Targeting a specific motor control process reveals an age-related compensation that adapts movement to gravity environment

Robin Mathieu*[1], Florian Chambellant[1], Elizabeth Thomas[1], Charalambos Papaxanthis[1,2], Pauline Hilt[1], Patrick Manckoundia[1,3], France Mourey[1], Jérémie Gaveau[1]

[1] Inserm UMR 1093-CAPS, Université de Bourgogne, UFR des Sciences du Sport, F-21000, 6 Dijon. Institut National de la Santé et de la Recherche Médicale : UMR 1093, Université de 7 Bourgogne, France.
[2] Pôle Recherche et Santé Publique, CHU Dijon Bourgogne, F-21000 Dijon, France
[2] Département de Gérontologie, Hôpital de Champmaillot, Centre Hospitalier Universitaire de Dijon, Dijon, France

*Corresponding author
Correspondence: robin.mathieu@u-bourgogne.fr

ABSTRACT

As the global population ages, it is crucial to understand sensorimotor compensation mechanisms that allow older adults to remain in good physical health, i.e. underlying successful aging. Although age-related compensation has long been conceptualized and despite important research efforts in varied gerontological subfields, behavioral compensatory processes and their underlying neural mechanisms remain essentially chimeras. This study investigates age-related compensation at the behavioral level. It tests the basic hypothesis that age-related compensatory processes may correspond to an adaptation process that changes movement strategy. More specifically, we focused on the ability of younger (n = 20; mean age = 23.6 years) and older adults (n = 24; mean age = 72 years) to generate movements that are energetically efficient in the gravitational environment. Previous results, from separate studies, suggest that aging differently alters energy efficiency in arm movement and whole-body movement tasks. With aging, energy efficiency seems to remain highly functional in arm movements but has been shown to decrease in whole-body movements. Here, we built on recent theoretical and experimental results demonstrating a behavioral process that optimally adapts human arm movements to the gravitational environment. Analyzing phasic muscle activation patterns, previous studies provided electromyographic measurements that quantified the output of an optimal strategy using gravity effects to discount muscle effort. Using these measurements, we probed the effort-minimization process in younger and older adults during arm movement and whole-body movement tasks. The key finding demonstrates that aging differently alters motor strategies for arm movements vs whole-body movements. Older adults used gravity effects to a similar extent as younger ones when performing arm movements, but to a lesser extent when performing whole body movements. These results provide clear experimental support for an adaptation strategy that down-regulates effort minimization in older adults.

Keywords: Aging, motor control, electromyography, gravity, sensorimotor compensation, equilibrium, posture

Introduction

Living old and healthy, also known as successful aging, is a blessing but is nonetheless associated with deterioration in various organs and functions. In terms of motor deterioration, aging is associated with loss of muscle mass (Larsson et al., 2019), sensory receptor degradation (Goble et al., 2009; Zalewski, 2015; Saftari & Kwon, 2018), and cortical atrophy (Hoffstaedter et al., 2015; Salat, 2004). Functionally, this translates into a decline in muscle strength and power (Larsson et al., 2019; Pousson et al., 2001), and movements that tend to become slower and more variable (Buckles, 1993; Darling et al., 1989). If the deteriorations are too great, they lead to reductions in quality of life and, ultimately, to dependency. Importantly, successful aging is thought to depend on compensatory processes that offset deterioration (Baltes & Baltes, 1990; Martin et al., 2015; Zhang & Radhakrishnan, 2018). Even the most elementary concept of health includes compensatory processes at its core, defining health as “the ability to adapt and to self-manage” (Huber et al., 2011). Thus, despite normal age-related deterioration, compensatory processes enable older adults to remain in good health and continue to perform their daily activities comfortably.

In a world with a rapidly aging population (Rudnicka et al., 2020), it is essential to understand the compensatory processes that enable older people to remain healthy. This represents a critical step toward implementing interventions aimed at detecting, preventing, or reducing frailty and later dependency (for reviews, see Barulli & Stern, 2013; Ouwehand et al., 2007; Poirier et al., 2021; Zhang & Radhakrishnan, 2018). Compensation has long been theorized and could be defined as "a response to loss in means (resources) used to maintain success or desired levels of functioning (outcomes)” (Baltes, 1997). In contexts of severe deterioration, the most basic form of compensation is the use of external aids (e.g., a crutch for walking). Such compensations are observed in frail or dependent older adults, i.e. when deterioration is severe. When considering more subtle deterioration levels, identifying compensation becomes challenging. In these cases, compensatory processes enable older adults to maintain behavioral performances similar to those of younger adults, at least for the less demanding tasks of daily life (Barulli & Stern, 2013). These compensatory processes are the result of neurophysiological and behavioral adaptations that are more difficult to observe with the naked eye. Almost thirty years ago, in his famous theory of selection, optimization, and compensation, Paul Baltes and his colleagues already noted this difficulty (Baltes, 1997; Baltes & Baltes, 1990).

Since then, countless studies have explored compensatory processes using powerful tools and analyses (for recent reviews, see Bunzeck et al., 2024; Fettrow et al., 2021; Poirier et al., 2021). These studies have considerably advanced the description and understanding of age-related neural alterations. Nevertheless, behavioral compensatory processes and their underlying neural mechanisms remain essentially chimeras. In the sensorimotor field, following the consens that aging is associated with increased activation and increased spatial recruitment, numerous studies have attempted to establish a correlation between neural activation and behavioral performance in older adults (for reviews, see Fettrow et al., 2021; Poirier et al., 2021; Seidler et al., 2010; Ward, 2006). This literature has not reached a consensus on the neural changes underlying compensatory mechanisms in older adults. Indeed, several studies reported a positive correlation (Cassady, Gagnon, et al., 2020; Clark et al., 2014; Harada et al., 2009; Heuninckx et al., 2008; Holtzer et al., 2015; Jor’dan et al., 2017; Larivière et al., 2019; Mattay et al., 2002; Spedden et al., 2019), and as many reported no correlation or even a negative correlation (Bernard & Seidler, 2012; Cassady et al., 2019; Cassady, Ruitenberg, et al., 2020; Fernandez et al., 2019; Hawkins et al., 2018; Holtzer et al., 2016; Loibl et al., 2011; Riecker et al., 2006; Ward et al., 2008). Several reasons may explain these discrepancies (for reviews see Fettrow et al., 2021; Morcom & Johnson, 2015; Poirier et al., 2021).

Building on the theoretical work of Krakauer et al. (2017), we recently proposed that an important reason for this failure may be that studies focusing on age-related neuronal alterations have used overly crude behavioral investigations (Poirier et al., 2021). Typically, these studies have used broad measures such as muscle strength or reaction time, and ambiguous experimental paradigms such as putting a peg in a hole or walking on a treadmill. Although these measures and paradigms tested important functional motor performances, they measured the combination of several behavioral strategies and even more neural mechanisms. Since these strategies and mechanisms likely showed different levels of age-related deterioration, broad behavioral measures, which could only quantify the net result, may have mixed deterioration and compensatory processes (Poirier et al., 2021). There's no denying that identifying neural compensation requires linking the brain to behavior and that, to establish this link, we need fine behavioral measures and experimental paradigms that allow approaching the constituent processes of a behavior and its underlying theoretical algorithms. (Krakauer et al., 2017; Pereira et al., 2020; Urai et al., 2022). It is therefore essential to develop detailed knowledge of age-related compensation at the behavioral level.

A number of studies have proposed that the differences observed between younger and older adults can be interpreted as compensations for age-related deteriorations. Of particular interest are studies from the last decade that have sought to investigate specific motor control processes rather than broad motor performance. For example, some of these studies indirectly suggested that older adults favor feedforward rather than feedback control (Moran et al., 2014; Wolpe et al., 2016) to compensate for the attenuation of sensory processing with increasing age (Moran et al., 2014; Parthasharathy et al., 2022; Saenen et al., 2023). Others indirectly suggested that older adults favor movement efficiency over precision (Healy et al., 2023; Poirier et al., 2020) to compensate for their increased energetic cost (Didier et al., 1993; Hortobagyi et al., 2003; John et al., 2009). Yet, because the focus of these studies was not on compensatory processes, they did not include dedicated experimental conditions, and a clear demonstration that these processes are indeed compensatory is lacking.

We sought to fill this gap by building upon the results of two different bodies of literature. On one hand, several studies have demonstrated that the brain plans efficient arm movements that take advantage of the mechanical effects of gravity to minimize muscle effort (Berret et al., 2008; Crevecoeur et al., 2009; Gaveau et al., 2014, 2016, 2021; Gaveau & Papaxanthis, 2011; Gueugneau et al., 2023; for a review, see White et al., 2020). Importantly, recent work demonstrates that this ability is maintained in older adults (Poirier et al., 2020, 2023); some results even suggest that older adults upregulate effort minimization compared to younger ones (Healy et al., 2023; Poirier et al., 2020). On the other hand, studies probing the control of movements performed with the entire body have reported a different conclusion. Even-though such movements involve especially increased effort in older compared to younger adults (Hortobagyi et al., 2003, 2011; Julius et al., 2012; VanSwearingen & Studenski, 2014), results from kinematic studies suggest that older adults plan movements that downregulate effort minimization (Casteran et al., 2018; Paizis et al., 2008). Combined with arm movement results showing that optimally efficient movement planning remains functional in older adults (Healy et al., 2023; Huang & Ahmed, 2014; Poirier et al., 2023), the down-regulation of effort minimization could support the hypothesis that a basic form of age-related compensation corresponds to an adaptation of movement strategy. However, as these literatures used very different experimental paradigms and measurements, this conclusion is highly speculative. More importantly, the results of numerous other studies could also interpret the age-related changes observed in whole-body movements as dysfunction (Goodpaster et al., 2006; Henry & Baudry, 2019; Quinlan et al., 2018; Vernazza-Martin et al., 2008), i.e. deterioration that impairs the ability to produce optimally efficient motor patterns. Here we specifically test the hypothesis that age-related alterations in movement efficiency correspond to an adaptation process, i.e. a process of compensation for other deteriorated sensorimotor components. To overcome the aforementioned limitations, using a specific muscle activation pattern analysis that has proven relevant to focusing on this precise process of effort efficiency (Chambellant et al., 2023; Gaveau et al., 2021; Poirier et al., 2020, 2022, 2023; Thomas et al., 2023), we compare older to younger adults on tasks involving either arm or whole-body movements.

Methods

Participants

Twenty younger adults (23.6 ± 2.1 y.o.) and twenty-four older adults (72 ± 5.3 y.o.) were included in the study after giving their oral informed consent. Participants had normal or corrected-to-normal vision and did not present any neurological or muscular disorders. The laterality index of each participant was superior to 60 (Edinburgh Handedness Inventory, Oldfield 1971), indicating that all participants were right-handed. The study was carried out following legal requirements and international norms (Declaration of Helsinki, 1964) and approved by the French National Ethics Committee (2019-A01558-49).

Experimental Protocol

All participants performed four tasks in a randomized order. Arm movements (Fig 1A), seat-to-stand/back-to-sit (STS/BTS, figure 1B), whole-body reaching toward a near target (WBR D1, figure 1C), and whole-body reaching toward a far target (WBR D2, figure 1D).

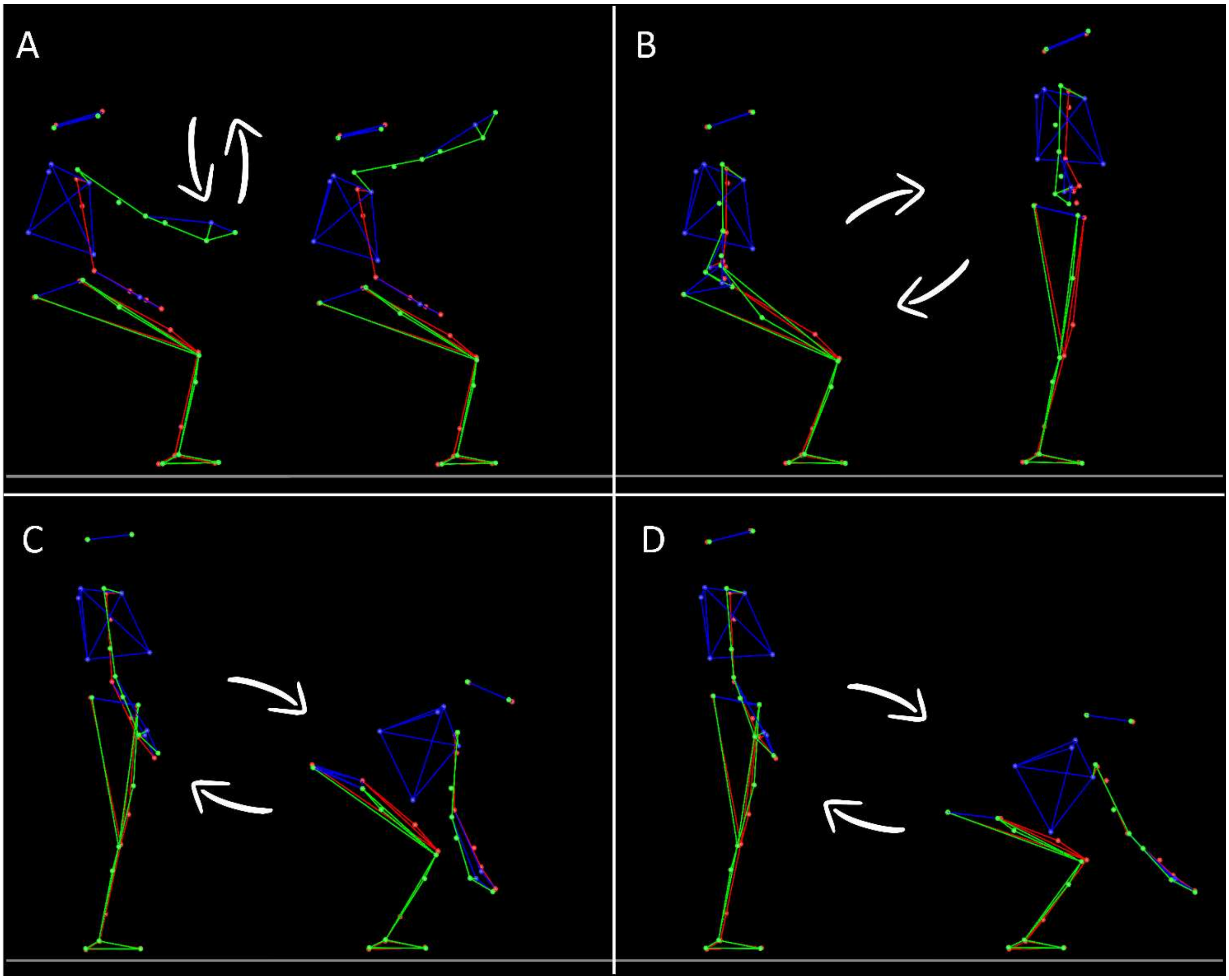

Figure 1. Illustration of the four tasks. Each panel illustrates the extreme body positions between which participants performed their movements. Each position was alternatively the starting or the ending target of a movement, depending on movement direction. **A**: Single degree of freedom arm movements around the shoulder joint. Participants performed upward and downward arm movements. **B**: Seat-to-stand/Back-to-sit movements. Participants performed vertical multi-articular whole-body movements to either stand up from the stool (upward movement) or sit on it (downward movement). **C**: Whole-body reaching task toward a near target. Participants performed vertical multi-articular whole-body movements to either reach towards targets that were located nearby the floor (downward movement) or to bounce back from this position toward a rest vertical standing position (upward movement). **D**: same as C but with targets that were placed farther away on the antero-posterior axis.

ARM task

This task was similar to a task used in several previous studies probing human movement adaptation to the gravity environment (Gaveau et al., 2014, 2016, 2021; Gaveau & Papaxanthis, 2011; Gentili et al., 2007; Hondzinski et al., 2016; Le Seac'h & McIntyre, 2007; Poirier et al., 2020, 2022; Yamamoto & Kushiro, 2014). Using their right arm, participants carried out single-degree-of-freedom vertical arm movements around the shoulder joint. Two blocks of arm movements were performed in a randomized order. One block consisted of six slow movements, and one block consisted of twelve fast movements. Two targets (diameter of 3 cm) were placed in front of the participant's right or left shoulder (in a parasagittal plane) at a distance corresponding to the length of their fully extended arm plus two centimeters. The prescribed movement amplitude between the two targets was 45°, corresponding to an 112.5° (upward target, 22.5° above horizontal) and 67.5° (downward target, 22.5° below horizontal) shoulder elevation.

STS/BTS task

Participants were seated on an armless stool whose height was adjusted to correspond to 30% of the participant's height. The hands were positioned on the hips, and the back was instructed to be maintained about vertical. Similarly to arm movements, participants executed two blocks of movements in a randomized order. One block consisted of six slow movements, and the other consisted of 12 fast movements.

WBR task

This task was similar to those of Casteran et al. (2018) and Paizis et al. (2008). Starting from an upright position, we asked participants to perform whole body reaching movements (WBR) toward two targets nearby the floor (10% of their heights above the floor). The targets (4 × 2 cm) were spaced by 0.5m on a medio-lateral axis and centered on the participant's sagittal axis. They were placed in front of the participant at two different distances, corresponding to 15% (D1) or 30% (D2) of her or his height on the antero-posterior axis. Distances were measured from the participant's big toe. Similarly to the previous two tasks, for each distance and in a randomized order, participants executed two blocks of trials performed at two different speeds. One block consisted of six slow movements and the other twelve fast movements (total of four blocks: two speeds * two distances).

Trial organization

The organization of a trial was similar for all tasks. It was carried out as follows: i) the experimenter indicated to get ready; ii) the participant adopted the requested initial position; iii) after a brief delay (~1 second), the experimenter verbally informed the participant that she/he was free to reach the requested final position whenever she or he wanted. Note that reaction time was not emphasized in our experiment; iv) the participant was requested to maintain the final position for a brief period (about 1 second); v) the experimenter instructed to move back to the starting position (reversed movement) whenever desired; vi) lastly, the participant was asked to relax. A short rest period (~20 s) separated trials to prevent muscle fatigue. Additionally, participants were free to rest as long as they wanted between blocks. Participants were allowed to perform a few practice trials (~3 trials) before each block. Low-speed and high-speed blocks were similar except that the instructions were to perform the movements in roughly 5 seconds or as fast as possible, respectively.

Data Collection

Kinematics

We used the Plug-In Gait full body model (Vicon, Oxford Metrics, UK). 39 reflective markers were placed on the participant's head (temples and backs of the head), back (C7, T10 and on the scapula), torso (Clavicle and sternum), shoulders (acromion), arms (upper lateral 1/3 left, 2/3 right), elbows (lateral epicondyle), forearms (lower lateral 1/3 left, 2/3 right), wrists (both cubitus styloid processes), fingers (second metacarp), pelvis (anterior and posterior superior iliac spine), thighs (upper lateral 1/3 left, 2/3 right), knees (flexion-extension axis), calves (upper lateral 1/3 left, 2/3 right), ankles (lateral malleolus), and feet (second metatarsal head and heel).

We recorded the position of all markers with an optoelectronic motion capture system (Vicon system, Oxford Metrics, UK; 18 cameras) at a sampling frequency of 200 Hz. The spatial variable error of the system was less than 0.5mm.

EMG

We placed sixteen bipolar surface electrodes (Cosmed, pico EMG, sampling frequency: 1000Hz) on the anterior (AD) and posterior (PD) heads of the deltoid, vastus lateralis (VL) biceps femoris (BF), spinal erectors on L1 (ESL1) and on D7 (ESD7), the soleus (SOL), and on the anterior tibialis (TA) to record EMG activity.

Electrodes were placed bilaterally. The location of each electrode was determined following the recommendations from Barbero et al. (2012).

The Giganet unit (Vicon, Oxford Metrics, UK) synchronously recorded kinematic and EMG data.

Data Analysis

We processed kinematic and EMG data using custom programs written in Matlab (Mathworks, Natick, MA). Data processing was inspired by previous studies (Gaveau et al., 2021; Poirier et al., 2022) and was similar for all tasks.

Kinematics analysis

First, we filtered position using a third-order low-pass Butterworth filter (5 Hz cut-off, zerophase distortion, "butter" and "filtfilt" functions). We then computed the amplitude of the movement using steady phases (200ms for fast movements and 500ms for slow movements) before and after the movement (Figure 2). The amplitude was computed on the Z axis for fast movements and on X, Y and Z axes for slow movements. For slow movements, we used 3D position to minimize detection error on signals that were more variable than those obtained during fast movements. Last, we automatically defined movement onset and offset as the moments when the displacement rose above or felt below a threshold corresponding to 5% and 95% of the total movement amplitude, respectively.

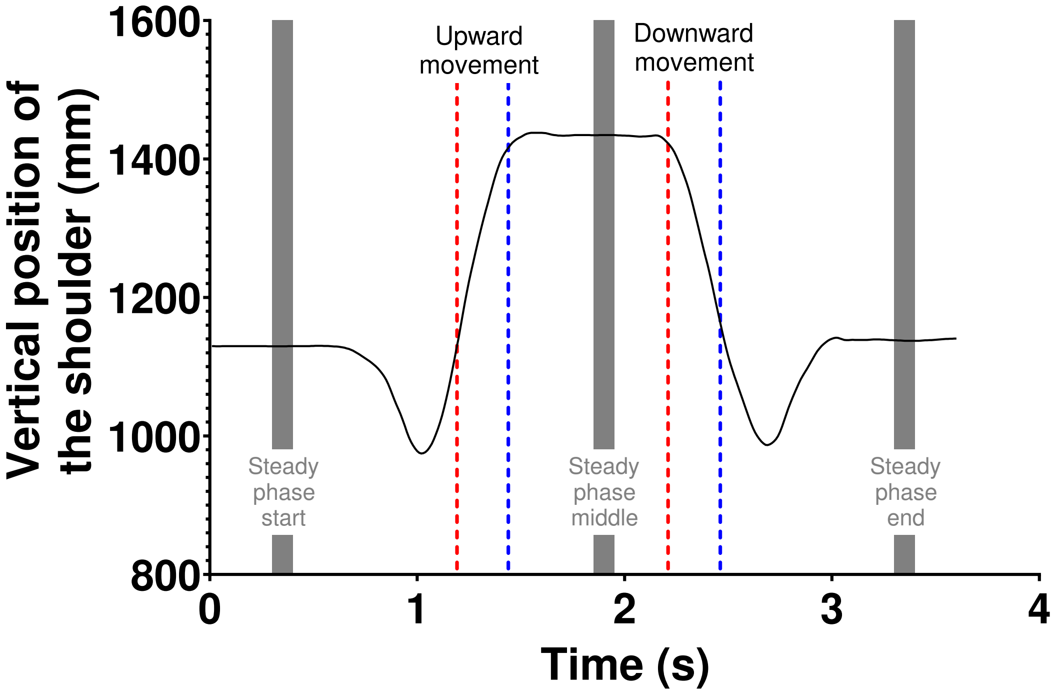

Figure 2. Detection of movement start and end. This panel displays the recording of two successively opposite fast Sit to stand / Back to sit movements. The black trace represents the position of a shoulder marker through time. Rest position is collected during steady phases, before and after each movement (ascending or descending). Based on the data obtained in steady phases, a recursive algorithm automatically defined movement onset and offset as the moments when the displacement rose above or felt below a threshold corresponding to 5% and 95% of the total movement amplitude, respectively.

EMG analysis

Pre-processing. EMG signals were first rectified and filtered using a bandpass third-order Butterworth filter (bandpass 30-300 Hz, zero-phase distortion, "butter" and "filtfilt" functions). Signals were integrated using a 100ms sliding window and cut off. For fast movements, EMG signals were cut off from 240ms before movement onset to 90ms after movement offset. For slow movements, EMG signals cut off from 75ms before movement onset to 75ms after movement offset. These timing values were obtained from preliminary analyses detecting EMG activity start and stop before and after all movements. The result is the average of all participants. Importantly, those values were kept constant for all participants and, thus, should not bias group comparisons.

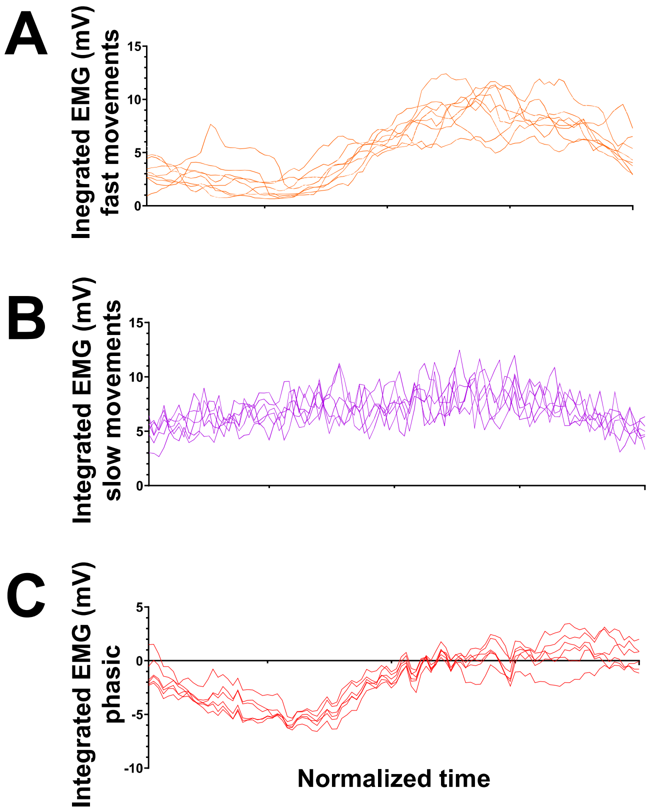

Figure 3. Illustration of the calculation method to obtain phasic EMG components. Electromyographic signals (mV) are presented as a function of time. Pattern duration and amplitude are normalized (see methods). **A**: Six integrated Vastus Lateralis EMG signals during fast BTS movements of a typical participant (BTS: Back-to-seat) ; **B**: Six integrated Vastus Lateralis EMG signals recorded during slow BTS movements of a typical participant . These signals represent the the tonic component. ; **C**: Integrated phasic EMG component computed using the six fast (panel A) and slow movements (panel B). The phasic is calculated by subtracting the mean of the slow acquisitions from the fast acquisitions (Phasic = Fast – Tonic).

Phasic/tonic separation. Last, before computing the EMG phasic component, signals were filtered using a low-pass third-order Butterworth filter to obtain the signal envelope (low-pass frequency: 20 Hz). We then computed the phasic component of each EMG signal using a well-known subtraction procedure that has mostly been used to study arm movements (Buneo et al., 1994; d'Avella et al., 2006, 2008; Flanders et al., 1994; Flanders & Herrmann, 1992; Gaveau et al., 2021). This processing allows quantifying how much the central nervous system takes advantage of the gravity torque when moving the body in the gravity environment (Gaveau et al., 2021; Poirier et al., 2022, 2023). Here, we customized this procedure to investigate whole body movements. First, the tonic signal was obtained as the mean of the six slow movements. Second, to improve signal to noise ratio, EMG traces of fast movements were ordered according to movement mean velocity and averaged across two trials (from the two slowest to the two fastest movements). This resulted in six EMG traces to be analyzed for each block. Each set of two traces was normalized in duration (corresponding to the mean duration of the two traces) before averaging. Third, the phasic component was obtained by subtracting the tonic EMG from the EMG trace of each fast movement. Finally, to set the data of all participants on a common scale, phasic activity was normalized by the maximal EMG value recorded in each task for each participant.

It was recently shown that the phasic EMG activity of antigravity muscles consistently exhibits negative epochs during vertical arm movements (Gaveau et al., 2021) when gravity is coherent with the arm acceleration sign (in the acceleration phase of downward movement and the deceleration phase of upward movements). This observation likely reflects an optimal predictive motor strategy where muscle activity is decreased when gravity assists arm movements, thereby discounting muscle effort. In the present study, we defined negative epochs as an interval where the phasic EMG signal was inferior to zero minus three times the standard deviation of the stable phase preceding the movement, and this for at least 40ms. We used this value as a threshold to automatically detect negativity onset and offset. On each negativity phase, we computed: i) a negativity index, defined as T x NA / TA, with NA the Negative Area integrated on the phasic signal between negativity onset and offset, TA the Tonic Area integrated on the tonic signal between the negativity onset and offset, and T the duration of the negative epoch normalized by movement duration; ii) negativity occurrence, defined as the number of trials where a negative epoch was automatically detected, divided by the total number of trials in the condition; iii) negativity duration, defined as the duration of the negative epoch normalized by movement duration; iv) negativity amplitude, defined as the minimal $Phasic\ value\ /\ Tonic\ Value \times 100$ during the negative period. A value of -100 indicates that the muscle is completely relaxed and a value of 0 indicates that the muscle exactly compensated the gravity torque.

As is often the case with EMG recordings, some of the EMG signals exhibited aberrant values. Those signals are usually due to poor contact between the electrodes and the skin. Supplementary Table 1 summarizes the issues encountered with all electrodes and participants.

Statistics

To compare results between groups, we used repeated measures ANCOVAs on JASP. The level of significance was set to 0.05 in all cases.

Machine Learning

We used a basic machine learning (ML) analysis to ensure that we focused the present study on muscles that contained important information to discriminate the muscle activation patterns recorded in younger adults from those recorded in older adults. For more details on similar use and operation of machine learning algorithms on EMG signals, please see Chambellant et al., 2023; Thomas et al., 2023. Here we present the results of a Linear Discriminant Analysis (LDA, Johnson & Wichern, 1988) but we verified that we obtained similar conclusions with two other algorithms, namely the Quadratic Discriminant Analysis (QDA, Cover, 1965) and the Support Vector Machine (SVM, Vapnik and Lerner, 1965). We used custom Matlab scripts [Mat, 2021] to perform all ML analyses. The ESL1G was not considered for these analyses because the electrode was defective for several younger participants (see Supplementary Table 1).

The input data was the phasic EMG signals of the 15 muscles taken individually or the whole set at once. These vectors were fed to the algorithms to it using binary classification setups, where the algorithm learned to distinguish between the EMGs of the two groups. To ensure robustness and generalization of the results, we employed a five-fold cross-validation method. This involved splitting the dataset into training and testing sets while ensuring equal representation of both directions in each set. By employing cross-validation, we could better estimate the algorithm's efficacy by testing it on multiple datasets, ultimately allowing us to compute an average accuracy across the testing sets. Finally, we could compare the efficiency of the algorithm for each muscle. Additionally, as performed in recent works (Chambellant et al., 2023; Thomas et al., 2023), we calculated the LDA distance as a further indicator of data separation.

Results

Movement duration varied between tasks and was slightly reduced in older compared to younger participants (see Supplementary Table 2 for detailed results). A repeated measures ANOVA (Age x Task) revealed that this age-difference was significant ($F_{(1,42)}$= 14.5, P=4.58E-05, η^2=0.256). For this reason, we used movement duration as a covariate in the following statistical analyses. Nevertheless, as revealed by figure 4, it is important to note that an important number of older adults moved with durations that were similar to those of younger adults.

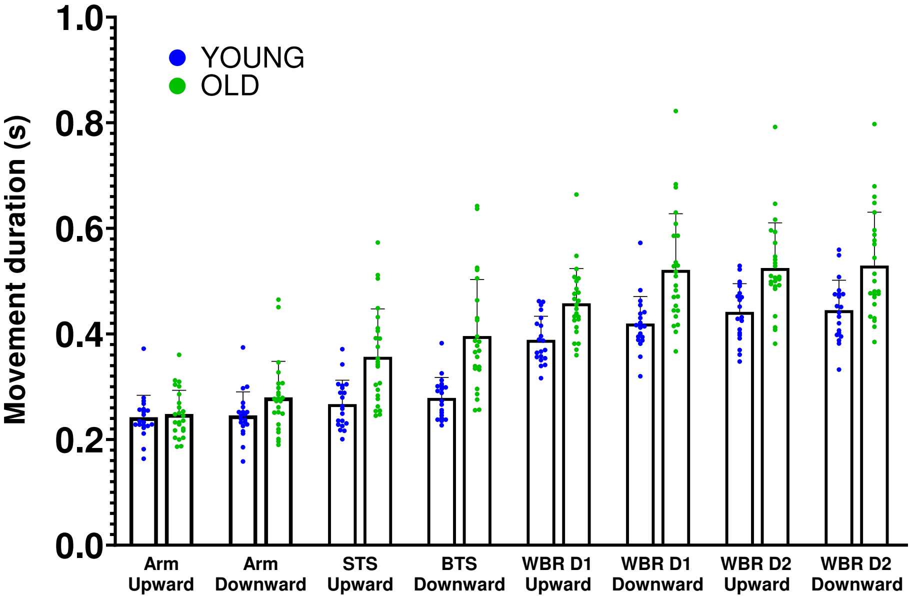

Figure 4. Mean ± SD movement durations (s) for all tasks and both groups (STS: Seat-to-stand, BTS: Back-to-seat, WBR: Whole-body-reaching, D1: Short distance=15% of the heigh of the subject and D2: Long distance=30% of the heigh of the subject). Each point correponds to the average duration of the trials of one participant. The blue points represent the young participants and the green points correpond to the older participants.

Figure 5 displays average phasic EMG profiles for each muscle, direction, and task. As recently reported, phasic EMG signals of arm movements show negative phases during the deceleration of upward and the acceleration of downward arm movements, i.e., where gravity torque helps generate the arm's motion (Gaveau et al., 2021; Poirier et al., 2022, 2023). Previous works demonstrated that this negativity is not erratic but systematic and indicate that muscles contract less than necessary to compensate for gravity effects. It is therefore especially prominent on antigravity muscles and reveals that the central nervous system (CNS) exploits gravity effects to produce efficient movements, i.e., motor patterns that save unnecessary muscle effort. Here, we extend this result to movements performed with the entire body. Indeed, for STS/BTS and WBR movements, Figure 2B-D unveils phasic EMG negativity during the deceleration of upward movements and the acceleration of downward movements, i.e. when gravity can help produce the motion. This first qualitative result demonstrates that movements that are performed with the entire body, similarly to more focal arm movements, exploit gravity effects to save unnecessary muscle effort (Gaveau et al., 2021). More importantly, the present results qualitatively reveal that older adults also use such an efficient strategy, both when moving their arm and their entire body.

The present study aimed to test for possible age-differences in the extent to which older and younger adults use gravity effects to minimize muscle effort. Using the theory-driven approach that we recently developed for arm movements, we were specifically interested in analyzing activation patterns of antigravity muscles, those that pull upwards (Gaveau et al., 2021; Poirier et al., 2022, 2023). To ensure that restricting the analysis to antigravity muscles would nonetheless provide significant information on how age alters muscle patterns, we used a machine learning approach. We trained models to classify the data from younger vs older adults.

Our rationale was the following: If the algorithm can successfully separate the data of younger and older adults, using antigravity muscle patterns, this would demonstrate that important information is contained in those muscles regarding age-related modifications in motor strategies. This analysis indeed revealed that antigravity muscles contained important information, allowing separating age-groups with some of the best success-rates (see Supplementary Figure 1 for results regarding LDA accuracy and LDA distance). Thus, building on the complementary results of the theory-driven approach (Gaveau et al., 2021; Poirier et al., 2022, 2023) and the present data-driven approach (Supplementary Figure 1), in the following we focus the analysis on antigravity muscles. Those muscles are the Anterior Deltoid for the arm task and the Vastus lateralis and Erector Spinae at L1 level for the tasks involving movements of the entire body (STS/BTS and WBR).

Main analysis

Following our primary hypothesis, we first analyzed a single metric quantifying phasic EMG negativity on an average muscle pattern, namely the negative area of phasic EMG patterns (see methods and Poirier et al., 2022, 2023). The bigger the negativity index, the more efficient the muscle contractions, in the sense that gravity effects were maximally exploited to minimize muscle effort (Gaveau et al., 2021). Figure 6 displays the results of this ANCOVA analysis (Age x Task), revealing a significant interaction between age and task factors ($F_{(1,42)}$= 5.48, P=2.44E-02, η^2=0.120). This result demonstrates that age differently alters motor strategies for arm movements vs entire body movements. Older adults used gravity effects to a similar extent as younger ones when performing arm movements (older adults, mean ± SD: -10.7 ± 5.6, 95% CI: [-8.4;-13.0]; younger adults, -11.4 ± 3.6, [-9.8;-13.0]), but to a lesser extent when performing whole body movements (older adults, -9.7 ± 3.2, [-8.0;-11.5]; younger adults, -15.6 ± 3.3, [-14.1;-17.0]). As recently reported by Poirier et al. (2023), similar arm results in younger and older adults suggest that the ability to plan movements that optimally use gravity effects to minimize muscle effort remains functional in older adults. The results obtained in whole-body movement tasks (STS/BTS and WBR) could thus suggest that the difference observed between older and younger adults does not reflect a deterioration of the ability to plan movements that are optimally adapted to the gravity environment. Instead, it would suggest a change in movement strategy that compensates for other deteriorated control processes.

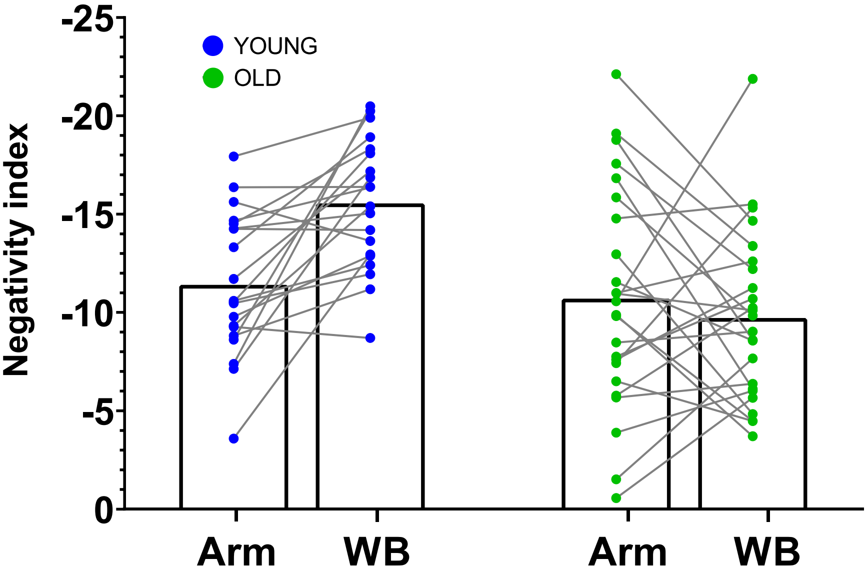

Figure 6. Negativity index computed for arm and whole-body movements in both groups (WB: Whole Body combines seat-to-stand/back-to-seat, whole body reaching from D1 and whole body reaching from D2). The negativity index, defined as T x NA / TA, with NA the Negative Area integrated on the phasic signal between negativity onset and offset, TA the Tonic Area integrated on the tonic signal between the negativity onset and offset, and T the duration of the negative epoch normalized by movement duration. The blue points correspond to the younger participants and the green points correpond to the older participants. Each point corresponds to the mean value of one participant (mean accross trials and antigravity muscles).

Previous studies have proposed that the change in kinematic strategies observed between older and younger adults during whole-body movements could be explained as a strategy maximizing equilibrium maintenance rather than muscular effort (Casteran et al., 2018; Paizis et al., 2008). Following this hypothesis, one would predict increasing differences between younger and older adults when the equilibrium constraint increases. In the present experiment, increased equilibrium constraint was produced by increasing the target distance during whole body reaching movements (WBR D1 vs WBR D2; alike Casteran et al., 2018). To specifically test this hypothesis, we conducted an ANCOVA with a between participant Age factor (Younger vs Older adults) and a within participant Distance Factor (WBR1 vs WBR2) on the index of negativity. This analysis did not reveal any significant interaction effect between Age and Distance ($F_{(1,40)}$= 1.6E-3, P=9.69E-1, η^2=3.89E-5), thereby providing inconclusive results regarding the hypothesis of a control that would favor equilibrium maintenance over effort minimization with increasing age.

Exploratory analyses

To provide a fine-grained analysis of the age effect on phasic EMG negativity, we probed negativity duration, negativity amplitude, and negativity occurrence across tasks and age-groups. Here also, the bigger the values, the bigger the use of gravity effects to produce body motion. A repeated measures ANCOVA (Age x Task x Direction) revealed a significant age effect where negativity duration was larger in younger compared to older participants ($F_{(1,36)}$= 21.49, P=4.54E-05, η^2=0.374). No interaction between Age and the other factors reached significance. The age effect did not reach significance for negativity occurrence ($F_{(1,36)}$= 3.62, P=0.065, η^2=0.091) nor for negativity amplitude ($F_{(1,36)}$= 1.16, P=0.28, η^2=0.031) but the Age x Task x Direction interaction did reach significance for both negativity occurrence ($F_{(1,36)}$= 5.50, P=2.25E-03, η^2=0.153) and negativity amplitude ($F_{(1,36)}$= 5.49, P=6.1E-03, η^2=0.132). Post-hoc comparisons nonetheless did not reveal any significant group difference on negativity occurrence (P>0.052 in all cases) or negativity amplitude (P>0.59 in all cases). Overall, all variables showed qualitatively smaller negativity on phasic EMGs, thus reduced use of gravity effects, in older compared to younger adult.

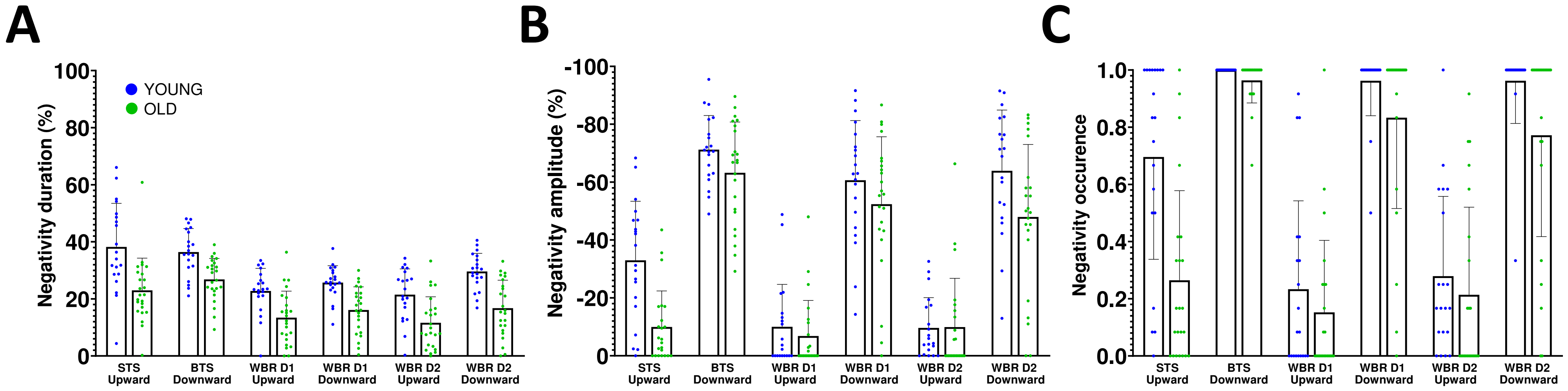

Figure 7. Mean ± SD negativity quantification for all tasks and groups (STS: Seat-to-stand, BTS: Back-to-seat, WBR: Whole-body-reaching, D1: Short distance=15% of the heigh of the subject and D2: Long distance=30% of the heigh of the subject). Quantification was carried out using three criteria: negativity duration, negativity amplitude an negativity occurrence. for the vastus lateralis (panel A) and the erector spinae L1 (panel B). The blue points correspond to the younger participants and the green points correpond to the older participants. Each point corresponds to the mean value accross trials and antigravity muscles.

Discussion

In younger and older adults, we investigated the muscle patterns responsible for arm and whole-body movements. The results revealed an age-related alteration of muscle commands that differ between tasks. Comparing older adults to younger ones, we found that a muscle marker of effort minimization was reduced during whole-body movements but not during arm movements. Previous works have demonstrated that this marker allows quantifying the output of a sensorimotor control process that adapts human movements to gravity (Gaveau et al., 2021; Poirier et al., 2022, 2023). More precisely, this marker allows for quantifying how much one harvests gravity effects to minimize muscle effort. Here, arm movement results reveal that this effort-discounting process remains functional in older adults. During whole-body movements, however, the present results reveal that effort-minimization was downregulated in older adults compared to younger adults. Overall, the present results suggest a compensation process that modulates planning strategies to maximize equilibrium in older adults.

The metabolic rate is known to influence resource use, body size, rate of senescence, and survival probability (Brown et al., 2004; DeLong et al., 2010; Strotz et al., 2018; Van Voorhies & Ward, 1999). The nervous system has therefore developed the ability to design movement strategies that minimize our every-day efforts (Cheval et al., 2018; Gaveau et al., 2016; Huang et al., 2012; Morel et al., 2017; Selinger et al., 2015; Shadmehr et al., 2016). The present findings confirm the results of previous arm movement studies that proposed a theory according to which motor control takes advantage of gravity effects to minimize muscle effort (Berret et al., 2008; Crevecoeur et al., 2009; Gaveau et al., 2014, 2016, 2021; Gaveau & Papaxanthis, 2011). Here, we focused on the muscle marker of gravity-related effort minimization, i.e. the negativity of phasic EMG. Previous modeling and experimental work demonstrated that this phasic EMG negativity results from an optimal control process that plans efficient arm movements in the gravity field (Gaveau et al., 2021). As reported by Poirier et al. (2023), we found similar phasic EMG negativity during arm movements in older and younger adults. Thus, arm movements equally optimized gravity effects in younger and older adults. These results align with those of studies that probed progressive motor adaptation to a new environment in older adults. Using locally induced force fields in a robotic environment, these studies revealed that older adults decreased their metabolic costs similarly to younger adults while adapting to new environmental dynamics (Healy et al., 2023; Huang & Ahmed, 2014). Overall, results from arm movement studies advocate for the maintenance of the ability to optimally integrate environmental dynamics and plan arm movements that minimize muscle effort in older adults.

Current results also extend the current knowledge on the planning of energetically efficient movements to more global movements, both in younger and older adults. They unravel that deactivating muscles, below the tonic level that would be necessary to compensate for external dynamics are not only relevant to control focal arm movement but also for whole-body movements. Using a combination of modeling and experimental work (Berret et al., 2008; Crevecoeur et al., 2009; Gaveau et al., 2014, 2016, 2021; Gaveau & Papaxanthis, 2011), previous studies demonstrated that healthy participants move their arms following trajectories and using muscular patterns that minimize muscle effort in the gravity environment. To isolate gravity effects, most studies focused on one-degree-of-freedom arm movements. Although those studies allowed us to clearly demonstrate how motor planning integrates gravity effects into motor planning, one-degree-of-freedom movements are hardly representative of the rich and complex human movement repertoire. The present study, using more ecological movements, basically extends the optimal integration of gravity effects theory to every-day movements.

Contrary to focal arm movements, we observed a strong age difference during global movements that engaged the entire body, here sit to stand / back to sit and whole-body reaching movements. Specifically, the negativity of phasic EMG was significantly reduced in older compared to younger adults. This suggests that whole-body movements are less energetically efficient in older adults than in younger ones. Previous kinematic studies suggested that older adults favor movement strategies that maximize balance maintenance rather than effort minimization (Casteran et al., 2018; Paizis et al., 2008). However, age differences observed during whole-body movements may also be interpreted as an inability to minimize muscle effort when coordinating complex movements (Vernazza-Martin et al., 2008). Here, contrasting results from arm and whole-body movements in the same participants, we provide clear support for a compensation process that adapts movement strategy in older adults rather than an inability to optimally coordinate whole-body movements. This adds to the general result that global movements are more energy-demanding for older adults compared to younger adults (Didier et al., 1993; Hortobagyi et al., 2003, 2011; John et al., 2009). Indeed, current results suggest that the increase in effort with age may not only be due to deterioration, such as lack of muscle strength or increased muscle coactivation, but also to compensation for this deterioration, which consists in a modification of the movement control strategy.

During the whole-body reaching task, reusing the protocol of previous studies (Casteran et al., 2018; Paizis et al., 2008), we varied the antero-posterior distance of the target to be reached. Casteran et al. (2018) found larger differences between younger and older participants when the target was further. Consequently, we hypothesized that the further away the target, the greater the age differences in the negativity epochs of phasic EMGs. The present results do not validate this hypothesis. We found no distance effect. Two explanations could be provided to account for this result. First, it is possible that our muscle activity criterion is not strongly correlated with the kinematic criterion used by Casteran et al. (2018). Secondly, it is possible that our sample of younger and older adults did not behave in the same way as in the study of Casteran et al. (2018), due to slight task specificities that we cannot clearly grasp here. Indeed, we did not observe the expected distance effect in younger people either, as it had been observed in Casteran et al. (2018). Future work should compare EMG to kinematic evaluations of movement strategies.

In conclusion, probing a specific motor control process, the present study provides a set of behavioral results that support the interpretation of a compensatory process that counterbalances other deteriorated processes in older adults. Probing age effects on specific sensorimotor control processes may help disentangle compensation from deterioration processes that occur through healthy aging (Poirier et al., 2021). We believe that understanding compensation at a behavioral level is an important step toward pinpointing its neural underpinning (Krakauer et al., 2017) and, later, preventing unhealthy aging (Baltes & Baltes, 1990; Martin et al., 2015; Zhang & Radhakrishnan, 2018).

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Data, scripts, code, and supplementary information availability

Data are available online: 10.5281/zenodo.10619701, webpage hosting the data: https://doi.org/10.5281/zenodo.10619701 (*citation of the data eg* Mathieu et al, 2023);

Scripts and code are available online: 10.5281/zenodo.10634004, webpage hosting the scripts: https://doi.org/10.5281/zenodo.10634004 (*citation of the scripts eg* Mathieu et al, 2023);

Supplementary information is available online: 10.5281/zenodo.10671496, webpage hosting the file: https://doi.org/10.5281/zenodo.10671496 (*citation of the supplementary file eg* Mathieu et al, 2023);

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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