

Anticipatory muscle activations to coordinate balance and movement during motor transitions: A narrative review

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ABSTRACT

BACKGROUND

3 Maintaining balance while moving is vital for day-to-day activities. A key challenge in the

- 4 comprehension of human movement is to determine how muscles contribute to balance-movement
- 5 coordination. Motor transitions, defined as movements executed between two steady balance states, are
- 6 particularly interesting phases to study balance-movement coordination because a large, discrete change
- 7 in whole-body momentum may disturb balance. During voluntarily-initiated motor transitions,
- 8 anticipatory muscle patterns provide the biomechanical conditions that are favourable to both
- 9 maintaining balance and executing the movement.

RESEARCH QUESTION

- What are the mechanical consequences of anticipatory muscle activations for balance-movement
- 12 coordination during voluntarily-initiated motor transitions?

METHODS

- We review the biomechanical contributions of the anticipatory muscle activations identified in the
- literature during four types of voluntarily-initiated motor transitions, through the prism of three balance
- mechanisms ('moving the centre of pressure (CoP)', 'counter-rotating segments', and 'applying new
- 17 external force(s)'). In particular, we investigate how anticipatory muscle activations modulate whole-
- body centre of mass acceleration.

RESULTS

- We show that the mechanical consequences of anticipatory muscle activations have been extensively
- described, but mainly using the 'moving the CoP' mechanism. Unlike their role during steady balance
- states, both 'moving the CoP' and 'applying new external force(s)' mechanisms create a required
- 23 mechanical instability during the anticipatory phase of motor transitions. The 'counter-rotating'
- 24 mechanism may act as a stabiliser during motor transitions, but additional research is needed to clarify
- 25 this assumption.

SIGNIFICANCE

This review establishes that muscle activation processes have different mechanical consequences for balance-movement coordination during the anticipatory phases of motor transitions, compared to steady balance states. Because the mechanical instability that is created can lead to falls, a better understanding of the mechanisms underlying motor transitions is needed to enable the design of more effective fall prevention programs and/or devices for population with balance deficits.

KEYWORDS

34 Transition; Anticipation; Coordination; Balance; Movement

Introduction

 The ability to maintain balance is often take for granted. It is only when a condition impedes its control that the vital role it plays in 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 movements disturb balance maintenance, and that appropriate muscle activations are required to compensate for these disturbing forces [1,2]. 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 [3,4]. Yet, understanding balance-movement coordination remains challenging. In this context, our narrative review 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. When these 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 is organised into three sections. In the first section, we introduce three key concepts of balance-movement coordination: balance, through the three main balance 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.

MAIN CONCEPTS RELATIVE TO BALANCE-MOVEMENT COORDINATION

MAINTENANCE OF BALANCE AND THE THREE MECHANISMS

Balance has originally been related to the regulation of posture, i.e., the ability to maintain the wholebody in a desired segmental configuration [5]. From this perspective, balance is described by considering the position of the whole-body centre of mass (CoM) relative to the base of support (i.e., the area surrounding all contact points with the environment) [6]. 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 [7], which characterise the maintenance of balance [8,9]. 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 [6]. 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 [6]. By computing the sum of external moments of a linearized inverted pendulum around the projection of the whole-body CoM in the transverse plane on the ground (M') (eq. 1), Hof [10] proposed three complementary balance mechanisms involved in motor tasks, which contribute to modifying whole-body CoM acceleration: (1) 'moving the CoP', (2) 'counter-rotating' segment(s), and (3) 'applying new external forces(s)' (Fig. 1). The whole-body CoM acceleration can then be computed along the antero-posterior and medio-lateral axes (eq. 2). See Nomenclature (table 1) for definition of all variables.

$d\vec{H}_{M} \longrightarrow d\vec{H}_{M}$	(eq. 1)
$\left(\overrightarrow{OP} - \overrightarrow{OM'}\right) \times \vec{F}_G - \frac{d\vec{H}_M}{dt} + \left(\overrightarrow{OE} - \overrightarrow{OM'}\right) \times \vec{F}_E = [0, l, 0]^T \times \vec{a}_M$	
ut	

$$\begin{bmatrix} a_{M_x} \\ a_{M_y} \\ a_{M_z} \end{bmatrix} = \begin{bmatrix} -\frac{(OP_x - OM_x') \times F_{G_y} - \frac{dH_{M_z}}{dt} + (OE_x - OM_x') \times F_{E_y}}{m. l} \\ -\frac{(OP_z - OM_z') \times F_{G_y} - \frac{dH_{M_x}}{dt} + (OE_z - OM_z') \times F_{E_y}}{m. l} \end{bmatrix}$$
 (eq. 2)

- Because *m.l* is considered constant for a linearized inverted pendulum, only the numerators are used to describe the three balance mechanisms.
 - 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 whole-body weight and external force vectors, and accelerates the whole-body CoM in the opposite direction (Fig 1.a) [6]. The contribution of this mechanism to whole-body CoM acceleration depends on the distance between P (the CoP) and M', and the magnitude of ground reaction forces (eq. 3).

$$\vec{a}_M = (\overrightarrow{OP} - \overrightarrow{OM}') \times \vec{F}_G \tag{eq. 3}$$

The 'counter-rotating' mechanism refers to all muscle actions that contribute to rotating body-segment(s) that are not directly in contact with a support. 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 (eq. 4):

$$\vec{H}_O = \vec{H}_M + \overrightarrow{OM} \times m. \vec{v}_M \tag{eq. 4}$$

 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 the global reference frame, H_M can be computed using eq. 5:

$$\vec{H}_{M} = \sum_{i=0}^{n} [I_{i} \cdot \vec{\omega}_{i} + (\overrightarrow{OM}_{i} - \overrightarrow{OM}) \times m_{i} (\vec{v}_{M_{i}} - \vec{v}_{M})]$$
 (eq. 5)

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57 121

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 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 [11]. 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 eq. 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 (Fig 1.b), especially when M' is outside the base of support [12].

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 [10]. Well-known examples of this mechanism are *hand* placement (Fig. 1c) and *foot* placement, which is largely used to maintain balance while walking (see [9] for a review). The contribution of this mechanism to whole-body CoM acceleration can be quantified using eq. 6:

$$\vec{a}_M = (\overrightarrow{OE} - \overrightarrow{OM}') \times \vec{F}_E \tag{eq. 6}$$

This equation is similar to eq. 3, with the difference that the distance $\overrightarrow{OE} - \overrightarrow{OM}'$ can be larger than the distance $\overrightarrow{OP} - \overrightarrow{OM}'$. It should be noted that the antero-posterior component of $\overrightarrow{F_G}$ (eq. 3) and $\overrightarrow{F_E}$ (eq. 6) is neglected, because the linearized inverted pendulum assumes no vertical displacement of the whole-body CoM.

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 wholebody CoM acceleration is impossible in humans) [13]. 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 [14].

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 [15,16]. 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 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) (Fig. 2): i) posture to posture, ii) posture to movement, iii) movement to posture, and iv) movement to movement.

ANTICIPATION

Humans have the remarkable ability to perform smooth movements that are temporally and spatially adapted to the objectives and constraints of the task [17]. It has been proposed that they achieve this by building internal models of the whole-body to predict their next whole-body state relative to the intended movement, based on the initial state and an efferent copy of the motor commands [18,19]. Because consequences of a voluntarily-initiated movement can be predicted, the nervous system can program

muscle activations adapted to both external and internal constraints, generating favourable biomechanical conditions for the execution of the forthcoming movement [20,21]. Such forward models appear to be essential in making motor responses coincide with predictable events, and overcoming the time delay present in the sensorimotor system when reactive control is not possible [1,22,23].

During voluntarily-initiated motor transitions, anticipatory muscle patterns have been defined as muscle activations or inhibitions preceding the prime mover muscle activation [4]. 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 [24], 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 (e.g., during change of direction [25], a movement to movement transition). 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 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 Fig. 2), could be more appropriate for all types of transitions. In turn, for the purposes of this review, we define motor anticipation as muscle patterns that have mechanical consequences on the whole-body CoM kinematics, initiating before the onset of the voluntary movement (e.g., raising the upper limb or lifting the foot to initiate gait). This definition enables us to consider the delay between muscle activation and muscle force production [26], without considering it as anticipation.

EVIDENCE OF ANTICIPATORY MUSCLE ACTIVATIONS MODULATING BALANCE

MECHANISMS DURING VOLUNTARILY-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 (Fig. 1), and focus our analysis on the anticipatory phase of the identified motor transitions (corresponding to subinterval (1) in Fig. 2). Since not all studies directly quantified the modulation of

each balance mechanism, in some cases we rely on findings from other studies to infer how anticipatory muscle activations modulated the balance mechanism(s).

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) [24], gait initiation, or squat jump (posture to movement) [27–29]. 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 [24,27,29,30] (Table 2). 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 [31–33]. The mechanical consequence of this anticipatory muscle pattern is to shift the CoP backward. According to eq. 3, this backward CoP shift is thought to generate forward wholebody CoM acceleration to initiate the voluntary movement [15,28,34–36] (Fig. 1a).

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 [37,38] (Table 2). 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 (eq. 3). The second is to progressively shift the CoP towards the stance foot, decelerating the wholebody CoM, enabling the swing foot unloading and lifting, while avoiding a fall towards the stance foot 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 (eq. 3). However, the second term, representing the ground reaction force vector in eq. 3, is generally not

considered, probably because it is not expected to change much during transitions with small momentum (posture to posture, and posture to movement).

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 [39–41].

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 [39]. 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 [41]. While these activations are likely to rotate the trunk in a forward direction, 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 [40,41] (Table 3).

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 trunk flexion preceding foot-off [40,42] (Table 3). 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 of base of support) [43], with the most important contribution coming from the trunk segment [44]. This

 point could be clarified by identifying whether the recorded flexion of the trunk 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 [40,41], and have suggested that these activations serve to limit the lateral trunk inclination towards the stance foot side, and direct the trunk towards the swing foot side [40]. This lateral 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 (posture to posture), some authors have reported an increase in H_M directed in a rotation towards the stance lower-limb in the frontal plane [43]. 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 [42,45]. 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 (eq. 5). 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 to whole-body CoM acceleration and, by extension, its impact on overall balance maintenance.

THE 'APPLYING NEW EXTERNAL FORCE(S)' MECHANISM

The 'applying new external force(s)' mechanism relates to motor transitions starting from a movement. In this case, there is a modification of the base of support, for example, adapting foot placement when walking on uneven terrain [46]. 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 [9], we only selected studies that considered modification of the foot placement.

Two distinct muscle activation mechanisms enable 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 [47]. Notably, it has been suggested that the gluteus medius actively modulates medio-lateral foot placement during gait [48] (Table 4). During

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 [47]. Notably, it has been suggested that the gluteus medius actively modulates medio-lateral foot placement during gait [48] (Table 4). 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 [49] (Table 4). 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 (eq. 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 [47]. While walking, foot placement is closely related to the current position and velocity of the whole-body CoM [9]. Authors have recorded biceps femoris activations during the penultimate step, before a change of direction [25]. 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 [50,51]. Other authors have suggested that while these activations may contribute to the last foot placement, they could also be related to the increase in ground reaction forces measured during gait termination (eq. 6) [52].

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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 ground reaction force vector has rarely been considered (eq. 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 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.

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 the 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 contributions of the three balance mechanisms proposed by Hof [10]—moving the CoP, counterrotating, 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 (Fig. 2). 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.

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 (eq. 3) [6]. During a movement, the foot is placed such that a steady velocity can be maintained [9]. 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', and 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 wholebody 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 (Table 2, 4). 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 [28,31]. 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 [53]. 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 [54]. During stepping (posture to posture), other authors have reported that the whole-body CoM

acceleration caused by the CoP shift is tuned to the planned foot placement, in both sagittal and frontal planes [34]. 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) [55]. 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 (eq. 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 ground reaction forces in eq. 3, and the new external force in eq. 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 [56,57]. 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 [58]. In another study, vestibular-stabilising responses to electrical stimulations were reported to be proactively down-regulated before different types of motor transitions [59]. 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 the roles of the 'moving the CoP' and 'applying new external force(s)' mechanisms differ between steady balance states and motor transitions. While they help maintaining balance during steady movements, these mechanisms increase mechanical instability during

the anticipatory phase of a motor transition, creating favourable conditions helping the nervous system to switch from the initial to the final steady balance state.

'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 [60,61]. Since it is very unlikely that the ankle muscles alone can regulate balance [62,63], especially if the distance between M and P is large (eq. 3), other mechanisms may limit excessive increases in wholebody 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 [10,64–66]. 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 [67,68]. In human movements, however, the role of the 'counter-rotating' mechanism remains unclear (Table 3). 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) [39]. During gait initiation (posture to movement), the trunk contribution to H_M in the sagittal plane is oriented in the opposite rotational direction to that of the stance limb [44], and that of an inverted pendulum. On the other hand, anticipatory trunk muscle activations and the associated trunk kinematics have been found to rotate in the direction of the voluntary movement during reaching tasks (posture to posture) [69], or in the final steady state direction during the penultimate step in a change of direction task (movement to movement) [53]. 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 literature review, we suggest that further research is needed to clarify the role of the 'counter-rotating' mechanism in balance-

movement coordination. Specifically, it is important to investigate the contribution of the 'counterrotating' 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 first step towards a better understanding of the 'counter-rotating' mechanism could be the quantification of each segment's angular momentum to H_M [53]. This would make it 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 [70,71], given that the link between muscle activations and segment dynamics is not straightforward. This would make it possible to determine direct cause and effect relationships between muscle activations and H_M , notably taking internal coupling and whole-body dynamics into account.

PRACTICAL PERSPECTIVES

In daily life, the "forces we exert on the environment during (loco)motion are anything but constant" [72]. 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 [73]. These motor transitions are therefore vital for everyone to move and interact safely within their environment. 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 [74].

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 [75], and their respective contributions can be analytically separated [10]. 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 older people have a larger range of H_M in the sagittal plane during stepping, compared to their younger counterparts [44]. 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 [76], and placed their recovery limb less accurately [77], 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 linearized inverted pendulum neglects the contribution of the 'counter-rotating' mechanism in the transverse plane (eq. 2). Future studies should identify specific situations in which individuals rely on '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 whether 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 [78]. 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 [79]. 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 [80]. Recently, hip exoskeletons were developed to modulate step width, and ensure balance during steady walking [81]. In an able-bodied population using a lower-limb exoskeleton, trunk motion and arm movements have been used to detect gait initiation [82], gait termination, and change of

direction intentions [83]. 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, further 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.

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 balance 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 the 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 2 **470** 3 devices. 5 **471** 6 **ACKNOWLEDGEMENTS** This work was funded by the Region Nouvelle-Aquitaine (France). The authors would like to thank Mrs 11 473 13 474 Elaine Seery for the English proofreading. 22 23 24 25 26 27 28 29 33 35 37 45

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688 TABLES

Table 1: Nomenclature for equation terms (All the variables are expressed in the global reference frame)

Term	Dimension	Description	
\vec{a}_{M}	3×1	Linear Acceleration of the whole-body centre of mass	
$d\vec{H}_{M}$	3×1	Variation of internal whole-body angular momentum	
dt	1	Variation of time	
$ec{F}_E$	3×1	New external force	
$ec{F}_G$	3×1	Ground reaction force	
$ec{H}_{O}$	3×1	Global whole-body angular momentum about the origin of the global reference frame	
$ec{H}_M$	3×1	Internal whole-body angular momentum about the whole-body centre of mass	
I_i	3×3	Inertia tensor of the i th segment around its centre of mass	
l	1	Effective pendulum length	
m	1	Mass of the whole-body	
m_i	1	Mass of the i th segment	
n	1	Number of segments of the multi-body model	
\overrightarrow{OE}	3×1	Position of the application point of the new external force	
ОM	3×1	Position of the whole-body centre of mass	
$\overrightarrow{OM'}$	3×1	Position of the projection of the whole-body centre of mass in the transverse plane on the ground	
\overrightarrow{OP}	3×1	Position of the centre of pressure	
$[x,y,z]^T$	3×1	Transpose of the row vector $[x, y, z]$	
\vec{v}_{M_i}	3×1	Linear velocity of the centre of mass of the i th segment	
\vec{v}_{M}	3×1	Linear velocity of the whole-body centre of mass	
×		Cross product between two vectors	
$ec{\omega}_i$	3×1	Angular velocity of the i th segment	

Table 2: 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 [24,27,29,30]	Sequentially [37,38], 1) Brief swing side Gluteus Medius activation 2) Decreased swing side Tibialis Anterior activation	
Biomechanical consequences of anticipatory muscle activations	Backward shift of the CoP, accelerating the whole-body CoM forward [15,34–36]	 Shift the CoP towards the swing foot, accelerating the CoM towards the stance foot Shift the CoP towards the stance foot, decelerating the CoM toward the swing foot [37,38] 	
Proposed role in 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 Enabling the initiation of the voluntary movement and maintaining balance	
Illustration	\overrightarrow{a}_{M} \overrightarrow{a}_{M}	Swing side	

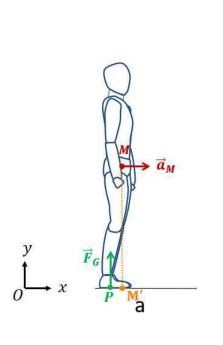
Table 3: Summary of the anticipatory muscle activations, biomechanical consequences, and proposed role in balance movement coordination for the 'counter-rotating' mechanism during transitions starting from a posture. The activations, biomechanical consequences and proposed role in the sagittal plane 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.

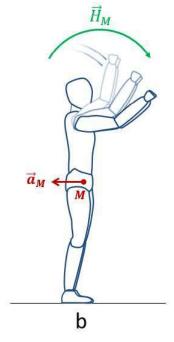
'Counter-rotating'	Transitions starting from a posture (e.g. upper-limb raising, gait initiation)	
	Sagittal Plane	Frontal Plane
Evidence of anticipatory muscle activations	Bilateral activation of rectus abdominis and obliquus abdominis, with a non- systematic inhibition of swing erector spinae [40,41]	Activation of erector spinae of the swing side [40,41]
Biomechanical consequences of anticipatory muscle activations	Trunk Flexion [40,42] But H_M is directed in a backward rotation [43]08/11/2024 12:42:00	Limit trunk lateral inclination towards the stance foot side [40], and direct H_M in rotation towards the swing foot side [43]
Proposed role in balance-movement coordination	Unclear The dissociation between pelvis/lower-limb and trunk should be further clarified in future studies	Limit the increase in H_M directed in a rotation towards the stance lower-limb side, probably to limit the increase in H_M and maintain balance
Illustration	\vec{a}_{M}	\overrightarrow{a}_{M} Swing side

Table 4: 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 wholebody 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	 Penultimate stance biceps femoris activation [25] Swing soleus and vastii activation [50,51] 	Activation of gluteus medius [48] (not directly assessed during motor transitions)	
Biomechanical consequences of anticipatory muscle activations	 Reduce gait velocity and step length [50,51] Increase in GRF during the last step [52] 	Reduction in the penultimate step width to reduce the CoM acceleration in the outward direction [49]	
Proposed role in 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	\vec{a}_M \vec{F}_E	Inside of the turn	

FIGURES





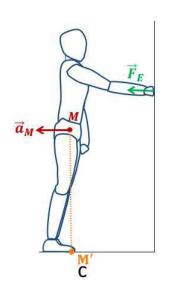


Fig. 1: Schematic representation of the three balance mechanisms that contribute to modifying whole-body CoM acceleration (red point M) [10], here illustrated in the antero-posterior direction. a) Moving the Centre of Pressure (green point P) location within the base of support to modify the distance between the centre of pressure and the projection of the whole-body COM in the transverse plane on the ground (orange point M'). b) Counter-rotating segments (trunk, upper limbs, etc.) modifies internal whole-body angular momentum about the whole-body centre of mass (H_M). c) Applying a new external force (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 indicate the primary biomechanical variables responsible for whole-body CoM acceleration within each of the three balance mechanisms (F_G , H_M and F_E , respectively), and red arrows represent whole-body CoM acceleration (\vec{a}_M).





Initial state = posture Initial state = movement b: Movement to movement a: Posture to posture $v_{init} = v_{final}$ \vec{a}_M d: Movement to posture c: Posture to movement \vec{v}_M $v_{init} \neq v_{final}$ Transition IS Transition FS IS FS time

Fig 2: Schematic representation of whole-body CoM acceleration (red) and velocity (green) during the 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 wholebody 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.