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Online control of anticipated postural adjustments in step initiation: Evidence from behavioral and computational approaches

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ABSTRACT

Anticipatory postural adjustments (APAs) prior to step execution are thought to be immutable once released. Here we challenge this assumption by testing whether APAs can be modified online if a body perturbation occurs during execution. Two directions of perturbation (resisting and assisting) relative to the body weight transfer were used during the execution of APAs. We found that APAs are modified online (increase in both ground pressure and muscle activity) to compensate for resisting perturbations. The outcomes of a biomechanical model confirmed that the early changes in the APAs resulted from an active control of the APAs and were not merely mechanical consequences of the perturbation. However, no modification of the initial feedforward command was observed for assisting perturbations. The motor command changes for the resisting perturbation may originate from the mismatch between passively originated forces and those actively specified by the central command when acting in the opposite direction. The absence of a mismatch in the assisting perturbation might explain why the central nervous system was not prompted to modify the APAs in this condition.

1. Introduction

According to recent models of motor control [1], expectation based on an internal predictive model that encodes muscle activation patterns is used to plan goal-directed movements. If somatosensory information is important in building this internal model, it is thought to have less importance in the initial phase of the movement. Alternatively, the feedforward internal model would then trigger this initial phase. This type of control would be used to trigger those postural adjustments aiming to prepare the conditions required for execution of the voluntary movement. This is indeed the case for gait initiation and leg raising which are preceded by an initial shift in the center of mass (CoM), both laterally toward the supporting leg (to unload the stepping leg), and forward to create favorable conditions for progression [2]. To provide the sideward acceleration of the CoM, a vigorous pressure on the ground, referred to as "thrust", is produced by an initial displacement of the center of pressure (CoP) toward the stepping leg [3,4]. This lateral thrust is generated by the co-activation of the tibialis anterior and gastrocnemius muscles of the stepping leg, which is scaled to the lateral force to overcome [4,5]. Occurring before the focal stepping movement, the thrust is defined as an anticipatory postural adjustment (APA).

MacKinnon et al. [6] have shown that the APAs are progressively assembled and stored well before (~1.5 s) being triggered. The scaling of the APAs relies on the ability to use sensory information before step initiation. For instance, Timmann and Horak [7] showed that the anticipatory phase that propels the CoM forward is reduced when a backward platform displacement, triggered during the planning phase of the stepping movement, tilts the body forward. This suggests that sensory inputs regarding the new standing condition can be rapidly processed to tune the APAs.

While several studies have examined the setting of APAs before they have been initiated, very few have investigated the influence of afferent feedback on APAs after being triggered off. The potential to change the unfolding APAs following vestibular stimulation (galvanic vestibular stimulation, GVS [8]) or leg muscle proprioception (tendon vibration [9]) has been investigated without conclusive results (namely, the APAs remained unchanged). This may suggest that APAs are resistant to sudden changes in sensory information and that they cannot be modified after initiation. In these studies, the sensory information related to body motion, evoked either by GVS or vibration, may have been superimposed and presumably masked by the massive sensory inputs (from other sensors) regarding body stability. Here we devised a paradigm that enabled us to determine if the initial phase of APAs (i.e., thrust) can be modified online when a real body disturbance occurs during

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their execution. We hypothesized that the body disturbance (namely pulling the body sideways) would evoke massive sensory input related to body motion that could be used to control the thrust online. As modification of the thrust could be the result of a purely mechanical effect of the body disturbance, we developed a biomechanical model of the CoM displacement to dissociate the passive effect of mechanical perturbation from active control of the APAs.

2. Methods

Seven healthy subjects aged 19–24 years old (170 cm mean height, 64 kg mean weight) participated in the experiment. Subjects stood barefoot on a force platform in a quiet standing position. They were asked to step over an obstacle (Fig. 1A) in a self-initiated manner. This task was chosen over a mere step initiation task to increase the balance constraints and therefore the importance of a fine-tuning of the APAs. A harness was fitted around the pelvis (i.e., near the CoM location) and attached to a steel cable on the right side. The length and tension of the cable was set such that the subject was unaware of the cable while standing still as well as during the thrust while the body was motionless. The cable was run laterally through a pulley to a load of 2.3 kg (Fig. 1A). At the start of each trial, the load was supported by an electromagnetic device, thereby preventing the subject from perceiving the mass. Switching off the electromagnet released the mass and pulled the body slightly to the right. The mass was sufficiently light as to not endanger the subject's equilibrium [10].

To set the threshold value of the lateral forces that would trigger the perturbation for each individual, the experimental session began by recording two blocks of five trials in which subjects stepped over the obstacle with either the right or left leg. Here the subject wore the harness, but was aware that no perturbation would occur (NP condition). Four conditions (M0, M1, M2, M3) were then tested in a randomized order. In the M0 condition, no perturbation was triggered. In the M1, M2 and M3 conditions, the online signal of the force platform was used to release the mass at the first third (96 ± 29 ms, ± referred to one standard deviation), second third (170 ± 28 ms) and last third (233 ± 71 ms) of the thrust, respectively (Fig. 1B). Ten trials for each condition were performed with the right stepping leg. As the mass release pulled the body in the opposite direction to the CoM shift, this mechanical perturbation was termed "resisting". In a second blocked session of 40 randomized trials, the stepping task was performed with the left stepping leg. This session was termed "assisting" as the mass release pulled the body in the same direction as the CoM shift (toward the supporting side). After visual inspection of the ground reaction force, four trials were rejected because they diverged drastically compared to trials within the same experimental condition therefore 98.85% of the trials were analyzed.

Movement kinematics were recorded at 100 Hz using the E.L.I.T.E. system® [11]. Markers were placed on the lateral and medial malleolus (right and left foot, respectively) and on the pelvis. Bipolar surface electromyogram (EMG) signals were recorded on the tibialis anterior (TA) and on gastrocnemius medialis (GM) muscles (i.e., ankle muscles, Fig. 1B). EMG signals were pre-amplified, sampled at 1000 Hz (band-pass filtered 20–250 Hz) and full wave rectified. Muscle activity was quantified for each muscle by computing the integral (iEMG) during the burst of activity, identified between the instants that the activity level exceeded (burst onset) and dropped below (burst offset) the mean baseline activity (recorded in a 200 ms time window during quiet standing [12]). Ground reaction forces were recorded at 500 Hz with an AMTI force platform to compute the center of pressure (CoP) displacement in the medio-lateral direction (Fig. 1B).

Horizontal CoM displacements were modeled as a point mass moving along the antero-posterior (AP) and medio-lateral (ML) axes (2D model [13–15]). Running the forward dynamic simulations (using Matlab and SimMechanics toolbox, Mathworks, Natick, MA, USA) permitted the prediction of CoM kinematics from the ground reaction forces. Consequently, for each trial, the inputs of the model were the ground reaction forces along both axes, the mass of the subject and the perturbation (i.e., mass of the dropping load multiplied by the gravitational acceleration modeled as a step input). The model output was the CoM displacement along both axes. Thereafter, we determined the maximum ML CoM displacement in all conditions of perturbation. The term M_{APA} represented the ML CoM displacement simulated when the ground reaction forces entered into the model and were taken from the recorded experimental data. The terms $M_{No\ APA}$ referred to the predicted ML CoM displacement computed when the perturbations were

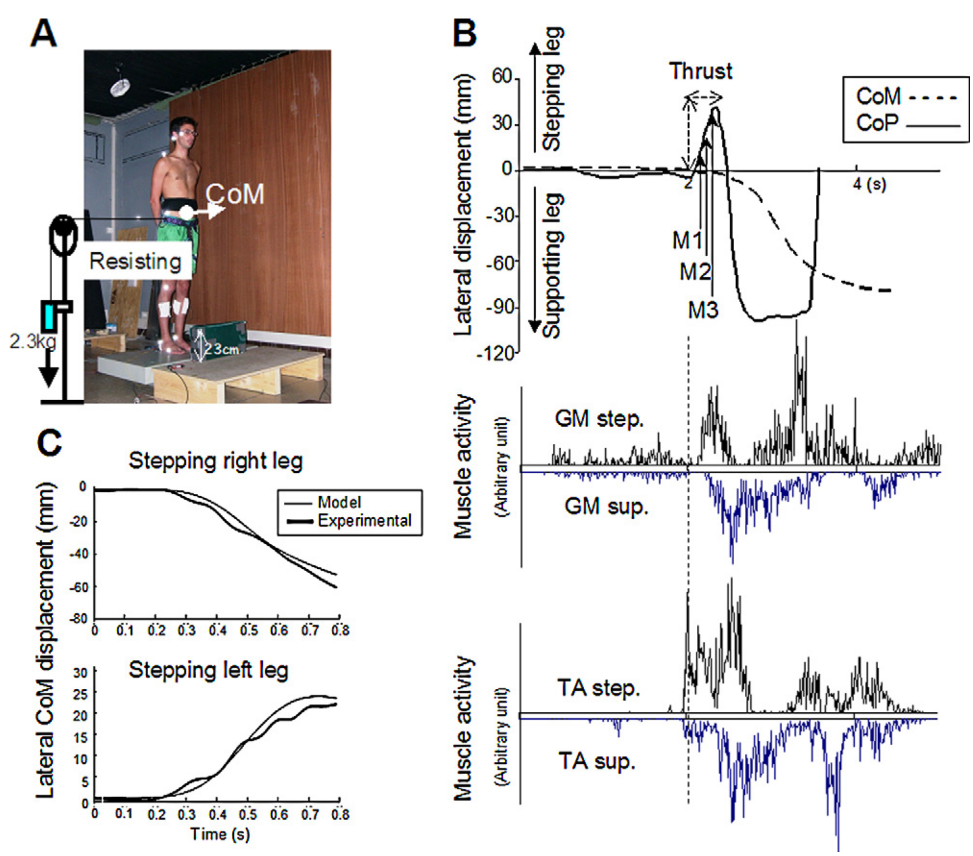

Fig. 1. (A) Experimental set up. The arrow represents the required direction of the center of mass (CoM) displacement for step initiation for the resisting perturbation. (B) Center of pressure (CoP) shift (solid line), center of mass (CoM) shift (pelvis marker, dashed line) and muscle activities averaged for the M0 condition for a typical subject. The arrow indicates the occurrence of the perturbation for M1, M2 and M3 and the dotted line indicates thrust onset. Note that the gastrocnemius medialis (GM step.) and the tibialis anterior (TA step.) of the stepping leg were co-activated during the thrust. Afterwards, the muscles recorded on the supporting leg (i.e., GM sup. and TA sup.) increased their activity when the CoP shifted toward the supporting side. (C) Mean experimental CoM displacement (i.e., pelvis marker)) and mean model prediction for stepping executed with the right and left feet. Data presented are for a typical subject for the M0 condition.

applied to the ground reaction forces recorded in condition M0, that is in the absence of perturbation (and putative active compensation) of the APAs. We reasoned that any difference in peak ML CoM displacement between M_{APA} and $M_{No\ APA}$ should be imputed to active modification of the APAs by the nervous system.

To verify the validity of the model, we compared the ML CoM displacement predicted by the model to the experimental ML CoM displacement (i.e., kinematics of the marker located at pelvis level) in the M0 condition (Fig. 1C). Afterward, the goodness-of-fit was determined by calculating the variance accounted for by the model. Overall, the model explained 92.8 ± 4.9% and 83.6 ± 12.6% of the variance for resisting and assisting perturbations, respectively. Consequently, although this model has several simplifications, the output closely matched the experimental CoM displacements (Fig. 1C). The unexplained variance may be due to measurement errors (e.g., participant's weight), estimation (CoM position using the marker located at the iliac crest) or the assumption that the CoM moves mainly along the horizontal plane.

Dependent variables were analyzed using two-way repeated measures analyses of variance (ANOVA) with two sides (resisting and assisting[1]) by five conditions (NP, M0, M1, M2, M3). Significant effects were analyzed using Newman–Keuls post hoc tests. The level of significance was set at 5%.

3. Results

To control whether the presetting of the APAs depended on the expectation of the perturbation, we specifically focused on any differences between the NP and M0 conditions within the two sides by five conditions analysis. NP and M0 were identical from a mechanical point of view (i.e., no perturbation), but differed with respect to the subject's expectation. Indeed, in the NP condition, subjects did not expect any perturbation during their stepping movement. This was contrary to the M0 condition where subjects were aware that a perturbation could occur. The ANOVA revealed a significant interaction between side and condition factors for both thrust amplitude and thrust duration ($F_{4,24}$ = 25.06; $p < 0.05$ and $F_{4,24}$ = 15.63; $p < 0.05$, respectively). The breakdown of the interaction revealed that in the resisting side, the amplitude of the thrust was greater in M0 than in NP conditions (Fig. 2). Conversely, for the assisting perturbation, the thrust was significantly lower and shorter in M0 than in the NP conditions (Fig. 2). Contrary to NP, which did not show differences in amplitude (p = 0.73) or duration (p = 0.66), M0 was significantly different between resisting and assisting sides for both amplitude and duration ($p < 0.05$).

Because the APAs were affected by the mere expectation of a perturbation, M0 was used as a control condition in the following analyses. The two-way repeated measures ANOVA showed a significant interaction between Side and Condition factors for both the amplitude ($F_{3,18}$ = 8.15; $p < 0.05$) and duration ($F_{3,18}$ = 11.74; $p < 0.05$) of the CoP thrust. Post hoc analyses showed that the statistical differences occurred only for the resisting side (Fig. 3A and B); the thrust amplitude was higher and longer in M1 (72 ± 6 mm; 389 ± 60 ms) and M2 (62 ± 7 mm; 346 ± 58 ms) relative to M0 (55 ± 4 mm; 290 ± 39 ms). The difference between the amplitude of the thrust in the M3 and M0 conditions just failed to reach conventional statistical significance (57 ± 7 mm; p = 0.056), but the duration of the thrust was significantly longer in M3 than in M0 (321 ± 46 ms; p = 0.029).

As any active modifications of the APAs by the nervous system should be associated with a change in muscle activity, we submitted the iEMG to separate one-way repeated measure ANOVAs for the resisting and assisting sides. Two-way ANOVAs were not used here as the muscles producing the thrust changed according to the side of the stepping leg and therefore according to the side of the perturbation. For the resisting perturbation, the ANOVA revealed a significant increase in the iEMG of the right GM burst ($F_{3,18}$ = 4.38; $p < 0.05$), but no significant change in burst duration ($F_{3,18}$ = 1.82; p = 0.179) (Fig. 3A). The analysis of the right TA muscle burst (not shown in the figure) did not reveal any significant modifications of the iEMG ($F_{3,18}$ = 1.64; p = 0.21), nor the burst duration ($F_{3,18}$ = 0.70; p = 0.56). For the assisting perturbation, the Condition had no significant effect on the iEMG or burst duration for both the left GM muscle ($F_{3,18}$ = 1.37; p = 0.28 and $F_{3,18}$ = 1.17; p = 0.34, respectively) and the left TA muscle ($F_{3,18}$ = 2.33; p = 0.107 and $F_{3,18}$ = 0.91; p = 0.454, respectively) (Fig. 3B). This indicates that subjects maintained the same motor command when the mechanical effect of the perturbation was in the same direction as the CoM displacement.

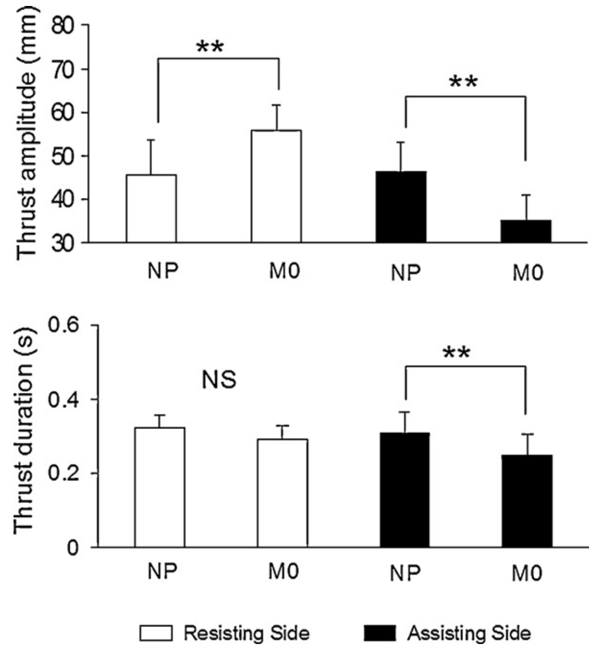

Fig. 2. Mean and standard deviation (SD) of the thrust amplitude and duration in the two conditions without perturbation. In NP there was no perturbation expectation and in M0, the subject was aware that a perturbation may occur (**$p < 0.01$; NS: not statistically significant).

To further test whether the CoM behavior resulted from an active control, we compared the model output based on the experimental data (i.e., M_{APA}) to the model output of the pure mechanical effect of the mass release (i.e., $M_{No\ APA}$). For the resisting perturbation, the two-way repeated measures ANOVA with two (Model outputs: M_{APA}, $M_{No\ APA}$) by three (Conditions: M1, M2, M3) showed a significant interaction for the peak CoM lateral displacement ($F_{2,12}$ = 6.67; $p < 0.05$). Post hoc analyses revealed that the CoM displacement was larger in $M1_{APA}$ than in $M1_{No\ APA}$ (Fig. 4), whereas in the other conditions, no significant effect was observed. The increase in CoM displacement suggests that for the early perturbation (i.e., M1), the motor commands were altered to preserve the planned CoM displacement, despite the resisting perturbation. For the assisting perturbation, the analysis did not reveal a significant effect for either Model outputs or Condition on the CoM displacement (Fig. 4, $F_{1,6}$ = 1.58; p = 0.25 and $F_{2,12}$ = 0.39; p = 0.68, respectively).

4. Discussion

The amplitude and duration of the thrust significantly increased when the subjects were slightly pulled in the opposite direction to the CoM shift during step initiation (i.e., resisting perturbation). Importantly, the active nature of these modifications was

[1] "Resisting" refers to stepping movements performed with the right leg; for these trials the mass release pulled the body in the opposite direction to the CoM shift.

"Assisting" refers to stepping movements performed with the left leg; for these trials the mass release pulled the body in the same direction as the CoM shift towards the supporting side.

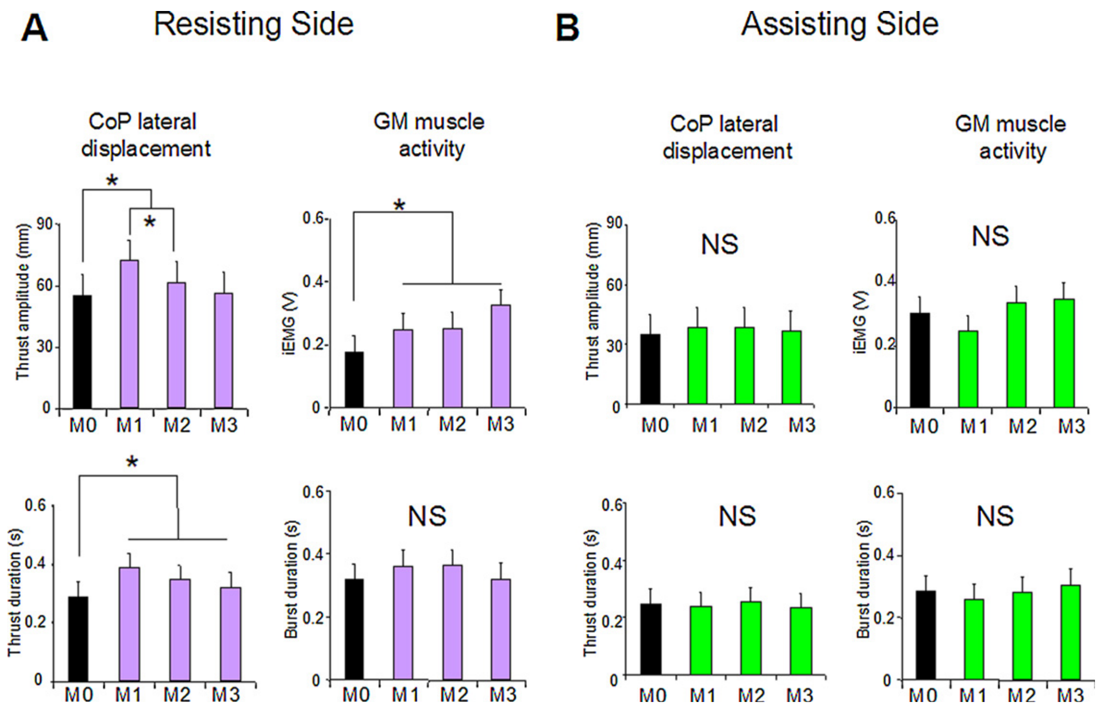

Fig. 3. Mean and SD of the thrust and right gastrocnemieus medialis (GM) muscle activation of the right stepping leg for the resisting side (A) and for the assisting side (B) ($^*p < 0.05$).

evidenced by both the analysis of ankle muscle activity and the model output, which showed that the CoM modification was not merely a passive mechanical consequence of the perturbation. These results provide the first experimental evidence for an online control of the initial phase of APAs (i.e., the thrust) during step initiation and the control of the APAs most certainly involved the processing of body afferent signals. Through rapid feedback loops, these signals (related to body motion) must have been used to update the central feedforward command of the APAs after their dispatch to the efferent system. Indeed, significant changes in the APAs were observed with short latencies (i.e., 389 ms for M1, 176 ms for M2 and 88 ms for M3, as measured from perturbation onset to thrust offset). The very short latency observed in the M3 condition corroborates the 80–120 ms latency of the postural muscles responses observed by Carpenter et al. [16] following motion of the base of support.

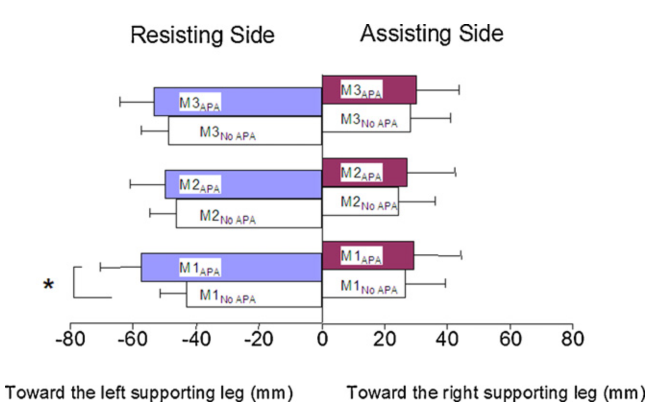

Fig. 4. Mean lateral peaks of CoM displacement simulated by the model. $M1_{APA}$, $M2_{APA}$, $M3_{APA}$ represent the peak CoM displacements simulated when the ground reaction forces entered into the model and were taken from the recorded experimental data. $M1_{No\ APA}$, $M2_{No\ APA}$, $M3_{No\ APA}$ refer to the predicted peak CoM displacements computed when the perturbations were applied to the ground reaction forces recorded in condition M0, that is in the absence of perturbation.

The fact that the perturbation trials were randomly presented and that the subjects were unaware of their occurrence also argues for a fast-tracking of mechanical perturbation and for an online control of the APAs (as opposed to a pre-set modification related to perturbation expectation as in the M0 condition). The discrepancy between the current and the expected somatosensory afferent [17] may have constituted the setting for triggering these online modifications. Indeed, the congruence between the afferents predicted by the central command of the lateral forces (i.e., thrust), and the current afferents was likely disrupted by the perturbation that provided resistance for tilting the body toward the supporting leg. Thereafter, an efferent signal lengthening and increasing the amplitude of the APAs may have been sent to accelerate the CoM toward the supporting side and compensate for the perturbation. This is in line with the role of the supplementary motor area [18–20], together with the basal ganglia, in scaling the duration of the APAs together to modulate the amplitude of the lateral APAs [21]. In contrast, given the small perturbations used here, the mismatch between the current and the expected afferent inflow may have gone undetected in the assisting perturbation. This might explain the lack of online control exerted over the thrust parameters in this condition.

Rogers et al. [22] have recently reported that the APAs that precede step initiation remain unchanged when an upward vertical perturbation of the supporting foot occurs during the early phase of the APA. In their study, the increased pressure under the supporting foot evoked by the upward perturbation was presumably compatible with the increase in pressure expected by the loading of the supporting foot during the body weight transfer. Therefore, the mismatch between the actual and expected sensory information was presumably negligible, leaving the APAs unchanged. In light of the present findings and those of Rogers et al. [22], it is possible that assisting perturbations have to be greater than resisting perturbations for prompting modifications in the initial phase of the APA. This idea is congruent with the results of Mille et al. [23–24] who did not observe changes in early APAs when the assistance was mild. Substantial assistance was necessary in these studies in order to reduce the early APAs and thus be of benefit to patients with Parkinson's disease. However, the lack of muscular activity recordings or model simulations in the studies by Mille et al. does not allow the determination of whether the observed changes resulted from the mechanical perturbation or from an active control by the nervous system.

Finally, the effect of the presence or absence of discrepancy between different sensory afferents, is consistent with Ivanenko et al. [25] who showed that when a confounding effect between proprioceptive information from vibrated muscles (leading to a postural response) and the information gathered regarding support surface instability is present, there is a decreased (or absent) in postural response. The effects of this sensory ambiguity were also suggested by Milner and Hinder [26] in goal-directed arm movement performed in a robot-generated force field.

Overall these results suggest that online control interferes with the feedforward command of anticipatory postural adjustments if the central nervous system can distinguish sensory inputs that arise from externally generated movements from those resulting from self-generated movements.

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Conflict of interest statement

None declared.

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