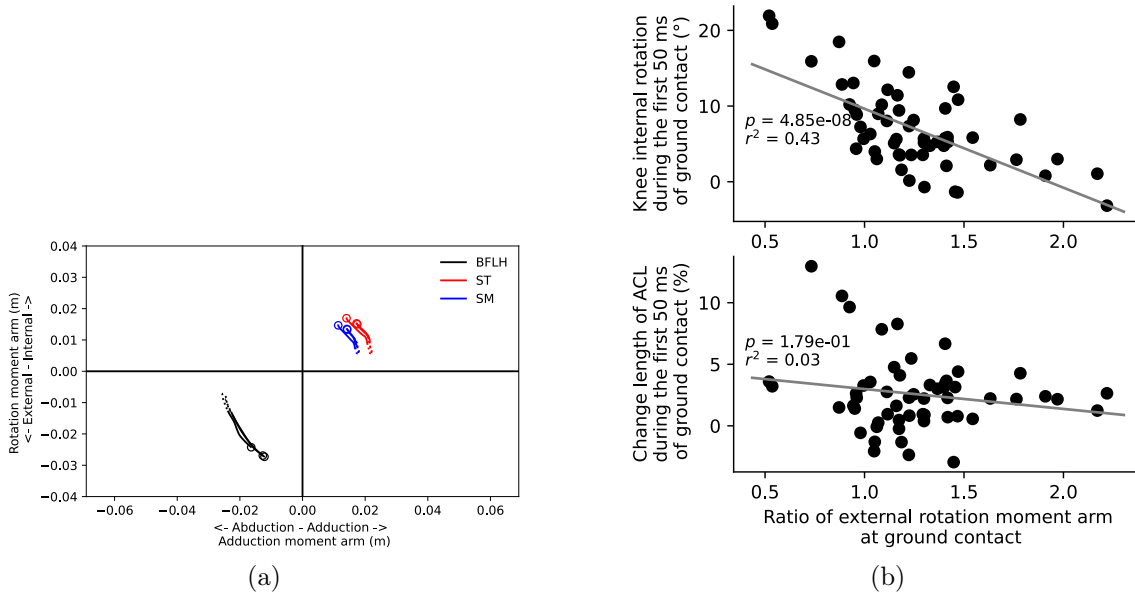


Figure 7.3: (a) Moment arms evolution for one typical participant. The dotted lines represent the evolution of the moment arms during 50 ms preceding ground contact, when the participant is in the air and the continuous lines represent the evolution of the moment arms during the first 50 ms of ground contact, with the circle indicating the 50th ms. Each line represents one trial. (b) Knee internal rotation ($^{\circ}$) (upper panel) and ACL length change (%) (lower panel) during the first 50 ms of ground contact, with respect to the ratio of external rotation moment arms at contact (see the methods section for definition).

produce force limiting knee internal rotation, and ultimately, protecting the ACL from too much strain and thus potential rupture.

7.4.1 MTU kinematics

Contrary to our hypothesis, the hamstring muscles did not lengthen, neither during the end of the anticipatory phase nor at the beginning of ground contact. During the last 50 ms before ground contact, the length of all three hamstring MTU we investigated did not change (figure 7.1). This indicates that the anticipated flexions of the hip and knee, as described in chapter 5, counterbalance each other, resulting in no net change in lengths of hamstrings MTU (see the fourth subplot of figure 7.1). Contrary to the hypothesis of Withrow et al. (2008), all three hamstrings MTU shortened on average during the beginning of ground contact. The hypothesis of hamstring MTU lengthening was appealing, since the ratio of moment arm between hip and knee flexion is between 2:1 and 3:1, depending on hip and knee joint angles. However, our data indicates that the larger increase in knee joint flexion, compared to hip flexion, led to MTU shortening.

The fact that hamstrings MTU lengths did not change before ground contact indicates that the coordination of the hip and knee joint flexions keeps constant MTU lengths. First, change in length of bi-articular MTU reflects the orientation of the lower-limb (excluding the foot) and is a marker of motor coordination (Ivanenko et al., 2007). By keeping the MTU length constant during the 50 ms preceding ground contact, participants seem to keep their lower-limb orientation (from the hip joint centre to the ankle joint centre)

constant before touching the ground. Moreover, the use of bi-articular muscles may improve perception of the lower-limb position by combining proprioceptive information from mono and bi-articular muscles, enhancing coordination between joints and reducing joint flexion errors (Herter et al., 2021). In chapter 5, we suggested that hip and knee joint angles and angular velocities at ground contact are important during landing tasks. Thus, humans may use proprioceptive information from both mono and bi-articular muscles to better sense hip and/or knee joint angles, and to ensure that adapted lower-limb joint flexion angles, as described in chapter 5, are reached to prepare coping with ground contact.

When looking at individual trials, we found weak correlations between change in MTU lengths for ST and SM and knee internal rotation during the first 50 ms of of ground contact, and even weaker correlations between change in MTU lengths and change in ACL length (figure 7.2): lower amplitudes of joint internal rotation and change in ACL length were observed when bi-articular MTU act isometrically. Overall, we recorded very few trials with SM and ST MTU lengthening, generally from the same participant. This may be because large MTU lengthening and lengthening velocity can damage muscle fascicles (Lieber & Friden, 1993), especially in hamstrings muscles (Kenneally-Dabrowski et al., 2019). Moreover, the majority of hamstrings injuries occurs in the BFLH (Ekstrand et al., 2012), and could explain why we did not find any correlation for the BFLH length change and knee internal rotation or ACL length change during this time interval.

7.4.2 Effects of anticipatory kinematic adjustments on MTU moment arms

Bi-articular MTU are well suited to stabilise joint because their anatomical structure enables to produce force perpendicular to the segment axis, *i.e.* in the frontal and transverse planes (Hof, 2001). One of the crucial factors influencing the resulted moment of force production is muscle moment arm (Sherman et al., 2013). When the knee joint is flexing, the moment arm of the BFLH contributing to the knee external rotation increases more than the moment of the SM and ST contributing to internal rotation (figure 7.3a). Thus, by anticipating knee joint flexion before ground contact, the ratio between the two quickly increases, generating *favourable conditions* for the BFLH to produce a moment of force that counter the internal rotation due to landing. In contrast, if there was no anticipatory knee joint flexion, participants would touch the ground with a very low moment arm of external rotation. Thus, BFLH would probably not be able to counter the internal rotation during the beginning of ground contact. This result highlights the determinant role of anticipatory muscle activations preceding ground contact in providing *favourable conditions*. it is amplified by the fact that very few muscles are knee external rotators, only the tensor fascia lata completes the action of the BFLH and BFSH, but has a very small moment arm.

To test this assumption, we correlated the ratio of external moment arm at ground contact with knee internal rotation during the first 50 ms of ground contact. The correlation, despite being moderate, suggests that the increase in external rotation moment arm due

7.4. DISCUSSION

to knee flexion helps protecting knee rotations in the transverse plane, and possibly to protect the ACL. Our results based on MTU moment arms thus confirm results from in vitro (Victor et al., 2010; Guelich et al., 2016) and in silico (Maniar et al., 2020) suggesting that BFLH force production reduces knee internal rotation, contrary to SM and ST which act as internal rotator. However, we found no correlation between the ratio of external moment arm at ground contact and ACL length change (figure 7.3b). This may be because ACL length depends on all of the knee degrees of freedom, that were not quantified in this study. In particular, we did not consider any translation of the leg relative to the thigh, which may bring uncertainties in our computation of ACL length. Moreover, ACL length change is not the only variable increasing its mechanical load. Forces acting to lengthen the ACL are also responsible for rupture, and were not quantified here.

It was recently suggested that ACL ruptures can occur following ligament fatigue, from repetitive strain of the ACL (Lipps et al., 2013; Wojtys et al., 2016). In light of this theory, our results suggest that humans can decrease the knee internal rotation experienced during each landing task by adapting their knee joint flexion at ground contact, to favour muscle force production from the BFLH to limit knee internal rotation and ultimately protect the ACL. These results complete results from chapter 5, where we suggested that anticipatory muscle activations have kinematic consequences enabling to prepare the whole-body coping with ground contact, to protect the skeletal system. Here, we can also suggest that these anticipatory processes are necessary to put bi-articular muscles in *favourable conditions* to limit knee joint rotating in the transverse plane. However, some prospective studies did not find different knee flexion angle at ground contact between participants with and without an ACL rupture (Hewett et al., 2005; Leppänen et al., 2017; Smeets et al., 2019). The absence of difference can be explained by different factors. First, these studies evaluated landing strategies during tasks known in advance, where participants can focus on the landing strategy, without any possible perturbation. In contrast, landings tasks during daily practice are often performed with additional cognitive load, making it difficult to fully focus on landing strategies. Second, in chapter 5, we suggested that initiating lower-limb joint rotations before ground contact enables to limit the change in lower-limb angular velocity during the beginning of ground contact, and possibly dissipate the increase of GRF required to accelerate the whole-body Centre of Mass (CoM) upward. Here, we can also suggest that reducing the GRF at the beginning of ground contact also enables to flex the knee and reach a more *favourable condition* in term of external rotation moment arm, to avoid applying too much GRF when the BFLH cannot exert much moment of force to resist the knee internal rotation. Thus, we suggest that quantifying the anticipatory kinematic adjustments during future prospective studies might confirm that participants without future injury are able to decrease the amount of GRF experienced when the BFLH is not in a configuration to develop large moment of force.

7.5 Conclusion

In this study, we quantified the hamstrings *MTU* lengths and moment arms during both the anticipatory phase and the beginning of ground contact of a drop landing task. We first showed that a precise coordination between the anticipated hip and knee joint flexions maintains the length of bi-articular hamstrings *MTU* constant. Moreover, we showed that the anticipated knee joint flexion modifies the knee external rotation moment arm of the *BFLH*, enabling the muscle to produce a large moment of force to resist the knee internal rotation, and potentially protect the *ACL*. These results complete the determinant role of anticipatory muscle activations preceding ground contact in providing *favourable conditions* for landing. The adjustments described here could be of key importance to prevent excessive knee joint rotation in the transverse plane and protect the *ACL*, and should be carefully considered in the future.

7.6 French summary

7.6.1 Introduction

La rupture du ligament croisé antérieur (LCA) est une blessure dramatique affectant énormément de personnes. Cette blessure a des conséquences aussi bien physiques que psychologiques. Malgré de nombreuses recherches, aucune cause définitive n'a été mise en avant, et le nombre de blessures ne baisse pas. Au contraire, il augmenterait même chez les adolescents (Kooy et al., 2023). Le LCA rompt lorsque la charge mécanique appliquée est supérieure à sa capacité. Il est donc crucial de comprendre les situations qui entraînent une charge mécanique importante sur le LCA. La majorité des mécanismes de rupture ont été déduits d'analyses vidéo à posteriori, il a donc été déduit que le LCA se rompt après une unique situation traumatique. Cependant, il a été récemment suggéré que la rupture du LCA pouvait intervenir suite à une fatigue ligamentaire (Lipps et al., 2013; Wojtys et al., 2016). L'accumulation des contraintes appliquées au ligament pourrait diminuer la capacité du LCA à encaisser des contraintes.

Les ruptures du LCA font généralement suite à une combinaison de trois mouvements de la jambe par rapport à la cuisse : la translation antérieure, la rotation interne et l'abduction, qui augmentent tous l'allongement du LCA. Grâce à des études in vitro, il a été suggéré que la combinaison de la translation antérieure interne et de la rotation interne allongeait plus le LCA que la combinaison de la translation antérieure et l'abduction (Oh et al., 2012). Il est donc nécessaire de trouver des stratégies motrices efficaces pour limiter la rotation interne du genou durant des tâches où les forces de réaction extérieures sont importantes.

Un autre facteur déterminant est la force générée par les ischios-jambiers, qui doit contrer la force produite par le quadriceps nécessaire pour décélérer la flexion du genou durant le contact au sol. La force générée par les ischios-jambiers va limiter la translation antérieure et augmenter la stabilité de l'articulation, et réduirait l'allongement du LCA en études in vitro (Withrow et al., 2008). Il a été suggéré qu'une contraction excentrique des ischios-jambiers permettrait de diminuer l'allongement du LCA (Withrow et al., 2008). Ainsi, une flexion de la hanche permettrait d'allonger les ischios-jambiers et protéger le LCA, mais n'a pas été testée expérimentalement.

Les résultats sur le rôle des ischios-jambiers sont à nuancer car tous les muscles n'ont pas le même rôle dans le plan transverse. Les muscles les plus médiaux (ST, SM) sont des rotateurs internes alors que les muscles les plus latéraux (BFLH, BFSH) sont rotateurs externes. Leurs rôles fonctionnels peuvent être analysés grâce à leurs bras de levier, qui représentent leur avantage mécanique. Il a donc été suggéré que l'activation des muscles latéraux limite l'allongement du LCA, alors que l'activation des muscles médiaux contribuerait à l'allonger (Guelich et al., 2016; Victor et al., 2010; Maniar et al., 2020). Le ratio entre les bras de levier des rotateurs internes et externes pourrait alors être déterminant dans la protection du LCA. La manière dont les bras de levier évoluent en fonction des angles articulaires durant des tâches traumatiques reste inconnue, mais paraît importante pour comprendre l'importance de chaque muscle des ischios-jambiers pour limiter la

rotation interne et l’allongement du LCA.

7.6.2 Méthode

A partir des modèles musculosquelettiques de chaque participant, les longueurs des complexes muscle tendon (MTU) et les bras de levier du BFLH, ST et SM ont été calculés grâce à l’outil Analyze d’OpenSim. Les longueurs des MTU ont été normalisées par leur longueur maximale (equation (7.1)). Ensuite, la contribution de chaque degré de liberté à la variation de la longueur des MTU a été calculée avec la méthode d’intégration du bras de levier equations (7.2) and (7.3) (voir nomenclature page [xix](#)). Nous avons calculé un ratio de bras de levier de rotation externe en divisant le bras de levier de rotation externe du BFLH par la valeur absolue du bras de levier de rotation interne du SM (qui a un bras de levier plus important que le ST) (equation (7.4)). Un ratio supérieur à 1 indique que le bras de levier de rotation externe du BFLH est supérieur au bras de levier de rotation interne du SM, et inversement. Enfin, nous avons estimé la longueur du LCA grâce aux données de [Pillet et al. \(2016\)](#).

7.6.3 Résultats

Nous avons trouvé qu’au début du contact au sol, les trois muscles bi-articulaires des ischios-jambiers se raccourcissent, avec une contribution de la flexion de genou plus importante que la contribution de la flexion de hanche. Le BFLH se raccourcit moins que le SM et le ST au début du contact. Lorsqu’une rotation interne de genou est présente, elle allonge légèrement le BFLH. Nous avons trouvé des corrélations très faibles et négatives entre la rotation interne du genou après 50 ms de contact et la variation de longueur du ST et SM ($p < 0.01$, $r^2 = 0.19$ et $r^2 = 0.20$). La figure [7.3a](#) présente un exemple de l’évolution des bras de levier des trois muscles bi-articulaires des ischios-jambiers pour un participant représentatif durant la phase d’anticipation et les 50 premières ms du temps de contact. Le bras de levier de rotation externe du BFLH augmente durant la phase anticipatoire, et augmente plus que le bras de levier de rotation interne du SM durant le contact. Nous avons trouvé une corrélation modérée négative entre le ratio de rotation externe à l’instant du contact et la rotation interne du genou au bout de 50 ms de contact (intervalle durant lequel le LCA se rompt) ($p < 0.01$, $r^2 = 0.43$).

7.6.4 Discussion

Contrairement à l’hypothèse de [Withrow et al. \(2008\)](#), les muscles bi-articulaires des ischios-jambiers ne s’allongent pas à la réception d’un saut. Durant la phase anticipatoire, ils changent très peu de longueur, indiquant que les flexions anticipées du genou et de la hanche se compensent parfaitement, bien que leurs bras de levier ne soient pas identiques. Ce résultat indique que les flexions anticipées décrites dans le chapitre [5](#) sont le résultat d’une coordination entre les deux articulations.

En regardant les essais individuellement, nous avons trouvé de faibles corrélations entre la variation de longueur des MTU du ST et SM et la rotation interne du genou durant

7.6. FRENCH SUMMARY

les 50 premières ms du contact. Au total, nous avons enregistré très peu d'essais avec un allongement du SM et ST, et venant presque tous du même participant. Cette absence d'allongement pourrait être expliquée par le fait que les contractions excentriques en présence de fortes forces de réaction du sol entraînent des dommages musculaires (Lieber & Friden, 1993) et principalement aux muscles des ischios-jambiers (Kenneally-Dabrowski et al., 2019).

Lorsque l'articulation du genou se fléchit, le bras de levier de rotation externe du BFLH augmente plus que le bras de levier de rotation interne du SM et du ST. En anticipant la flexion du genou avant le contact au sol, le ratio de bras de levier devient rapidement favorable à la rotation externe, générant une *condition favorable* à la production de force du BFLH pour contrer la rotation interne induite par le contact au sol. À l'inverse, s'il n'y avait pas de flexion anticipée, les participants toucheraient le sol dans une configuration où le BFLH ne pourrait pas produire beaucoup de force. Ce résultat souligne l'importance du rôle des activations musculaires anticipées et des ajustements cinématiques afin d'apporter des *conditions favorables* et protéger le système squelettique. Ceci est d'autant plus accentué par le fait que très peu de muscles sont rotateurs externes du genou. En plus du BFLH et BFSH, seul le tenseur du fascia lata peut réaliser cette action, mais a un très faible bras de levier.

Il avait été suggéré que les ruptures du LCA peuvent intervenir suite à une fatigue ligamentaire. Nos résultats suggèrent qu'en adoptant les bonnes cinématiques anticipées lors de tâches de réception, il serait possible de diminuer la rotation interne du genou et donc l'allongement du LCA lors de tâches communes, et ainsi protéger le LCA de dommages quotidiens.

Dans cette étude, nous avons quantifié les longueurs des MTU des ischios-jambiers et les bras de levier durant la période d'anticipation et le début du contact de tâches de réception. Nous avons montré premièrement qu'une coordination précise entre les flexions anticipées de la hanche et du genou maintient la longueur des MTU constante. De plus, nous avons montré que la flexion anticipée du genou modifie le bras de levier de rotation externe du BFLH, permettant au muscle de produire un moment de force plus important qui s'oppose à la rotation interne du genou. Ces résultats complètent le rôle déterminant des activations musculaires anticipées durant des tâches de réception. Les ajustements décrits peuvent être importants pour éviter une rotation interne trop importante et protéger le LCA.

CHAPTER 8

General Discussion

On all its many values, the greatest must
be the freedom to doubt.

Richard P. Feynman

8.1. ANTICIPATORY MUSCLE ACTIVATIONS PROVIDE FAVOURABLE CONDITIONS FOR MOVEMENT EXECUTION

The general aim of the thesis was to complete the fundamental understanding on the underlying mechanisms the nervous system uses anticipatory muscle activations to generate *favourable conditions* during motor transitions. We investigated two different, yet complementary, contexts of motor anticipation, to infer on the *favourable conditions* provided by anticipatory muscle activations. We showed that anticipatory muscle activations have mechanical consequences before the initiation of movement that are not directly linked to the voluntary movement itself, but enables to maintain balance, to cope with gravity and protect the skeletal system. These results demonstrate that there are various objectives the nervous system must satisfy when executing a movement. These objectives have to be achieved at different times, and must be considered to provide adapted rehabilitation programs and assistive devices to enable mobility to everyone.

8.1 Anticipatory muscle activations provide favourable conditions for movement execution

We started this thesis stating that the computational theory level theorised by Marr (1982) remains understudied in human movement. In other words, it remains unclear which task objectives the nervous system tries to satisfy when executing a movement. In this thesis, we investigated anticipatory processes during motor transitions to clarify the objectives of the nervous system when executing movements. As expected, we found that anticipatory muscle activations provide different *favourable conditions* to the movement execution.

Despite very different contexts between the two tasks we investigated, our results suggest some similarities in the roles of anticipatory processes we described. Indeed, anticipatory processes **increase the duration of motor transitions**. During gait initiation, the whole-body **Centre of Mass (CoM)** is increasingly accelerated, so that the increase in whole-body **CoM** velocity is progressive, and not abrupt (figure 4.4) (Breniere & Do, 1986; Jian et al., 1993). Similarly, there is no abrupt change in hip and knee joint angles and angular velocities during anticipation of contact (figures 5.1 to 5.3). This adaptation enables to limit the peak of vertical **Ground Reaction Forces (GRF)** but lengthens the time required to accelerate the whole-body **CoM** upwards. This increase in the duration of motor transitions can be interpreted in different ways.

First, the increase in the duration of motor transitions enables to **protect the physical integrity**, by avoiding both falls and musculoskeletal injuries. In the definition of motor transitions (section 2.2.1.2), we argued that these situations are the most critical for balance maintenance because of the distinct change in whole-body **CoM** acceleration. With the increase in the duration of motor transitions, we can infer that the nervous system acts to limit the change in whole-body **CoM** acceleration when possible. In the same way, too much of an increase in **GRF** during foot contact can lead to various lower-limb injuries (Dufek & Bates, 1991). By increasing the duration of the motor transition, it also enables to avoid large **GRF** at the beginning of ground contact when anticipating contact, to let the knee flex and reach a configuration when muscles can produce more force to avoid injury

chapter 7. Overall, the system seems to adapt the duration of motor transition, to smooth its magnitude (*i.e.* change of acceleration of the whole-body CoM and GRF applied to the whole-body), to provide *favourable conditions* to limit the risk of falling or musculoskeletal injuries. These adjustments need to be considered when evaluating the computational theory level of theory of Marr (1982), because they would represent a objective that the nervous system has to satisfy when executing movement.

Second, the increase in the duration of motor transitions would enable to **limit resources required to perform motor transitions**. During gait initiation, the forward trunk inclination first enables to accelerate the whole-body CoM forward using little muscle activity, thanks to the action of gravity. Then, this forward inclination is quickly limited to avoid a state where large muscle force from the lower-back muscles is required to reduce the mechanical instability. During anticipation of contact, anticipatory kinematic flexion of the knee joint enables to limit the peak of GRF at the beginning of ground contact, and limit joint moments (and thus force production requirement), compared to shorter transitions (Devita & Skelly, 1992). Recently, during walking on uneven terrains, minimisation of mechanical work using a simple mechanical model allowed to explain experimental speed fluctuations (Darici & Kuo, 2023). However, this approach considers the whole-body as a simplified mechanical model, neglecting the 'counter-rotating' mechanism (section 2.2.1.1). Using such approach to predict the time evolution of all degrees of freedom appears difficult, because it requires the level of activation of each muscle, also obtained through an optimisation (Erdemir et al., 2007). These two optimisations are a combination of the two first level of analysis detailed by Marr (1982) (table 1.1). Thus, if movement trajectory is based on a minimisation of muscle force required, it would indicate that the nervous system performs both the computational theory and the representation and algorithm levels suggested by Marr (1982) at the same time and not sequentially.

Finally, while we suggested that one of the *favourable conditions* provided by anticipatory muscle activations is to increase the duration of motor transitions, we have to mention that too much increase may be detrimental. We argued that motor transitions are periods of mechanical instability, with whole-body CoM acceleration increasing during the anticipatory phase (figure 4.4). Thus, if the duration is too long, the mechanical instability may become too important and difficult to recover. This is especially true in situations where unexpected perturbations can happen. In the same way, flexing too much the lower-limb joints during landing tasks may result in large joint angular velocities, requiring greater muscle force to slow down.

In conclusion, the nervous system seems to use anticipatory processes to lengthen the duration of motor transitions, providing *favourable conditions* to protect the physical integrity of the system. The increase in duration of motor transitions enables to reduce the changes in whole-body CoM acceleration and GRF that may lead to loss of balance and risk of injury. Such situations would also require more muscle force, and seem to be avoided by the nervous system when programming voluntary movements.

8.2 Different phases of anticipation

A second similarity we observed among the two contexts of anticipation we investigated in this thesis is the presence of different periods of anticipation. The presence of different periods of anticipation is a new reason why the system lengthens the duration of motor transitions, and particularly the anticipatory period, as stated in the previous section. During gait initiation, we detailed two phases of anticipation: a first one when all segments rotate forward, contributing together to accelerate the whole-body CoM backward, and a second one where some segments start counter-rotating, contributing to accelerate the whole-body CoM forward (chapter 4). During anticipation of ground contact, we showed that lower-limb joint angles first need to be extended, to then be actively flexing at ground contact (chapter 6).

In both cases, the first anticipatory period could not have been predicted by the model of Kawato (1999)(figure 2.2). In this model, forward model programs anticipatory muscle activations adapted to the predicted consequences of the voluntary movement (von Holst & Mittelstaedt, 1971; Miall et al., 1993). Then, anticipatory processes are programmed to provide some *favourable conditions* to the movement execution. In this thesis, we suggested that, before the nervous system can program anticipatory processes, it should place the whole-body in a state that enables these actions. In the case of balance-movement coordination, the predicted consequence of the voluntary movement is the rotational mechanical instability. The *favourable conditions* provided are the counter-rotation of the trunk segment. Before starting counter-rotating the trunk, every body segments must be put into rotation. In the case of anticipation of contact, the predicted consequences are the impact forces upon contact. The *favourable conditions* are the initiation of hip and knee joint flexions. Before starting these flexions, the lower-limbs need to be extended. These two periods of anticipation indicate that, in addition to the multiple objectives the nervous system must satisfy when executing a movement (*i.e.* perform the movement, maintain balance, protect the skeletal system), it must also satisfy at least two objectives during the anticipatory phases. This completes the number of objectives we need to consider at the computational theory level of Marr (1982).

These two phases of anticipation question whether the whole period of anticipation is programmed in advance as a whole sequence or separately as two successive steps required to anticipate a motor transition. In the later case, some feedback control may intervene to indicate when switching from one anticipatory phase to another. During gait initiation, it remains unknown whether a specific state is required to switch from the first phase of anticipation to the second, such as a given whole-body CoM velocity or an acceleration sufficient to initiate the movement. We can suggest that varying the initial states of the transition would provide valuable information in this purpose. For example, the duration of relative phases may vary depending on the distribution of GRF under each lower-limb (Azuma et al., 2007; Caderby et al., 2017), suggesting that a particular state needs to be reached before switching phases. The nature of such state remains unknown, and may be found by using the phases delimitation we proposed in (chapter 4), based on \dot{H}_M . During

anticipation of contact, the onset of hip and knee joint flexion seems to depend on an initial joint configuration, enabling to initiate joint flexion leading to adequate joint angle and angular velocity at contact (chapter 6). These adaptation may suggest that the period of anticipation is programmed separately as successive steps.

Finally, the presence of two phases of anticipation also questions how far humans can anticipate in advance a given voluntary movement. For example, a recent study found lower magnitude of H_M around the antero-posterior axis when participants must ascent stairs after change of direction, compared to a simple change of direction (Li et al., 2020). This suggested that *favourable conditions* are adapted to future transitions, particularly to maintain balance during multiple transitions. Moreover, it is possible that, the final state of a stepping task (*i.e.* a posture) is already anticipated when initiating the movement, leading to a larger magnitude of H_M directed backward around the medio-lateral axis compared to gait initiation. A comparison between gait initiation and stepping tasks would enable to determine whether final states of motor transitions are anticipated or not.

In summary, results we had over different movement contexts suggest that anticipatory processes are divided into at least two phases. The first phase could be a necessary requirement to accomplish the second phase, identified as the one providing the *favourable condition* to movement execution. However, it remains unknown whether these two phases are programmed as a whole sequence or not.

8.3 Perspectives

8.3.1 Generalisation of the results

The roles and phases of anticipatory processes we proposed in the previous sections were based on a limited number of experiments. To be more robust, we must be able to generalise our results to other types of transitions. Particularly, we could generalise the use of the counter-rotating mechanism found during gait initiation to other motor transitions occurring during walking, such as gait termination (a movement to posture) and change of direction (a movement to movement transition). The role of the trunk segment started to be investigated during change of direction, and it seems to show two phases based on H_M around the antero-posterior axis: it first rotates towards the inside lower-limb, and then rotates towards the outside lower-limb during the penultimate and the step of the change of direction (Nolasco et al., 2019). These results appear similar to those we presented in chapter 4, with a first increase of H_M towards the movement direction, then followed by a decrease. Characterising the role of the counter-rotating mechanism during different types of motor transitions will also help design effective devices such as exoskeleton improving mobility by adapting the contribution of determinant body segments such as the trunk. In this end, the goal is to improve both balance maintenance and balance confidence for users (Hamza et al., 2020). Moreover, a more complete understanding of the use of the counter-rotating mechanism will also improve the design of rehabilitation programs, by effectively considering the contribution of all body segments.

8.4. GENERAL CONCLUSION

8.3.2 Linking the two contexts

In this thesis, we investigated two different contexts independently, anticipation for balance-movement coordination, and the anticipation of contact. Although different, these two contexts are complementary, through the 'applying new external force(s)' balance mechanism proposed by Hof (2007) (section 2.2.1.1). Indeed, foot placement is largely used to maintain balance during locomotion (Bruijn & van Dieën, 2018) because it is an effective solution to accelerate the whole-body CoM in a desired direction. Thus, foot placement has been demonstrated to be modulated to react to an external perturbation (Maki & McIlroy, 1997), to terminate gait (Tirosh & Sparrow, 2004) and to perform change of direction (Patla et al., 1999). The same adjustments should also be present during the anticipation of contact context such as drop-landing tasks. We quickly tested whether foot placement was adapted during different landing contexts, even though we did not have conditions where the horizontal whole-body CoM velocity during air time was experimentally manipulated. We compared drop-landing from 0.35 m, where participants had some horizontal whole-body CoM velocity during the air time ($0.59 \pm 0.07 \text{ m.s}^{-1}$), with landing from a counter-movement jump, where participants had no horizontal whole-body CoM velocity during the air time ($0.04 \pm 0.11 \text{ m.s}^{-1}$). We found that the foot was positioned in front of the whole-body CoM ($0.10 \pm 0.02 \text{ m}$) during drop-landing, when there was an horizontal whole-body CoM velocity, but underneath the whole-body CoM ($0.02 \pm 0.03 \text{ m}$) during counter-movement jump, where there was no horizontal whole-body CoM velocity. Among the anticipatory kinematic adjustments we recorded (chapter 5), the anticipated hip flexion contributes to a forward acceleration of the foot, and the anticipated knee flexion contributes to a backward acceleration of the foot. Although these anticipatory joint flexions seem modulated to adapt the foot position at contact, it remains to determine the nature of these modulations, to satisfy both foot placement and coping with gravity. Altogether, we showed that the nervous system must satisfy different objectives when programming a movement, and future research is required to determine how these different objectives are combined to provided *favourable conditions* to each objective.

8.4 General Conclusion

In this thesis, we wanted to complete the fundamental understanding of anticipatory muscle activations in generating *favourable conditions* to movement execution. We investigated anticipatory processes to highlight the task objectives the nervous system tries to satisfy when executing a movement. We focused on motor transitions, distinct changes of steady-balance states, because there are the most crucial situations to enable mobility. Through the investigation of two different contexts of anticipation, we found that anticipatory muscle activations provide various *favourable conditions* to the movement execution that are not directly linked to the voluntary movement itself. Indeed, we showed that anticipatory muscle activations enable to maintain balance, to cope with gravity and protect the skeletal system. We also discussed similarities between the two contexts of motor anticipation. Anticipatory muscle activations enable to increase the duration of motor transition,

CHAPTER 8. GENERAL DISCUSSION

to protect the physical integrity of the human body, and multiple periods of anticipation seem to success each other, to provide different *favourable conditions* for the motor transition. Since motor transitions are ubiquitous in daily-life, these *favourable conditions* are necessary to movement execution and may be incorporated in future adapted devices and rehabilitation programs for population with impairments.

8.5 French summary

L'objectif général de cette thèse était de compléter la compréhension fondamentale des mécanismes sous-jacents par lesquels le système nerveux utilise les activations musculaires anticipatives pour générer des conditions favorables lors des transitions motrices. Nous avons étudié deux différents contextes d'anticipation afin d'inférer sur les *conditions favorables* apportées par les activations musculaires anticipées. Nous avons montré que les activations musculaires anticipées ont des conséquences mécaniques avant le début du mouvement, qui ne sont pas directement liées au mouvement volontaire en tant que tel, mais permettent de maintenir l'équilibre, de faire face à la gravité et de protéger le système squelettique. Ces résultats démontrent que plusieurs objectifs liés à la tâche doivent être satisfaits par le système nerveux lors de l'exécution d'un mouvement. Ces objectifs doivent être atteints à différents instants de la phase d'anticipation, et devront être considérés dans la conception de programmes de rééducation et de matériels d'assistance adéquats pour permettre la mobilité à tout le monde.

8.5.1 Les activations musculaires anticipées apportent différentes conditions favorables à l'exécution du mouvement

Nous avons débuté cette thèse en déclarant que le niveau calculatoire théorisé par Marr (1982) était sous-étudié dans le cas du mouvement humain. En d'autres termes, il n'apparaît pas clairement quels objectifs liés à la tâche le système nerveux essaie de satisfaire lors de l'exécution d'un mouvement. Dans cette thèse, nous avons investigué les processus anticipés durant des transitions motrices pour clarifier les objectifs du système nerveux. Comme attendu, nous avons trouvé que les activations musculaires anticipées apportent différentes *conditions favorables* à l'exécution du mouvement.

Malgré les deux contextes d'anticipation différents étudiés, nos résultats suggèrent des similarités dans le rôle des activations musculaires anticipées. En effet, nous avons trouvé que les processus anticipés permettent **d'augmenter la durée des transitions motrices**. Durant l'initiation à la marche, le centre de masse du corps complet est accéléré graduellement, de telle manière que l'augmentation de sa vitesse ne soit pas abrupte. De la même manière, il n'y a pas de changement abrupt des angles et des vitesses angulaires de flexion de la hanche et du genou lors de l'anticipation du contact. Ces adaptations permettent de limiter le pic de force de réaction verticale, mais augmentent le temps nécessaire pour accélérer le centre de masse vers le haut. Cette augmentation de la durée des transitions peut être interprétée de différentes manières.

Premièrement, cette augmentation de la durée des transitions permet de protéger l'intégrité physique, en évitant aussi bien les chutes que les blessures. Dans notre définition des transitions motrices, nous avons mis en avant que ces situations étaient les plus critiques pour le maintien de l'équilibre à cause d'un changement net d'accélération du centre de masse du corps complet. Ici, nous pouvons suggérer que le système nerveux cherche à lisser ce changement d'accélération. De la même manière, des forces de réaction trop

importantes apportent des blessures. En augmentant la durée de la transition, cela permet d'éviter des pics de forces extérieures trop importants, de laisser le genou se fléchir pour se mettre dans une configuration où il peut produire plus de force. Ces ajustements doivent être considérés lors de l'évaluation du niveau calculatoire de Marr (1982), parce qu'ils pourraient représenter des objectifs importants pour le système nerveux lors de l'exécution d'un mouvement.

Deuxièmement, l'augmentation de la durée des transitions motrices pourrait permettre de **limiter les ressources nécessaires pour effectuer une transition motrice**. Durant l'initiation à la marche, l'inclinaison vers l'avant du tronc permet d'accélérer le centre de masse du corps complet vers l'avant en utilisant peu de force musculaire. Ensuite, cette inclinaison vers l'avant du tronc est rapidement limitée pour éviter d'avoir à utiliser beaucoup de force en cas de perturbation externe. Durant l'anticipation du contact, les flexions anticipées permettent de limiter l'intensité des forces de réaction au début du contact, en limitant les moments de forces articulaires contrairement à des transitions plus courtes (Devita & Skelly, 1992). Une étude récente met également en avant le fait que les humains minimiseraient le coût mécanique durant de la marche sur un terrain non-plat (Darici & Kuo, 2023), en faisant varier leur vitesse aux instants les plus propices.

Enfin, bien que nous ayons suggéré que les activations musculaires anticipées permettent d'augmenter la durée des transitions, cette augmentation ne peut pas être trop importante. Etant donné que les transitions sont un instant d'instabilité mécanique, augmenter la durée de la transition de manière trop importante pourrait mener à une instabilité trop importante. Ceci est d'autant plus vrai dans les situations où des perturbations externes peuvent intervenir. De la même manière, fléchir les articulations du membre inférieur de manière exagérée en anticipation d'un contact pourrait résulter en des vitesses angulaires trop importantes et impossibles à ralentir.

8.5.2 Différentes phases d'anticipation

La seconde similarité observée durant l'étude des deux contextes d'anticipation est la présence de différentes périodes d'anticipation. La présence de plusieurs périodes d'anticipation est également une des raisons entraînant l'augmentation de la durée des transitions, et particulièrement de la période d'anticipation. Durant l'initiation à la marche, nous avons détaillé deux phases d'anticipation : une où tous les segments du corps tournent vers l'avant contribuant à l'accélération du centre de masse du corps complet vers l'avant, et une seconde où certains segments initient une contre-rotation, contribuant à limiter l'accélération vers l'avant. Durant l'anticipation du contact, nous avons montré que les articulations du membre inférieur devaient premièrement être en position d'extension avant de pouvoir être activement fléchies.

Dans les deux cas, la première période d'anticipation n'aurait pas pu être prédite par le modèle de Kawato (1999)(figure 2.2). Le modèle Forward programme des activations musculaires adaptées aux conséquences prévues du mouvement volontaire, permettant d'apporter des *conditions favorables à l'exécution du mouvement*. Dans cette thèse, nous

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suggérons que, avant que le système nerveux ne puisse programmer des activations musculaires anticipées, il doit placer le corps complet dans un état qui permette la réalisation de ces activations. Dans le cas de l'initiation à la marche, les conséquences prédites du mouvement sont l'instabilité mécanique. Les *conditions favorables* sont la contre-rotation des segments. Avant de pouvoir commencer la contre-rotation, le corps complet doit être suffisamment accéléré pour réaliser la transition. Dans le cas de l'anticipation du contact, les conséquences prédites sont les forces d'impact suite au contact. Les *conditions favorables* sont l'initiation de la flexion de la hanche et du genou. Avant de pouvoir initier ces flexions, le membre inférieur doit être en extension. Ces deux périodes d'anticipation semblent indiquer de nouveaux objectifs que le système nerveux doit assurer pendant l'exécution d'un mouvement.

8.5.3 Perspectives

Premièrement, les rôles et les phases d'anticipation proposés dans les précédentes sections sont basés sur un nombre limité d'expériences. Pour que ces rôles et ces phases soient plus robustes, nous devons être capables de généraliser ces résultats à d'autres types de transitions, et plus particulièrement le rôle de la contre-rotation durant la terminaison de la marche, une transition mouvement à posture, et durant des changements de direction, une transition mouvement à mouvement. Le rôle du tronc a commencé à être étudié pendant des changements de direction, avec deux phases qui pourraient correspondre à celles que nous avons décrites dans le chapitre 4 (Nolasco et al., 2019).

Ensuite, nous avons étudié deux contextes différents de l'anticipation. Bien que différents, ces deux contextes sont complémentaires, notamment via l'utilisation du mécanisme de l'équilibre d'application d'une nouvelle force extérieure. Le placement du pied est largement utilisé pour maintenir l'équilibre durant la locomotion (Bruijn & van Dieën, 2018) car c'est une solution efficace pour accélérer le centre de masse du corps complet dans la direction désirée. Le placement du pied est ajusté en réaction à une perturbation externe (Maki & McIlroy, 1997), pour terminer la marche (Tirosch & Sparrow, 2004) et pour réaliser un changement de direction (Patla et al., 1999). Des ajustements similaires devraient être visibles durant l'anticipation d'un contact comme des situations de réception. Nous avons rapidement testé si le placement du pied en antéro-postérieur était ajusté selon la vitesse horizontale du centre de masse du corps complet. Nous avons trouvé que le pied était positionné de manière plus antérieure si la vitesse du centre de masse était non nulle. Parmi les ajustements cinématiques décrits dans le chapitre 5, la flexion de la hanche contribue à accélérer le pied vers l'avant, et la flexion du genou à accélérer le pied vers l'arrière. Bien que ces flexions semblent être adaptées pour le placement du pied, la nature de ces adaptations pour satisfaire à la fois la position du pied et la contrainte gravitaire reste à être étudiée. Dans l'ensemble, bien que nous ayons montré que le système nerveux doit satisfaire différents objectifs lors de l'exécution de mouvements, des recherches futures sont nécessaires pour déterminer comment ces objectifs sont combinés pour apporter des *conditions favorables* à chaque objectif.

8.5.4 Conclusion générale

Dans cette thèse, nous voulions compléter la compréhension fondamentale des activations musculaires anticipées et des *conditions favorables* qu'elles apportent pour l'exécution du mouvement. Nous avons étudié les processus anticipés pour mettre en évidence les objectifs liés à la tâche que le système nerveux essaie de satisfaire lors de l'exécution du mouvement. Nous nous sommes plus particulièrement intéressés aux transitions motrices, définies comme des changements distincts d'états d'équilibre, parce qu'elles représentent les situations les plus critiques pour permettre la mobilité. Par l'étude de deux contextes d'anticipation différents, nous avons trouvé que les activations musculaires anticipées permettent d'apporter différentes *conditions favorables* pour l'exécution du mouvement qui ne sont pas reliées aux objectifs de la tâche en tant que tels. En effet, nous avons montré que les activations musculaires anticipées permettent de maintenir l'équilibre, de faire face à la gravité, et de protéger le système squelettique. Nous avons également discuté des similarités entre les deux contextes d'anticipation. Les activations musculaires anticipées permettent d'augmenter la durée des transitions motrices pour protéger l'intégrité physique du corps humain, et différentes périodes d'anticipation se succèdent, apportant différentes *conditions favorables* à l'exécution de la transition motrice. Étant donné que les transitions motrices sont omniprésentes dans la vie quotidienne, ces *conditions favorables* sont nécessaires à l'exécution de n'importe quel mouvement et devront être considérées pour les futurs programmes de rééducation et le matériel d'assistance destiné aux personnes à mobilité réduite.

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