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► To cite this version:

Eric Yiou, Teddy Caderby, Tarek Hussein. Adaptability of anticipatory postural adjustments associated with voluntary movement. World Journal of Orthopedics, 2012, 3 (6), pp.75–86. 10.5312/wjo.v3.i6.75 . hal-01232313

HAL Id: hal-01232313

<https://hal.univ-reunion.fr/hal-01232313>

Submitted on 27 Oct 2016

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Adaptability of anticipatory postural adjustments associated with voluntary movement

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Supported by UFR STAPS of the University of Paris 11, France

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Received: December 4, 2011 Revised: May 2, 2012

Accepted: June 5, 2012

Published online: June 18, 2012

constraints. However, it seems that, depending on the constraint, the "priority" of the CNS was focused on postural stability maintenance, on body protection and/or on maintenance of focal movement performance.

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Key words: Anticipatory postural adjustments; Adaptability; Voluntary movement; Balance; Biomechanics; Motor control

Peer reviewer: Vassilis Paschalis, PhD, Department of Physical Education and Sport Science, University of Thessaly, Karies, 42100 Trikala, Greece

Yiou E, Caderby T, Hussein T. Adaptability of anticipatory postural adjustments associated with voluntary movement. *World J Orthop* 2012; 3(6): 75-86 Available from: URL: <http://www.wjgnet.com/2218-5836/full/v3/i6/75.htm> DOI: <http://dx.doi.org/10.5312/wjo.v3.i6.75>

Abstract

The control of balance is crucial for efficiently performing most of our daily motor tasks, such as those involving goal-directed arm movements or whole body displacement. The purpose of this article is twofold. Firstly, it is to recall how balance can be maintained despite the different sources of postural perturbation arising during voluntary movement. The importance of the so-called "anticipatory postural adjustments" (APA), taken as a "line of defence" against the destabilizing effect induced by a predicted perturbation, is emphasized. Secondly, it is to report the results of recent studies that questioned the adaptability of APA to various constraints imposed on the postural system. The postural constraints envisaged here are classified into biomechanical (postural stability, superimposition of motor tasks), (neuro) physiological (fatigue), temporal (time pressure) and psychological (fear of falling, emotion). Overall, the results of these studies point out the capacity of the central nervous system (CNS) to adapt the spatio-temporal features of APA to each of these

INTRODUCTION

The control of balance is crucial for efficiently performing most of our daily motor tasks, such as those involving goal-directed arm movements or whole body displacement. Humans, as in all terrestrial species, indeed evolve in a gravity field that permanently tends to induce postural destabilization by its attracting effect towards the center of the earth. The control of these gravitational forces is necessary to maintain balance in a given posture, which constitutes a prerequisite in efficiently performing goal-directed movements and also to displace our body in the intended direction. In addition, movements themselves perturb our balance and can be considered as self-inflicted perturbation. This perturbation originates from the internal forces and torques elicited by the movements which are transmitted through the whole body to the support surface, where ground reaction forces are produced (the latter are external forces).

es). According to the laws of mechanics, these external forces act to destabilize the whole body in the direction opposite to that of the movement. For example, raising the arm forwards to the horizontal induces internal forces and torques at the shoulder level that initially tend to destabilize the rest of the body backwards and downwards. In addition, raising the arm displaces the center of gravity which disrupts the initial conditions of balance. A biomechanical model of the human body showed that the perturbation elicited by a rapid arm raising movement from the erect posture may potentially leave the subject “to fall flat on their face”^[1].

The purpose of this article is twofold. Firstly, it is to recall how balance can be maintained during voluntary movement despite these different sources of perturbation. The importance of the so-called “anticipatory postural adjustments” (APA), taken as a “line of defence” against the destabilizing effect induced by a predicted perturbation, will be emphasized. In daily situations, this line of defence might be challenged by various constraints imposed on the postural system (or “postural constraints”). Examples of postural constraints are fatigue of the postural musculature, instability, time pressure (i.e., having to perform a motor task in a limited time), “fear of falling” (e.g., when one is to move on an elevated surface) and so on. When facing such constraints, the central nervous system has to develop adaptive postural strategies to efficiently perform the intended motor task and maintain balance. The second purpose of this review is to report the results of recent studies that questioned the adaptability of APA to various postural constraints in healthy young adults.

BALANCE MAINTENANCE DURING VOLUNTARY MOVEMENT

The way that balance can be maintained during voluntary movement has inspired many authors, at least since Leonardo da Vinci, and it is still a matter of intensive research. One common statement stressed in most of these researches is that voluntary movements are subjected to two antagonistic constraints. One is to move the “focal” segment(s) (i.e., the body segments directly involved in the voluntary action) towards a goal; the other is to stabilize the “postural” segment(s) (i.e., the body segments not directly involved in the voluntary action) in order to maintain balance. This process of postural stabilization necessarily involves that dynamical phenomena take place in the postural segments that act to minimize the self-inflicted perturbation. These dynamical phenomena correspond to the “postural adjustments”. The following paragraph traces back a brief history of this notion of postural adjustment (for more details on this aspect, the reader may refer to the reviews by^[2-4]), with an emphasis on those postural adjustments that precede the onset of the voluntary movement, i.e., on APA.

Brief history of the “postural adjustment” concept

de Vinci^[5] wrote in around 1500: “I maintain that, when

a man stands motionless upon his feet, if he extends his arm in front of his chest, he must move backwards a natural weight equal to that, both natural and accidental, which he moves towards the front” (cited from Gahery^[3]). This backward body movement corresponds to what we now call “postural adjustments”. The existence of postural phenomena related to voluntary movement was described more recently by Babinski^[6] at the end of the nineteenth century. Babinski observed that when healthy subjects were asked to voluntarily bend their head and trunk backwards, their knees systematically flexed. Thank to this postural adjustment, the center of gravity remains over the base of support and balance is maintained. Babinski also noted that this compensatory leg movement was absent in cerebellar patients, which caused them to fall backward. Although important, this observation was limited because it did not provide information regarding the timing of these postural adjustments in relationship to the onset and termination of the voluntary movement. The necessity to develop postural adjustments during voluntary movement was also emphasized by Hess^[7] in the middle of the twentieth century. Hess distinguished three components in his model of voluntary movement. Each component was symbolized by one character: the first one, the leaper was to jump from the shoulders of the second character, the postural frameworker. This second character also requires the intervention of the third character, the supporter, to maintain balance during the jump. The jump is efficient when the three characters properly coordinate their activity. The jump is unsuccessful when there is a lack of coordination between the three characters. In this model, the activity of the leaper, qualified as “teleokinetic”, was distinguished from the postural activity of the frameworker and of the supporter, qualified as “ereismatic”.

The modern view of postural adjustments associated with a voluntary movement integrates these different historical sources. The “Posturo-Kinetic Capacity” (PKC) has been defined as the capacity of an individual to generate efficient postural adjustments in response to a perturbation (internal or external) (see^[2,8,9] for reviews). The PKC theory emphasizes the necessity to develop postural adjustments in anticipation of the forthcoming perturbation in order to optimize the control of balance. These postural adjustments correspond to the so-called APA and are related to the “action equilibration” mechanisms of André-Thomas^[10]. Because of their precedence relative to the onset of the voluntary movement, APA has been thought to reflect the existence of an internal forward model within the central nervous system that takes into account the dynamic consequence of an expected perturbation and that generates responses to counteract these consequences^[11]. The PKC theory also emphasized the importance of postural joint mobility to ensure an efficient postural counter perturbation. Specifically, this theory predicts that any factor constraining postural joint mobility (e.g., with aging or pathology) would alter the focal movement performance (e.g., the maximal ve-

locity of a pointing task) and the postural stability. The performance of a voluntary movement and postural stability would thus tightly depend on the PKC, which is in agreement with the Hess's model of posture and movement coordination^[7]. Recent experimental data are in agreement with this theory (see paragraph III.1).

Anticipatory postural adjustments

To date, it is to the merit of the Russian school to report the existence of APA in human^[12] and animals^[13]. Specifically, authors reported an activation of the ipsilateral biceps femoris muscle (hip extensor/knee flexor) prior to the activation of the focal muscle (deltoides anterior) during rapid arm raising from the erect posture in humans^[12]. The existence of APA was later confirmed by several authors during a more or less similar paradigm involving the upper limb and it was completed with an exhaustive description of the complex patterns of anticipatory activation/inhibition of the postural muscle within the legs and trunk segments^[14-17].

The function of APA during an upper limb task performed from a quiet standing posture was argued based on experimental data obtained with a force plate^[18,19]. Specifically, authors showed that the onset of voluntary arm raising was systematically preceded by a dynamical phenomena detected by the force plate, which included forward and upward acceleration of the center of gravity. As these phenomena cannot be due to the transmission of forces associated with the focal movement to the support surface (because they precede it), they are necessarily due to postural movements. The latter correspond to APA. It is noteworthy that the biomechanical effects of these APA are opposite in sign to the biomechanical effects of the perturbation associated with the forthcoming arm movement, which is initially directed backwards and downwards as described above. For this reason, it was proposed that the function of the APA is to counter the perturbation associated with the forthcoming voluntary movement in advance^[18,19]. The result is that the APA duration and/or amplitude increases with the velocity of the arm and when an inertia is added to the wrist^[18-21], i.e., when the postural perturbation is increased in line with this function of postural counter perturbation. As proposed in a recent study by Yiou *et al.*^[22], the need to counter this perturbation in advance might stem from the existence of electromechanical delay between the onset of postural muscle activation and the onset of the counter perturbing inertial forces generated by the postural segments. This delay ranged from 80 ms to 100 ms, depending on the muscle^[23]. Thanks to this anticipatory activation of postural muscles, the postural counter perturbation could be effective at the beginning of the voluntary movement, i.e., at the beginning of the perturbation. It is now generally admitted that APA do not totally compensate for the postural perturbation. Postural adjustments occurring during and after the voluntary movement were also described in the literature (albeit to a much less extent^[19,24-26]). The latter are termed "consecutive postural adjustments" (CPA)

and deal with the actual postural perturbation.

Besides the fact that APA are associated with motor tasks performed from a fixed base of support (e.g., arm raising from the erect posture), APA are also described in various motor tasks involving a change in the size of the base of support, such as during leg flexion, rising on the toes, gait initiation, *etc.* Gait initiation has classically been defined as the transient period between a quiet standing posture and steady walking^[27]. It can be decomposed into an APA period, which is the period between the onset of the mechanical or electromyographical (EMG) changes from the background level and the time of swing heel off (which corresponds to the onset of the voluntary movement), and an execution phase that ends at the time of swing foot contact with the support surface. Balance in the initial standing posture is disrupted during APA by backward center of pressure displacement, which promotes the propulsive forces necessary to displace the center of gravity forwards during the execution phase^[27,28]. This anticipatory center of pressure displacement is induced by ankle synergy (bilateral soleus inhibition followed by strong tibialis anterior activation). APA along the anteroposterior direction thus serve to create dynamical conditions necessary for gait progression. Authors have shown that the amplitude of these APA (in terms of maximal backward center of pressure displacement) is predictive of the progression velocity of the center of gravity, i.e., gait initiation performance^[27]. Along the axis orthogonal to the progression axis (mediolateral axis), APA are also generated and act to stabilize the whole body during the execution phase^[28-32]. Indeed, it is noteworthy that the act of lifting the swing foot induces a reduction in the base of support size, which is then limited to the single stance foot's contact with the ground. It follows that if the center of gravity is not repositioned above the base of support before the time of swing foot off, the whole body will become unstable during the execution phase and will tend to fall laterally towards the swing leg side under the effect of gravity. During voluntary gait initiation, this natural tendency toward instability is invariably countered in advance by mediolateral APA. These mediolateral APA are manifested as a center of pressure displacement towards the swing leg side which serves to shift the center of gravity in the opposite direction and to provide an initial velocity at the start of the execution phase. During rapid gait initiation, it is known that the center of gravity is not propelled directly above the base of support^[29,30]. Nevertheless, in moving the center of gravity closer to the point of support, i.e., by reducing the mediolateral "gap" between the center of pressure and the center of gravity at the time of swing foot off, the disequilibrium torque at the onset of the execution phase is reduced so the subsequent mediolateral shift of the center of gravity is attenuated. Thus, although mediolateral APA could also serve other functions (e.g., unloading of the swing leg), they appear to be crucial in minimizing postural instability during the execution phase of gait initiation.

ADAPTABILITY OF APA ASSOCIATED WITH VOLUNTARY MOVEMENT

In many daily situations, factors of a different nature may constrain the development of APA and thus affect balance and/or the focal movement performance. This paragraph reports the results of recent studies that questioned the adaptability of APA to various constraints imposed on the postural system. Those postural constraints envisaged here can be classified into biomechanical (postural stability, superimposition of tasks), (neuro) physiological (fatigue), temporal (time pressure) and psychological (fear of falling, emotion).

APA and postural stability

The question of the focal movement performance and the associated APA scale with changes in postural stability has been thoroughly investigated in the literature. As stressed by authors, postural stability depends on both strictly mechanical factors (e.g., the initial height of the center of gravity, the size of the base of support, the presence of an additive support) and on strictly neurophysiological factors, i.e., on the capacity of the postural muscle system to efficiently counter an external or internal perturbation^[2,33]. When the posture is mechanically highly stable, e.g., when standing upright with an additive thoracic support^[14], when leaning against a wall^[15] or when sitting or lying^[34], APA have been reported to be attenuated, very likely because they are then not crucial to maintain posture and balance during task execution. When the posture is mechanically highly unstable, e.g., when the base of support size is drastically reduced in the direction of the perturbation applied to posture, attenuation of APA has also been reported. This attenuation has been thought to reflect a protective strategy directed to minimize the potential destabilizing effect by APA themselves^[35-37].

Results of recent studies illustrate the relationship between base of support size, APA and focal movement performance. For example, in the study of Yiou *et al.*^[37], subjects performed a series of forward arm pointing tasks at maximal velocity, from five postures that differed by the anteroposterior distance between the heels (Figure 1). This distance was decreased stepwise from 40 cm (P40 condition) to 0 cm (P0 condition with feet in contact). Kinetics data were collected with a large force plate and kinematics data of the pointing was collected with a bi-axial accelerometer fixed at the wrist (Figure 1). Results showed that the amplitude (maximal backward center of pressure displacement) and the efficiency of the APA (anticipatory forward center of gravity velocity), as well as the pointing performance (maximal hand velocity towards the target), all statistically decreased from P40 to P0. In contrast, the duration of APA did not change with the base of support size. These results provided support to the PKC theory, according to which the performance of the focal component of a motor

task tightly depends on the capacity of the postural component to develop efficient anticipatory dynamics^[2,8,9]. This capacity is hindered when the base of support size is reduced in the direction of the perturbation.

In the continuity of these results, Yiou *et al.*^[33] questioned how young healthy subjects control their balance in situation of instability specifically elicited by a reduced capacity of force production in the postural muscle system. Subjects displaced a horizontal bar forwards with both hands at a maximal velocity towards a target while standing on one or both legs. It is noteworthy that, in terms of mechanics, the postural stability along the anteroposterior direction is roughly equivalent in these two conditions since the base of support length remained unchanged. In contrast, the postural stability along the mediolateral direction was lower in the unipedal compared to the bipedal stance since the base of support width was reduced. The focal movement was expected to induce very low mediolateral perturbation as it was symmetrical with respect to the sagittal plane. Thus, it was assumed that any change in APA parameters or in focal movement performance in the unipedal stance predominantly reflected adaptation to the reduced postural muscle system efficiency, rather than adaptation to the reduced mediolateral base of support size. The main results showed that, along the anteroposterior axis, APA were twice as long in the unipedal stance than in the bipedal stance, while the anticipatory inertia forces directed to offset the forthcoming perturbation remained equivalent. The focal movement performance was maintained without any additive postural perturbation during task execution. These results showed that young healthy subjects do not use a “protective strategy of APA attenuation”^[35,36] when exposed to a situation of instability specifically elicited by reduced postural muscle system efficiency. Instead, when confronted with such a situation herein experimentally elicited by having subjects standing on one leg, they lengthen APA duration in order to reach an as efficient anticipatory postural counter perturbation as under the more stable bipedal posture (in terms of whole body anticipatory inertia forces). As a consequence, they could maintain an equivalent focal movement performance (maximal velocity) without any additive postural perturbation. This postural adaptation was possible here because the possibility of center of pressure shift in the direction of the perturbation remained unchanged across conditions.

Overall, these studies suggest that when APA cannot be adapted to the perturbation induced by the voluntary movement, the perturbation, and hence the focal movement performance, is reduced. When APA can adapt to the perturbation, the focal movement performance remains optimal.

APA and fatigue

The question of how the central nervous system adapts APA in order to take into account the internal pertur-

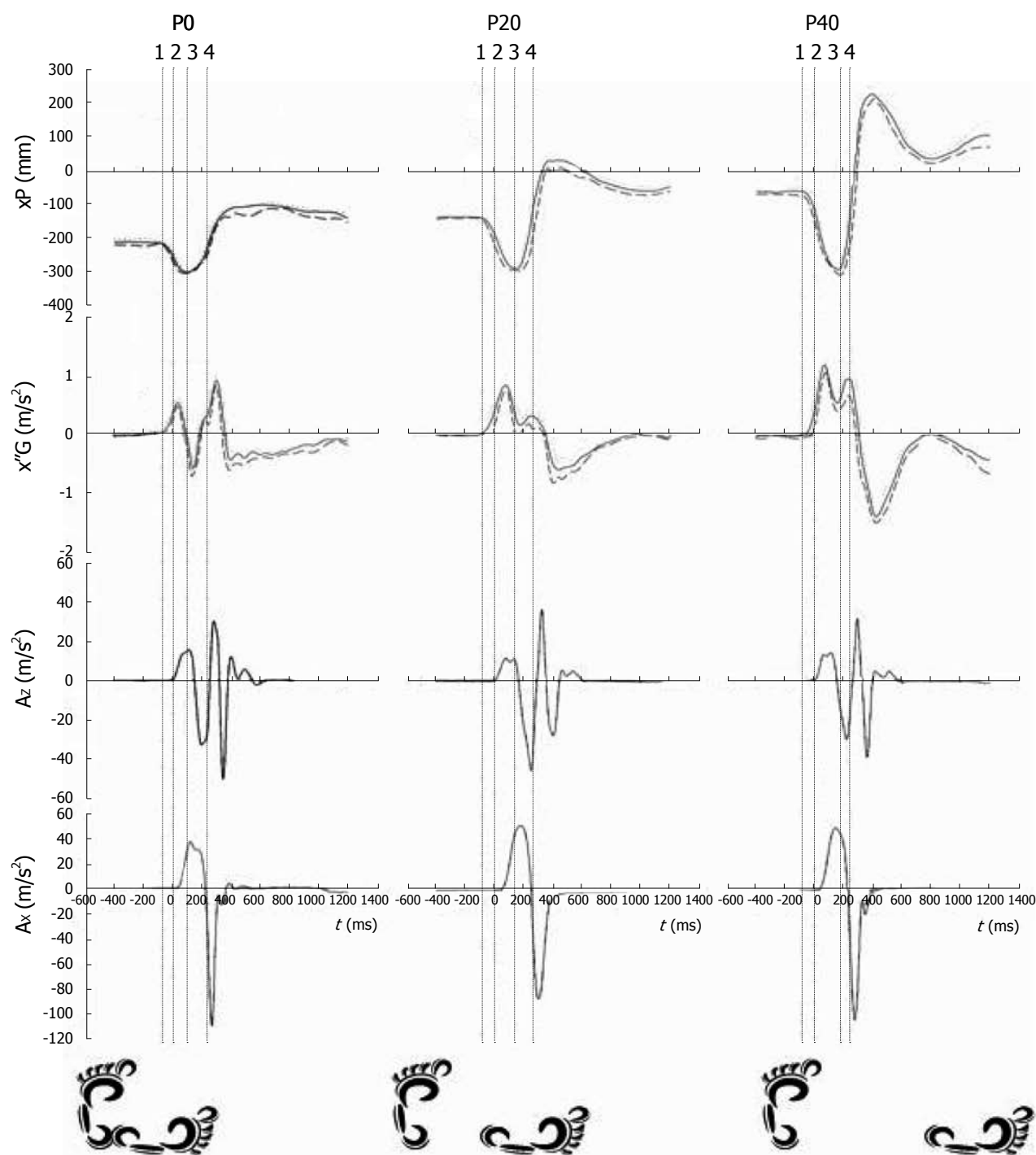


Figure 1 Example of biomechanical profiles associated with forward arm pointing in the P0 (heels in contact), P20 (20 cm between the heels) and P40 conditions (40 cm between the heels), and feet position (below panels). Mean traces (± 1 STD) are presented in one representative subject ($n = 7$ trials) pointing the arm to the right of the figure. xP, x''G, Az, Ax: Anteroposterior center of pressure displacement, anteroposterior center of gravity acceleration, vertical and anteroposterior hand acceleration, respectively. Line 1: Onset of biomechanical traces/onset of anticipatory postural adjustments (APA); Line 2: Onset of voluntary hand acceleration; Line 3: Peak of maximal center of pressure displacement/end of APA; Line 4: Target hit. An upward variation indicates a forward or an upward oriented displacement or acceleration. The time scales reported at the bottom of the figure are the same for all panels. The y-scales reported on the left side are the same for the panels in the P0, P20 and P40 conditions. (From Yiou *et al.*^[37]).

bation induced by postural muscle fatigue (hereafter referred to as “fatigue”) has been addressed in several recent studies^[38-42]. In these studies, subjects performed a series of rapid discrete motor tasks involving one or both arms from a bipedal stance, before and after a fatiguing procedure designed to obtain fatigue in the

postural musculature [generally in the upper leg (hamstrings) and/or the trunk muscles]. The fatiguing procedure typically consisted of a series of low to moderate level isometric contractions i.e., isometric contractions ranging from 7% of maximal voluntary isometric contraction (MIC) to 50% MIC, that were performed until

exhaustion. As an alternative procedure, exhausting aerobic exercise was used by Strang *et al.*^[43] to fatigue the whole postural musculature. These studies repeatedly reported that, under such experimental conditions, the level of muscle excitation was drastically decreased in the fatigued state compared to the normal state and that APA onset occurred earlier, which was responsible for a longer APA duration. Because the amplitude of the motor outcome (as measured with the anticipatory displacement of the center of pressure) remained unchanged with fatigue^[38,40], this longer APA duration was thought to reflect adaptive change to the reduced capability of force production in the postural muscle system^[38-43].

In contrast with these latter studies, Yiou *et al.*^[26] reported that, following fatigue of the dorsal part of leg muscles induced by series of high level isometric contractions (60% MIC), neither the level of excitation of the fatigued muscles (hamstrings), APA onset, postural joint kinematics nor anticipatory center of pressure displacement changed. In this study, the motor task was to displace forwards a 2 kg bar (grasp bar) with both arms at a maximal velocity towards a target from a bipedal stance [bilateral forward reach (BFR)]. To explain this discrepancy with the literature, it was proposed that the effects of fatigue on APA might be dependent on the adequacy between the motor units fatigued during the fatiguing procedure and those motor units recruited during the APA. This interpretation was based on the well-known “size principle”^[44], according to which slow and fatigue-resistant motor units [i.e., motor units of type I (MU_I)] are recruited before fast, more fatigable motor units [i.e., motor units of type II (MU_{II})]. In this hypothesis, those motor units that were fatigued by the high level isometric contractions (MU_{II}) were not those predominantly recruited during the APA (MU_I) because the force level required in the postural musculature to counterbalance the destabilizing effect of the BFR was too weak. Consequently, no adaptive EMG change of APA was required following the fatiguing procedure to ensure an equivalent motor outcome.

The results of this latter study further raised the question whether and how the central nervous system adapts the anticipatory EMG activity in the fatigued postural muscles if the force level required in these muscles to counterbalance the destabilizing effect of the BFR was elevated^[45]. In such a condition, the fatigued muscular fibers might then indeed partly match with those used during the APA. Consequently, adaptive EMG changes in the fatigued postural muscles would then be required unless biomechanical features of APA (peaks of anticipatory center of pressure displacement/anticipatory center of gravity acceleration) would be altered. In order to increase the force level required in the postural musculature (in particular in the hamstrings) to counterbalance the destabilizing effect of the BFR, the subjects stood upright on one single leg (unipedal stance) rather than on both legs. The mass of the grasp bar to

be displaced forward was also purposely doubled compared to the study described above (4 kg *vs* 2 kg in Yiou *et al.*^[26]). Subjects performed a series of bilateral forward reach tasks (BFR) under a unipedal stance (dominant and non dominant) before [“no fatigue” condition (NF)] and after [“fatigue” condition (F)] a procedure designed to obtain major fatigue in hamstrings. Center of gravity acceleration, center of pressure displacement and electrical activity of trunk and leg muscles were recorded and quantified within a time window typical of APA. The main results showed that there was no significant effect of fatigue on the level of muscle excitation and APA onset in any of the postural muscles recorded. Similarly, no change in APA onset could be detected from the biomechanical traces. In contrast, the results showed that the peaks of anticipatory center of pressure displacement and anticipatory center of gravity acceleration were much lower in F than in NF. These results suggest that, following the fatiguing series of high level isometric contractions, the capacity of the central nervous system to adapt APA to the reduced muscular efficiency might be altered. Subjects might then possibly more strongly rely on postural adjustments occurring during and/or following the voluntary movement to maintain postural stability. These results markedly contrast with the previous studies reporting adaptive anticipatory changes in the electrical activity of the fatigued postural (and in particular an earlier APA onset), along with an equivalent motor outcome^[38,40]. This discrepancy with the literature might possibly be ascribed to the different intensity of isometric contractions used to elicit fatigue in the postural muscle system, with low to medium level isometric contractions generating lower perturbation of the proprioceptive information sources used to control posture and balance than high level isometric contractions. This effect might be exacerbated when subjects stood on one single leg.

The generality of these latter results obtained with upper limb tasks from a quiet standing posture was recently tested with another experimental model of posture and movement coordination, stepping initiation^[22]. Specifically, the question was how the central nervous system organizes the APA associated with stepping initiation under acute fatigue of ankle dorsiflexors (tibialis anterior, *primum movens* of anticipatory backward center of pressure shift during APA; see Figure 2 for examples of biomechanical and electromyographical traces). The subjects performed a series of stepping initiation at spontaneous velocity before NF and after F, a protocol designed to induce tibialis anterior fatigue on both sides. The main results showed that the level of tibialis anterior activation during the APA, the amplitude of anticipatory dynamical phenomena and the peak of center of gravity velocity (motor performance) decreased with fatigue, while the duration of the APA and the execution phase increased. Subjects were, however, able to increase the level of tibialis anterior activation and thus reach a greater center of gravity velocity when the instruction was to step faster. It

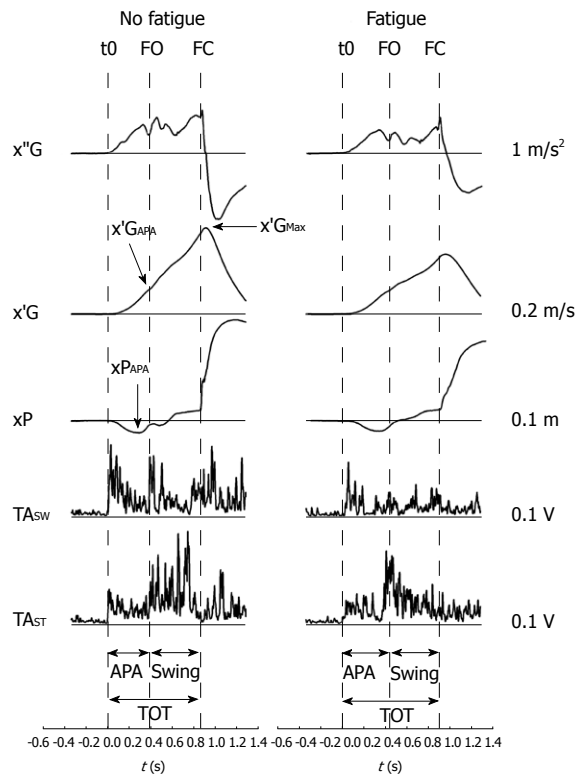


Figure 2 Example of biomechanical and electromyographical profiles of stepping initiation in the fatigue and no fatigue condition (one representative participant at spontaneous speed). $x''G$, $x'G$, xP : Anteroposterior center of gravity acceleration, center of gravity velocity and center of pressure displacement, respectively; t_0 , FO, FC: Onset rise of $x''G$ trace, swing foot off, swing foot contact, respectively; TA: Rectified electrical activity of tibialis anterior; SW, ST: Swing and stance leg, respectively; APA, SW, TOT: Anticipatory postural adjustments, swing phase and total stepping initiation time windows, respectively; $x'G_{APA}$, $x'G_{Max}$, xP_{APA} : Peak of center of gravity velocity, center of gravity velocity at foot off, peak of backward center of pressure displacement, respectively. Positive variation of the biomechanical traces indicates forward displacement, velocity or acceleration. Negative variation of these traces indicates backward displacement, velocity or acceleration (from Yiou *et al.*^[22]).

was proposed that the changes in stepping initiation parameters with fatigue might reflect the existence of protective strategy directed to preserve the fatigued muscles, rather than muscle weakness associated with fatigue. In other words, priority was given to body protection rather than to motor performance maintenance.

Overall, these studies suggest that the adaptability of APA to fatigue depends upon the motor task to be performed and upon the way in which fatigue is induced.

APA and temporal constraints

Voluntary movements can be performed in at least two conditions of temporal constraint: a reaction time condition in response to an external signal and a self-triggered condition in which movement initiation is self-initiated^[46,47]. A literature review showed that the duration of APA in various motor tasks, such as upper limb task^[48,49] and gait initiation^[50,51], was shortened in a reaction time condition compared to a self-triggered condition. A recent study by Yiou *et al.*^[52] tested the hypothesis that, during rapid leg flexion, this shortening of APA could be compensated

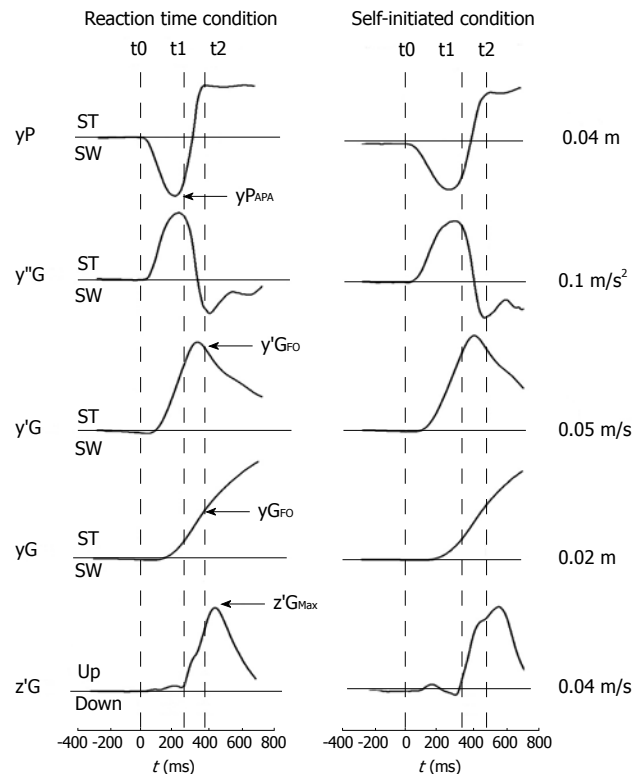


Figure 3 Example of the biomechanical traces of leg flexion in the reaction time and self-initiated conditions (one trial in one representative participant). The figure presents the main experimental variables: yP , $y'G$, yG , yG , $z'G$, medio-lateral (ML) center of pressure (CoP) displacement, ML center of gravity (CoG) acceleration, ML CoG velocity, ML CoG displacement and vertical CoG velocity. The markers t_0 , t_1 , t_2 represent respectively the onset variation of the $y'G$ trace from the baseline, swing heel off and swing foot off. SW and ST indicate the swing and stance leg side, respectively. Finally, yP_{APA} , $y'G_{FO}$, yG_{FO} , $z'G_{Max}$ are the peak of ML CoP displacement during APA, ML CoG velocity/displacement at the foot off time, peak of vertical CoG velocity (motor performance), respectively (from Yiou *et al.*^[52]).

by a larger APA amplitude so that the dynamic stability reached at the foot off time (i.e., at the end of APA) remains the same as in the self-triggered condition. Young healthy participants performed series of leg flexions (1) as soon as possible in response to an acoustic signal (reaction time condition; condition with temporal pressure); and (2) in a self-triggered condition (no temporal pressure). In this study, the focus was on the anticipatory postural control of mediolateral stability, i.e., mediolateral dynamics was mainly considered (Figure 3). Results showed that the swing foot off was triggered sooner in the reaction time condition compared to the self-triggered condition. As a consequence, the APA duration was shorter in the former condition; this shortening was compensated by an increase in the medio-lateral anticipatory center of pressure displacement so that the dynamic stability reached at the foot off time remained unchanged. Overall, these results showed that when a complex task is performed under temporal pressure, the central nervous system is able to adapt the spatio-temporal features of APA in a way to both hasten the initiation of the voluntary movement and maintain optimal conditions of dynamic

stability. It therefore seems that the central nervous system does not “trade off optimal stability for speed of movement initiation under reaction time condition”, as it had been proposed in the literature^[53]. Now, these results must be taken with caution since it remains to be verified whether a more challenging task (e.g., with higher precision requirement on the leg movement, as in Bertuccio *et al.*^[54]), would affect motor performance and/or dynamic stability in the condition with temporal pressure.

APA and superimposition of motor tasks

In many daily situations, humans have to perform goal-directed arm movements in multiple possible directions while voluntarily displacing the whole body, i.e., they have to superimpose “elementary” motor tasks. As stated above, each of these elementary motor tasks necessitates the development of specific APA, in terms of duration, amplitude and direction. In a series of recent papers^[55-59], the question was asked how the central nervous system organizes the APA associated with each of these elementary tasks when they are superimposed in a motor sequence. The experimental model used in these studies was typically composed of two elementary tasks that both required APA. These tasks were either performed in isolation or superimposed in a sequence. For example, in Yiou *et al.*^[60], the three following experimental conditions were carried out: (1) “Isolated stepping” (the stepping initiation was performed alone); (2) “Isolated pointing” (the pointing was performed alone); and (3) “Experimental sequence” (the pointing and stepping were combined). In this study, the question was whether the APA associated with the coordination of arm pointing and stepping initiation resulted from the sole juxtaposition of APA associated with each isolated elementary tasks (“juxtaposition hypothesis”). The postural dynamics of a “theoretical sequence” was purposely calculated based on the linear summation of the acceleration of the center of gravity and the displacement of the center of pressure traces recorded in conditions (1) and (2) (elementary tasks performed in isolation). The “juxtaposition hypothesis” was tested by between condition comparisons of postural dynamics computed during APA for stepping (stepping APA). The main results showed that: (1) The amplitude of the stepping APA was higher in the “experimental sequence” than in the “theoretical sequence”; (2) The stepping APA amplitude was higher in the “isolated stepping” than in the “theoretical sequence” while, in contrast, the model of the “juxtaposition” predicted that it should be lower; and (3) The stepping APA amplitude was higher in the “experimental sequence” than in the “isolated stepping” condition. These results showed that the arm movement facilitated the stepping initiation rather than hindering it, as predicted from the “juxtaposition hypothesis”. It was therefore proposed that the APA generated during the experimental sequence did not result from a simple juxtaposition of isolated elementary tasks. Rather, it was proposed that the central nervous system was able to adapt the APA associated with the arm movement to

fit with the biomechanical constraints associated with the stepping initiation.

Conversely, the question was asked in Yiou and Do’s study whether the central nervous system was able to adapt the APA associated with stepping initiation to take into account the postural perturbation induced by voluntary arm movement. In this study, the focus was on the anticipatory postural control of mediolateral stability during the stepping initiation. Subjects purposely initiate stepping in isolation (“isolated stepping”) or in combination with a lateral arm raising (“motor sequence”). Stepping initiation was carried out with the leg ipsilateral or contralateral to raising arm (ipsilateral and contralateral sequence, respectively) (Figure 4). The arm movement was expected to accentuate the lateral fall of the center of gravity towards the swing leg in the ipsilateral sequence (destabilizing effect) while it is expected to attenuate its fall in the contralateral sequence (stabilizing effect).

The main results showed that the amplitude of APA along the mediolateral direction increased from “ipsilateral isolated stepping” to “ipsilateral sequence”, but did not change in conditions involving the contralateral leg. In addition, the mediolateral instability increased from “ipsilateral isolated stepping” to “ipsilateral sequence”, but decreased from “contralateral isolated stepping” to “contralateral sequence”. These changes were exacerbated when inertia was added at the hand during raising (Figure 5). The results of this study showed that markedly different strategies are used to control mediolateral stability in the “ipsilateral sequence” and the “contralateral sequence”. In the “ipsilateral sequence”, the central nervous system increased the amplitude of APA for stepping to counter the destabilizing effect induced by the forthcoming arm raising. This strategy of up-regulation was, however, not sufficient to completely offset this additive destabilizing effect. Part of this additive destabilizing effect was therefore probably taken charge of during the CPA. In the “contralateral sequence”, the APA amplitude did not change and even tended to decrease as the inertia became higher and instability was lower. In this case, the central nervous system may then simply take advantage of the postural dynamics induced by arm raising to facilitate the process of postural stabilization during CPA. Altogether, these results support the hypothesis that, in young healthy subjects, the central nervous system scales the amplitude of APA for stepping as a function of the biomechanical consequences of forthcoming arm raising on postural stability.

Overall, these studies suggest that during sequential tasks involving whole body displacement, the central nervous system is able to adapt the APA associated with each elementary task to facilitate both whole body progression and postural stability.

APA and psychological factors

Fear of falling: In addition to biomechanical factors such as those reported above, recent studies have shown that psychological factors, such as fear of falling (FoF)

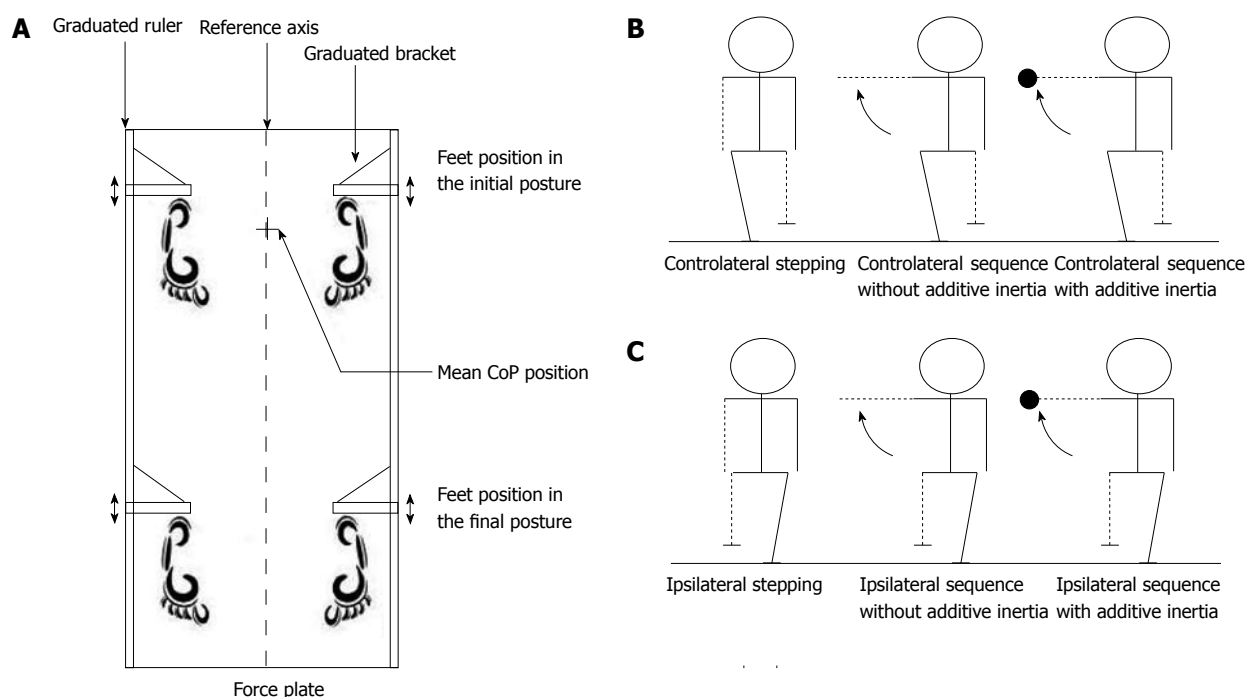


Figure 4 Example of experimental tasks and setup to investigate the organization of anticipatory postural adjustments in a motor sequence. A: Experimental setup. The center of pressure and center of gravity displacement are determined relative to the reference line passing through the center of pressure position in the initial posture; B: Experimental tasks involving the controlateral leg for stepping; C: Experimental tasks involving the ipsilateral leg for stepping. Dotted lines represent the body segments involved in raising and stepping (from Yiou *et al.*^[32]). CoP: Center of pressure.

and related concepts such as low balance confidence, may induce adaptive changes in the way postural equilibrium is controlled^[61-63]. For example, we examined in a recent study^[64] how FoF may influence the anticipatory postural control of mediolateral stability during rapid leg flexion. Young healthy participants performed a series of leg flexions at maximal velocity from low and high surface heights (6 cm and 66 cm above ground, respectively). In the latter condition with increased FoF, the stance foot was placed at the lateral edge of the support surface to induce a maximal postural threat. Results showed that the peak of mediolateral center of gravity velocity reached during APA decreased with FoF; this decrease was compensated by an increase in APA duration (which resulted in a longer reaction time) so that the center of gravity position at the time of swing foot off was located further towards the stance leg side. With these changes in APA, the center of gravity was propelled in the same final (unipodal) position above the stance foot as in the condition with low FoF, i.e., it reached an as stable position. The focal movement performance also remained unchanged. Based on these results, it was suggested that, in the condition with increased FoF, the central nervous system was able to compensate for the lower initial center of gravity velocity by an increase in the APA duration so that the center of gravity could be propelled further towards the stance leg side at the foot off time. With this strategy, the center of gravity was brought nearer to its position of equilibrium at the time when the voluntary leg raising was initiated. It thus

seems that the central nervous system more carefully ensured that the conditions of stability could effectively be reached in the final posture before triggering the voluntary movement. It was thus proposed that the changes in APA with FoF reflected an adaptive strategy directed to simultaneously avoid lateral fall towards the edge of the support surface and to maintain stability in the final unipodal posture.

Emotion: Darwin already proposed a relationship between emotional states and postural changes in man and animals^[65]. Nowadays, there is growing evidence from psychology and neurophysiology that human motor control centers and emotion centers are largely intertwined and reciprocally interrelated^[66]. The so-called “motivational direction hypothesis”^[67] is founded on Darwin’s theory of adaptation of species to their environment. This hypothesis proposes that unpleasant emotions activate defensive circuitry and prime avoidance behaviors, whereas pleasant emotions activate appetitive circuitry that prime approach behaviors. This theory has initially been supported by experiments that manipulate emotional states prior to or during the execution of upper extremity movements that are made towards or away from the body, e.g., wrist flexion or extension^[68]. Only very recently, studies investigated the influence of the emotional state on APA associated with complex task involving whole body displacement such as gait initiation^[69-71]. In these studies, emotional state was elicited by the presentation of unpleasant (e.g., mutilation) or

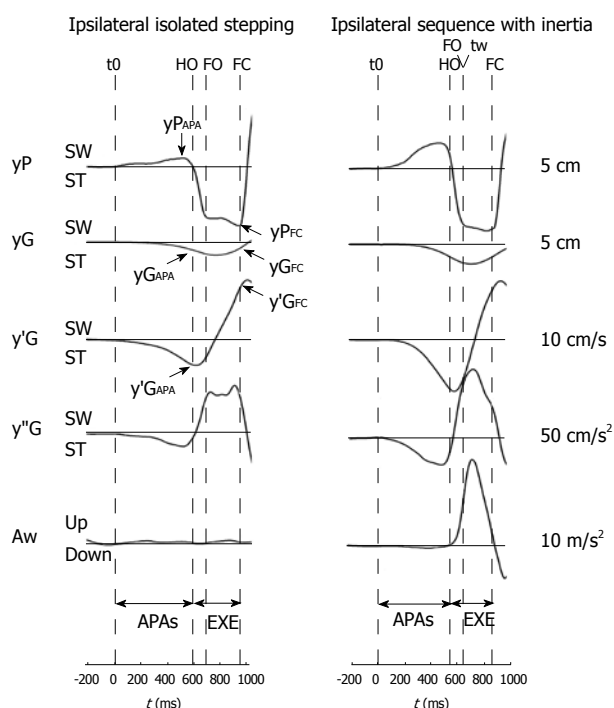


Figure 5 Example of biomechanical traces in “ipsilateral isolated stepping” and “ipsilateral stepping + arm raising sequence” with additional inertia (one trial in one representative subject). yP, yG, y'G, y''G, Aw: Medio-lateral (ML) center of pressure and center of gravity displacement, ML center of gravity acceleration, ML center of gravity velocity and tangential wrist acceleration, respectively; t0, HO, FO, FC, tw: Onset variation of the yP trace from the reference line, swing heel off, swing foot off, swing foot contact and onset of raising, respectively; SW, ST: Swing and stance leg side, respectively; APAs, EXE: Anticipatory postural adjustments and stepping execution phase, respectively. Main postural variables were reported only in the traces of the “ipsilateral isolated stepping”; yPAPA, yGAPA, y'GAPA: Maximal center of pressure displacement, center of gravity displacement and velocity during APAs; yPFC, yGFC, y'GFC: Center of pressure displacement, center of gravity displacement and velocity at time of swing foot contact. Positive variation of the traces indicates displacement, velocity or acceleration towards the swing leg side. Negative variation of the traces indicates displacement, velocity or acceleration towards the stance leg side (from Yiou *et al.*^[32]).

pleasant (e.g., erotic, baby faces) pictures. In brief, these results showed that pleasant images induced an increase in APA amplitude and therefore facilitated forward gait initiation, whereas unpleasant images induced a decrease in APA amplitude and therefore hindered gait initiation. This latter result was interpreted as reflecting a defensive response, probably associated with freezing like behavior. The results of these studies are thought to be in agreement with the “motivational direction hypothesis” and would reflect adaptive changes of APA to environmental stimuli.

Overall, these studies suggest that changes of APA with FoF or emotion might reflect adaptive behavior to the subject's environment.

CONCLUSION

This paper first addressed the question of how balance is controlled during voluntary movement, with a focus on APA, considered as a major “line of defence”

against self-inflicted postural perturbations. Results of recent studies that focused on the adaptability of APA to various sources of constraints imposed to the postural system (biomechanical, temporal and psychological) were then reviewed. Overall, these results point out the capacity of the central nervous system to adapt the APA parameters to each of these constraints, but in specific way. Hence, depending on the constraints, it seems that the “priority” of the central nervous system was focused on postural stability maintenance, on body protection and/or on maintenance of focal movement performance. Knowing how balance is controlled during voluntary movement and how this control adapts to postural constraints may be beneficial for the clinicians to better understand the etiology of falls in populations with postural impairments (e.g., the elderly or persons with Parkinson disease) and to better individualize rehabilitation programs.

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