Comparing arm to whole-body motor control disambiguates age-related deterioration from compensation

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, Dijon. Institut National de la Santé et de la Recherche Médicale : UMR 1093, Université de Bourgogne, France.

[2] Pôle Recherche et Santé Publique, CHU Dijon Bourgogne, F-21000 Dijon, France

[3] 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. These mechanisms are thought to enable older adults to remain in good physical health, but despite important research efforts, they remain essentially chimeras. A major problem with their identification is the ambiguous interpretation of age-related alterations. Whether a change reflects deterioration or compensation is difficult to determine. Here we compared the electromyographic and kinematic patterns of different motor tasks in younger (n = 20; mean age = 23.6 years) and older adults (n = 24; mean age = 72 years). Building on the knowledge that humans take advantage of gravity effects to minimize their muscle effort, we probed the ability of younger and older adults to plan energetically efficient movement during arm-only and whole-body movements. In line with previous studies and compared to younger adults, muscle activation patterns revealed that older adults used a less efficient movement strategy during whole-body movement tasks. We found that this age-related alteration was task-specific. It did not affect arm movements, thereby supporting the hypothesis that healthy older adults maintain the ability to plan energetically efficient movements. More importantly, we found that the reduced whole-body movement efficiency was correlated with kinematic measures of balance control (i.e., the center-of-mass movement amplitude and speed). The more efficient the movement strategy, the more challenging the balance. Overall, these results suggest that reduced movement efficiency in healthy older adults does not reflect a deterioration but rather a compensation process that adapts movement strategy to the task specificities. When balance is at stake, healthy older adults prefer stability to energy efficiency.

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 deteriorations (Baltes & Baltes, 1990; Martin et al., 2015; Zhang & Radhakrishnan, 2018). Even the most elementary concept of health includes compensatory processes at its core. The World Health Organization defined health as "a state of complete physical, mental, and social well-being and not merely the absence of disease or infirmity" (1948). Scientists and clinicians later redefined it even more generally as "the ability to adapt and to self-manage" (Huber et al., 2011; The Lancet, 2009). So, despite the normal deterioration associated with age, compensatory processes enable older adults to adapt and remain in good health (i.e., aging successfully) and thus continue to live 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. 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 neural alterations have used overly crude behavioral paradigms (Poirier et al., 2021). Typically, these studies have used broad measures such as muscle strength, reaction time, or movement time. Although these measures and paradigms tested important functional motor performances, they measured the combination of several behavioral strategies and subtending neural mechanisms. Since these strategies and mechanisms likely showed different levels of age-related deterioration, previous studies have likely mixed deterioration and compensation processes (Poirier et al., 2021). Identifying neural compensation requires linking the brain to behavior, and to establish a precise link, we need fine behavioral measures and experimental paradigms that allow approaching the constituent processes of a behavior (Krakauer et al., 2017; Pereira et al., 2020; Urai et al., 2022). It is therefore essential to first develop detailed knowledge of age-related compensation at the behavioral level.

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 save muscle effort, thus to save energy (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 and maybe even upregulated in older adults (Healy et al., 2023; Huang & Ahmed, 2014; Poirier et al., 2020; Summerside et al., 2024). On the other hand, studies probing the control of movements performed with the entire body have reported a different conclusion. Kinematic results suggest that older adults plan whole-body movements that are less energy-efficient than younger adults (Casteran et al., 2018; Paizis et al., 2008). This is unexpected

93 because such movements require more energy expense in older adults than in younger adults (Hortobagyi et
94 al., 2003, 2011; Julius et al., 2012; VanSwearingen & Studenski, 2014). Since the ability to plan efficient
95 movements is maintained in older adults, as testified by arm movements studies, one may speculate that this
96 decreased efficiency reflects an age-related compensation that changes movement strategy (i.e., an age-
97 related motor adaptation process). However, because this literature used very different experimental
98 paradigms and measurements, this conclusion is highly speculative. More importantly, the results of numerous
99 other studies could also interpret the decreased efficiency observed in whole-body movements as a
100 deterioration of the ability to produce efficient motor patterns (Goodpaster et al., 2006; Henry & Baudry, 2019;
101 Quinlan et al., 2018; Vernazza-Martin et al., 2008). Here we test the hypothesis that age-related alterations in
102 movement efficiency correspond to an adaptation process, i.e., a change in movement strategy that
103 compensates for other deteriorated sensorimotor components. To overcome the aforementioned limitations,
104 using a specific muscle activation pattern analysis that has proven relevant to focusing on this precise process
105 of energetic efficiency (Chambellant et al., 2023; Gaveau et al., 2021; Poirier et al., 2022, 2024; Thomas et al.,
106 2023), we compare older to younger adults on tasks involving either arm or whole-body movements. We then
107 test whether energy efficiency is correlated to balance control.

Methods

Participants

110 Because we had no prior data to calculate the ideal sample size, we included as many participants as
111 possible over a fixed recruitment period. Twenty younger adults (23.6 ± 2.1 y.o.) and twenty-four older adults
112 (72 ± 5.3 y.o.) were included in the study after giving their oral informed consent. Participants had normal or
113 corrected-to-normal vision and did not present any neurological or muscular disorders. The laterality index of
114 each participant was superior to 60 (Edinburgh Handedness Inventory, Oldfield 1971), indicating that all
115 participants were right-handed. The study was carried out following legal requirements and international
116 norms (Declaration of Helsinki, 1964) and approved by the French National Ethics Committee (2019-A01558-
117 49). Each participant was included in the study by a medical doctor.

Experimental Protocol

119 All participants performed four tasks in a randomized order. These tasks either required moving the arm
120 only (Figure 1A) or the whole-body (Figure 1B-D). Whole-body movements consisted of seat-to-stand/back-to-
121 sit (STS/BTS, Figure 1B), whole-body reaching toward near targets (WBR D1, Figure 1C), and whole-body
122 reaching toward far targets (WBR D2, Figure 1D). The arm task was selected because it is the reference task
123 that has been studied to demonstrate how muscle patterns take advantage of gravity effects to save energy.
124 The whole-body tasks were selected because they include an equilibrium constraint, are movements of the

daily life, and they have been investigated in previous studies (Casteran et al., 2018; Jeon et al., 2021; Manckoundia et al., 2006; Millington et al., 1992; Mourey et al., 1998; Paizis et al., 2008).
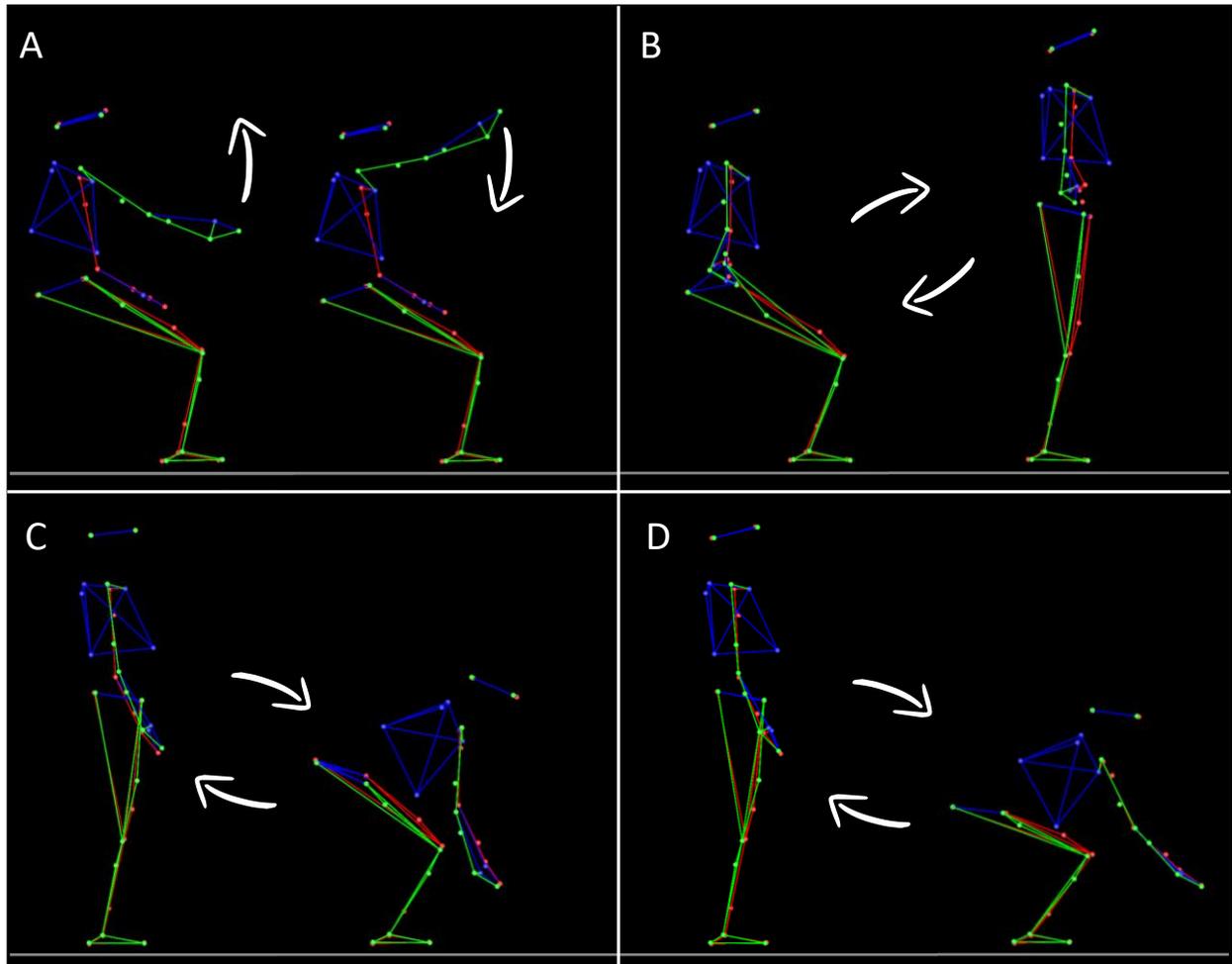

Figure 1. Illustration of the four tasks. Each panel illustrates the extreme body positions between which participants performed their movements. Each position was alternatively the starting or ending target of a movement, depending on movement direction. **A**: Single degree of freedom arm movements flexion/extension around the shoulder joint (flexion/extension). 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 resting vertical standing position (upward movement). **D**: same as C but with targets that were placed farther away on the antero-posterior axis.

ARM task

Over a variety of arm movement tasks, including single or muti-degree of freedom pointing movements, drawing movement, reach to grasp movements, or arm movements that transport a hand-grasped object, the results consensually support an optimization principle that shapes arm motor patterns to take advantage of gravity effects in saving energy (Crevecoeur et al., 2009; Gaveau et al., 2011; Gaveau & Papaxanthis, 2011; Le Seac'h & McIntyre, 2007; Paizis et al., 2008; Papaxanthis et al., 1998, 2005; Yamamoto & Kushiro, 2014a). Thus, to make the protocol doable in a single session with each participant, we only included one arm task in the present experiment. 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, 2014a). Using their right arm, participants carried out single-degree-of-freedom vertical arm flexion/extension 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 shoulder (in a

141 parasagittal plane) at a distance corresponding to the length of their fully extended arm plus two centimeters.
142 The prescribed movement amplitude between the two targets was 45°, corresponding to 112.5° (upward
143 target, 22.5° above horizontal) and 67.5° (downward target, 22.5° below horizontal) shoulder
144 flexion/extension.

145 *STS/BTS task*
146 This task was similar to those of previous studies (Jeon et al., 2021; Manckoundia et al., 2006; Millington
147 et al., 1992; Mourey et al., 1998). Participants were seated on an armless stool whose height was adjusted to
148 correspond to 30% of the participant's height. The hands were positioned on the hips, and the back was
149 instructed to be maintained about vertical. Participants were asked to stand up from the stool, make a short
150 pause (about 2s), and then sit back on the stool. Similarly to arm movements, participants executed two blocks
151 of movements in a randomized order. One block consisted of six slow movements, and the other consisted of
152 12 fast movements.

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

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

175 **Data Collection**

176 *Kinematics*
177 We used the Plug-In Gait full body model (Vicon, Oxford Metrics, UK) following their recommendations to
178 place the 39 reflective markers on the participant's head (temples and backs of the head to form a rigid plan
179 with the head), back (C7, T10 and on the right scapula), torso (jugular notch where the clavicles meet the
180 sternum and on the xiphoid of the sternum), shoulders (acromion), arms (upper lateral 1/3 for the left arm,
181 and 2/3 for the right arm), elbows (lateral epicondyle), forearms (lower lateral 1/3 for the left forearm, and
182 2/3 for the right forearm), wrists (both cubitus styloid processes), hands (middle of the proximal knuckle of the
183 index), pelvis (anterior and posterior superior iliac spine), thighs (upper lateral 1/3 for the left leg, and 2/3 for
184 the right leg), knees (lateral side of the flexion-extension axis), calves (upper lateral 1/3 for the left calf, and
185 2/3 for the right calf), ankles (lateral malleolus), and feet (second metatarsal head and heel). The markers on
186 the scapula, on the arms, on the forearms, on the thighs, and on the calves have been deliberately placed
187 asymmetrically so that the model can best dissociate the right and left sides; these markers are not used for
188 the analyses presented in this manuscript.

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

192 *EMG*
193 We placed sixteen bipolar surface electrodes (Cosmed, pico EMG, sampling frequency: 1000Hz) on the
194 anterior (AD) and posterior (PD) heads of the deltoid, vastus lateralis (VL), biceps femoris (BF), spinal erectors
195 on L1 (ESL1) and on T7 (EST7), the soleus (SOL), and on the tibialis anterior (TA) to record EMG activity.
196 Electrodes were placed bilaterally. The location of each electrode was determined following the
197 recommendations from Barbero et al. (2012).
198 The Giganet unit (Vicon, Oxford Metrics, UK) synchronously recorded kinematic and EMG data.

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

203 *Kinematics analysis*
204 First, we filtered position using a third-order low-pass Butterworth filter (5 Hz cut-off, zerophase distortion,
205 "butter" and "filtfilt" functions). We then computed the amplitude of the movement using steady phases
206 (200ms for fast movements and 500ms for slow movements) before and after the movement, using the marker
207 of the right shoulder (for whole-body movements, see Figure 2) or the right finger (for arm movements). The
208 amplitude was computed on the Z axis for fast movements and on X, Y, and Z axes for slow movements. For
209 slow movements, we used 3D position to minimize detection error on signals that were more variable than
210 those obtained during fast movements. Last, we automatically defined movement onset and offset as the
211 moments when the displacement rose above or felt below a threshold corresponding to 5% and 95% of the
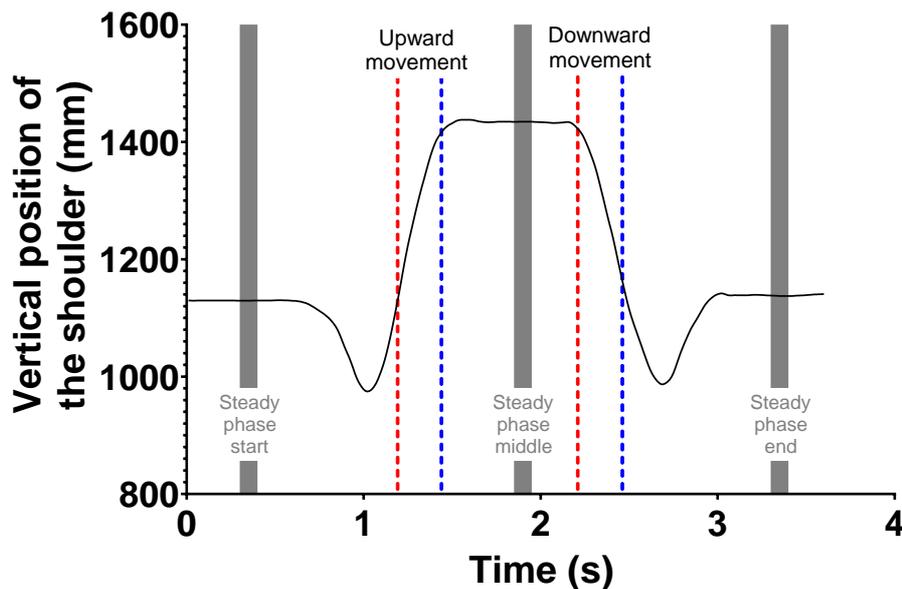212 total movement amplitude, respectively.

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.

213 On behalf of using the kinematics to define the start and end of movement, we analyzed the displacement
214 of the Center of Mass (CoM) in three dimensions to understand how equilibrium was maintained during the
215 whole-body tasks. This was done to reproduce the work of Casteran et al., (2018) and Paizis et al., (2008), but

216 also, and more importantly, to perform a simple analysis testing whether our main criterion, quantified via
217 electromyographic activity, is linked to a simple, interpretable kinematic change. Our analysis utilized a seven-
218 segment mathematical model incorporating rigid segments such as the Trunk, Thigh, Shank, Foot, Upper arm,
219 Forearm, and Hand. We used anthropometric data from Winter (2009), as performed by previous studies
220 (Berret et al., 2009; Stapley et al., 1999). Our choice of movement segmentation for this specific kinematic
221 analysis has been guided by the works of Casteran et al., (2018) and Paizis et al., (2008). We determined
222 movement onset and offset on velocity profiles, using a threshold of 5% of the peak velocity. We further
223 explored the kinematics of the whole-body tasks using two simple parameters: i) the total displacement of the
224 center of mass, calculated as the distance between the start and end positions and normalized by the subject's
225 height; and ii) the peak velocity of the center of mass. We focused on downard movements, as these are the
226 ones that have been studied and present the greatest challenge to balance. The specific process to compute
227 criteria used by previous studies (Casteran et al., 2018 and Paizis et al., 2008) is detailed and available in
228 Supplementary Figure 1.

229 *EMG analysis*
230   Below, following methodologies developed by several previous studies, we detail how we obtain EMG
231 marker.
232   **Pre-processing**. EMG signals were first rectified and filtered using a bandpass third-order Butterworth filter
233 (bandpass 30-300 Hz, zero-phase distortion, "butter" and "filtfilt" functions) followed by a low-pass third-order
234 Butterworth filter (low-pass frequency: 5 Hz) to highlight important features of muscular activities. Signals
235 were integrated using a 100ms sliding window using trapezoidal numerical integration from Matlab
236 (Mathworks, Natick, MA) and cut off. For fast movements, EMG signals were cut off from 240ms before
237 movement onset to 90ms after movement offset. For slow movements, EMG signals cut off from 75ms before
238 movement onset to 75ms after movement offset. These timing values were obtained from preliminary
239 analyses detecting EMG activity start and stop before and after all movements. The result is the average of all
240 participants. Importantly, those values were kept constant for all participants and, thus, should not bias group
241 comparisons.
242   **Phasic/tonic separation**. We then computed the phasic component of each EMG signal using a well-known
243 subtraction procedure that has mostly been used to study arm movements (Buneo et al., 1994; d'Avella et al.,
244 2006, 2008; Flanders et al., 1994; Flanders & Herrmann, 1992; Gaveau et al., 2021). This processing allows
245 quantifying how much the central nervous system takes advantage of the gravity torque when moving the
246 body in the gravity environment (Gaveau et al., 2021; Poirier et al., 2022, 2024). Here, we customized this
247 procedure to investigate whole body movements since movements are not one-degree-of-freedom
248 movements. First, the tonic signal was obtained from the six slow movements. For that purpose, the cut
249 movements (as described earlier with delays) were normalized in duration to be finally averaged together in
250 one tonic signal. Second, to improve signal to noise ratio, EMG traces of fast movements were ordered
251 according to movement mean velocity and averaged across two trials (from the two slowest to the two fastest
252 movements). This resulted in six EMG traces to be analyzed for each block. Each set of two traces was
253 normalized in duration (corresponding to the mean duration of the two traces) before averaging. Third, the
254 phasic component was obtained by subtracting the tonic EMG from the EMG trace of each pair of fast

movements. 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.
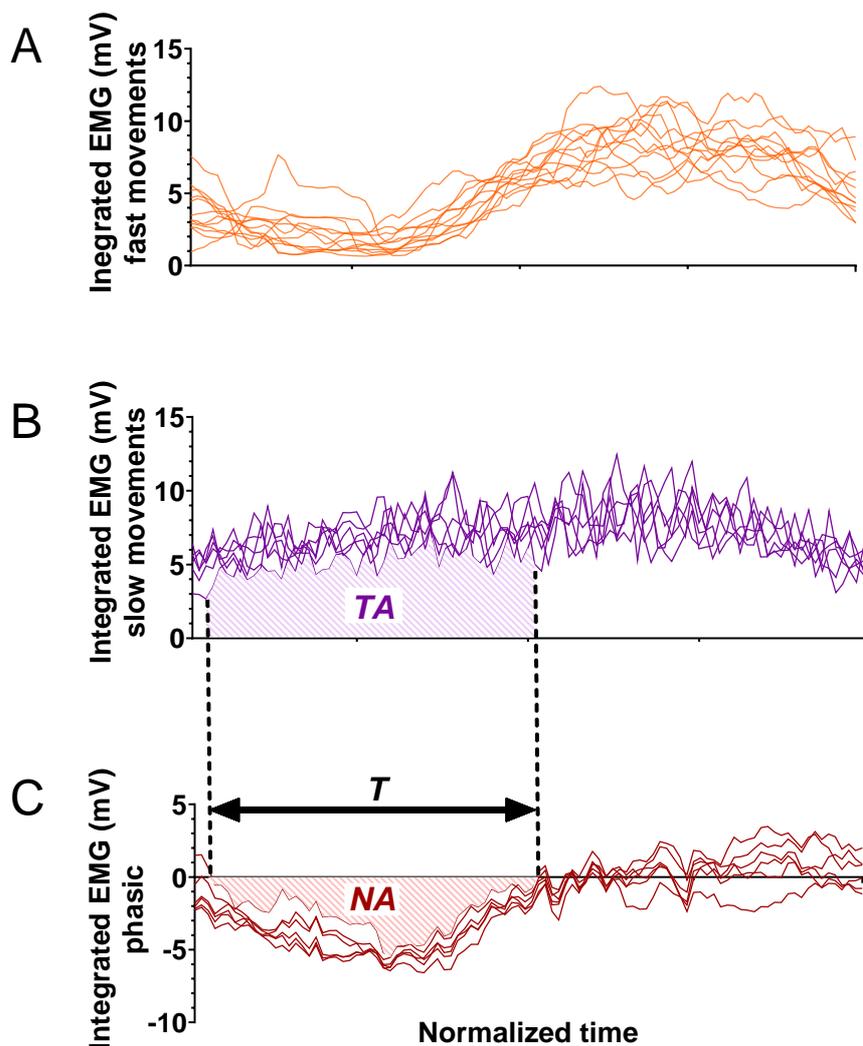

Figure 3: Illustration of the calculation method to obtain phasic EMG components. Electromyographic signals (mV) are presented as a function of time. Pattern duration and amplitude are normalized (see methods). **A**: Six integrated Vastus Lateralis EMG signals during fast BTS movements of a typical 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 tonic component. TA: Tonic Area integrated on the tonic signal between the negativity onset and offset; **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). T: the duration of the negative epoch normalized by movement duration and NA: the Negative Area integrated on the phasic signal between negativity onset and offset.

Muscles selection. It was recently shown that the phasic EMG activity of antigravity muscles, those that pull against the gravity vector, consistently exhibits negative epochs (Chambellant et al., 2024; Gaveau et al., 2021; Poirier et al., 2022; Thomas et al., 2023) when the arm acceleration sign is coherent with the gravity acceleration sign (i.e., in the acceleration phase of downward movement and in 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 saving energy (Gaveau et al., 2021). In the present study, the antigravity muscles are: i) the Anterior Deltoïd (DA), flexing the shoulder joint; ii) the Vastus Lateralis (VL), extending the knee joint; iii) the Erector Spinae L1 (ESL1), extending the rachis; iv) the Erector Spinae T7 (EST7), extending the rachis; v) the Soleus (SOL), flexing the ankle in the plantar direction. Because the Erector Spinae T7 and the Soleus muscles did not play a strong focal role but a rather postural one in the present tasks, we focused our analyses on the remaining three muscles (DA, VL, and ESL1). Probing the

activation of a postural muscle, per definition, is not appropriate to test whether the nervous system takes advantage of gravity effects to move our body limbs. Compared to other joints (e.g., hips and knees), the ankle and upper rachis were only minimally mobilized in the tasks we investigated here (see stick diagrams in Figure 1). Including these muscles in our analyses would thus add noise to our dependent variables and likely impede our ability to test our hypothesis. Therefore, we focused on DA during arm movements and on VL and ESL1 during movement of the entire body.

Quantifying negativity. 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. This duration has been chosen after preliminary tests to avoid detecting false-positives. We kept it constant for all analyses. 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 (see Figure 3). This value is always negative or null. The lower the value, the greater the efficiency; 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.

Machine Learning

We used custom Matlab (Mathworks, Natick, MA) scripts to perform all machine learning 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 using binary classification setups, where the algorithm learned to distinguish between the EMGs of the two groups. To ensure robustness of the results, we employed a five-fold cross-validation method. This involved splitting the whole dataset into five sets while ensuring equal representation of both directions in each set. The algorithm was trained on four of those sets before being evaluated on the fifth set (containing data unknown to the trained algorithm). This operation was repeated five times, so each set was tested once. Cross-validation allowed computing the average accuracy and its variance across the testing sets, thereby providing a reliable estimate of the accuracy obtained by the algorithm. Finally, we could compare the accuracy of the algorithm for each muscle.

Univariate Statistics

After an initial kinematic analysis (detailed in the results section), we observed a difference in movement duration between younger and older adults (conducting a repeated measure analyses of variance with a between factor *Age* with two levels: Young/Older and a within factor *Task-type* with two levels: Arm/Whole-body movements). Because movement duration is known to influence phasic EMG negativity (Poirier et al., 2023), we added movement duration as a covariate. We performed repeated measure analyses of covariance (ANCOVA) using JASP software. Two ANCOVA analyses were carried out. We first used a mixed ANCOVA with a between factor *Age* (two levels: Young/Older) and a within factor *Task-type* (two levels: Arm/Whole-body movements) to test whether age effects on movement control depended on the type of task being performed. Second, to detail the age differences observed during movements of the entire body, we used a mixed ANCOVA with a between factor *Age* (two levels: Young/Older) and a within factor *Whole-Body-Tasks* (three levels: STS_BTS/WBR D1/WBR D2). In all cases, the significance level was set to 0.05.

To test for a possible beneficial effect (i.e., compensation) of the EMG alterations that we observed with aging, we performed a kinematic analysis of the center of mass. We then used independent Student-tests and Pearson correlation coefficients to study potential differences between groups and associations between variables.

321   **Results**

322   Movement duration of fast movements varied between tasks and was slightly reduced in younger
323   compared to older participants (see Figure 4 and Supplementary Table 2 for detailed results). Overall, older
324   adults were 3.5% slower than younger adults. A repeated measures ANOVA revealed that this age-difference
325   was significant ($F_{(1,42)}$= 14.5, P=4.58E-05, η^2=0.256). For this reason, we used movement duration as a
326   covariate in the following statistical analyses. Nevertheless, as revealed by Figure 4, it is important to note that
327   an important number of older adults moved with durations that were similar to those of younger adults.
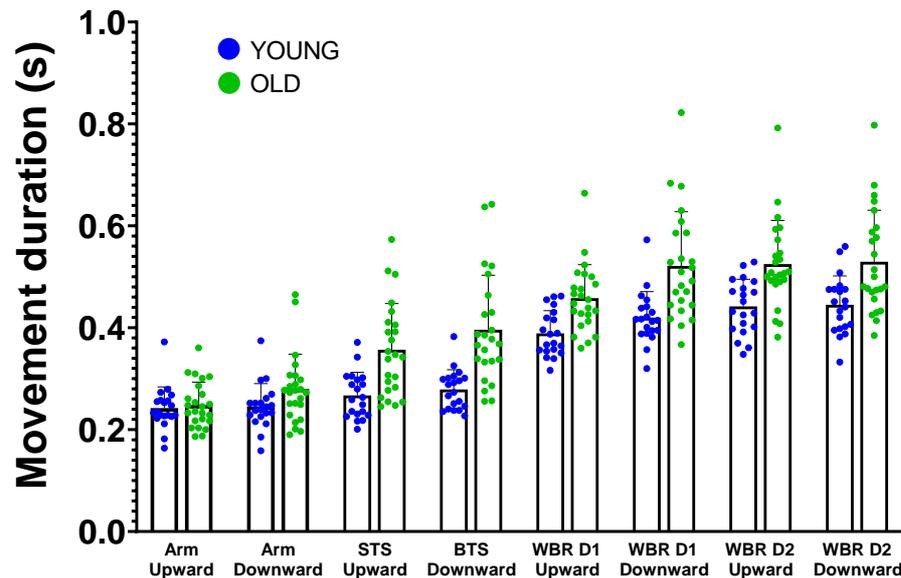

Figure 4. Mean ± SD movement durations (s) for fast movements performed in all tasks and both groups (STS: Seat-to-stand,
BTS: Back-to-seat, WBR: Whole-body-reaching, D1: Short distance=15% of the height of the subject, and D2: Long distance=30%
of the height of the subject). Each point corresponds to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

328   A body of computational studies has demonstrated that human arm movements take advantage of gravity
329   effects to save energy (Berret et al., 2008; Crevecoeur et al., 2009; Gaveau et al., 2011, 2014, 2016, 2021).
330   Most of these studies used mathematical models that minimized the absolute work of muscle force to produce
331   the arm displacement (Berret et al., 2008; Gaveau et al., 2011, 2014, 2016, 2021). More specifically, the study
332   from Berret et al. (2008) formally demonstrated that this muscle work cost, and associated behavior,
333   corresponded to an energetic-like optimum. Because previous studies have shown that the amplitude of
334   kinematic and electromygographic markers directly relates to energetic efficiency (Gaveau et al., 2016; Poirier
335   et al., 2022), here we compare the amplitude of an EMG marker between younger and older adults. If the EMG
336   marker increases, this means that energetic efficiency increases – i.e., the minimization process is upregulated
337   – and thus muscle work decreases. If the EMG marker decreases, this means that energetic efficiency
338   decreases – i.e., the minimization process is downregulated – and thus muscle work increases.
339   Figure 5 displays average phasic EMG profiles for each muscle, direction, and task. As recently reported,
340   phasic EMG signals of arm movements show negative phases during the deceleration of upward and the
341   acceleration of downward arm movements, i.e., where gravity torque helps generate the arm's motion
342   (Gaveau et al., 2021; Poirier et al., 2022, 2024). Previous works demonstrated that this negativity is not erratic
343   but systematic and indicate that muscles contract less than necessary to compensate for gravity effects. It is
344   therefore especially prominent on antigravity muscles and reveals that the central nervous system (CNS)
345   exploits gravity effects to produce efficient movements, i.e., motor patterns that save unnecessary muscle
346   work. Here, we extend this result to movements performed with the entire body. Indeed, for STS/BTS and WBR
347   movements, Figure 5B-D unveils phasic EMG negativity during the deceleration of upward movements and the
348   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 work (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.

Main analysis

Following our primary hypothesis, we first analyzed a single metric quantifying phasic EMG negativity on an average muscle activation pattern (vastus lateralis and erector spinae in L1 were averaged for whole-body tasks and deltoid anterior was used for arm tasks), namely the negative area of phasic EMG patterns (see methods and Poirier et al., 2022, 2024). The bigger the negativity index, the more efficient the muscle contractions, in the sense that gravity effects were maximally exploited to save energy (Gaveau et al., 2021).
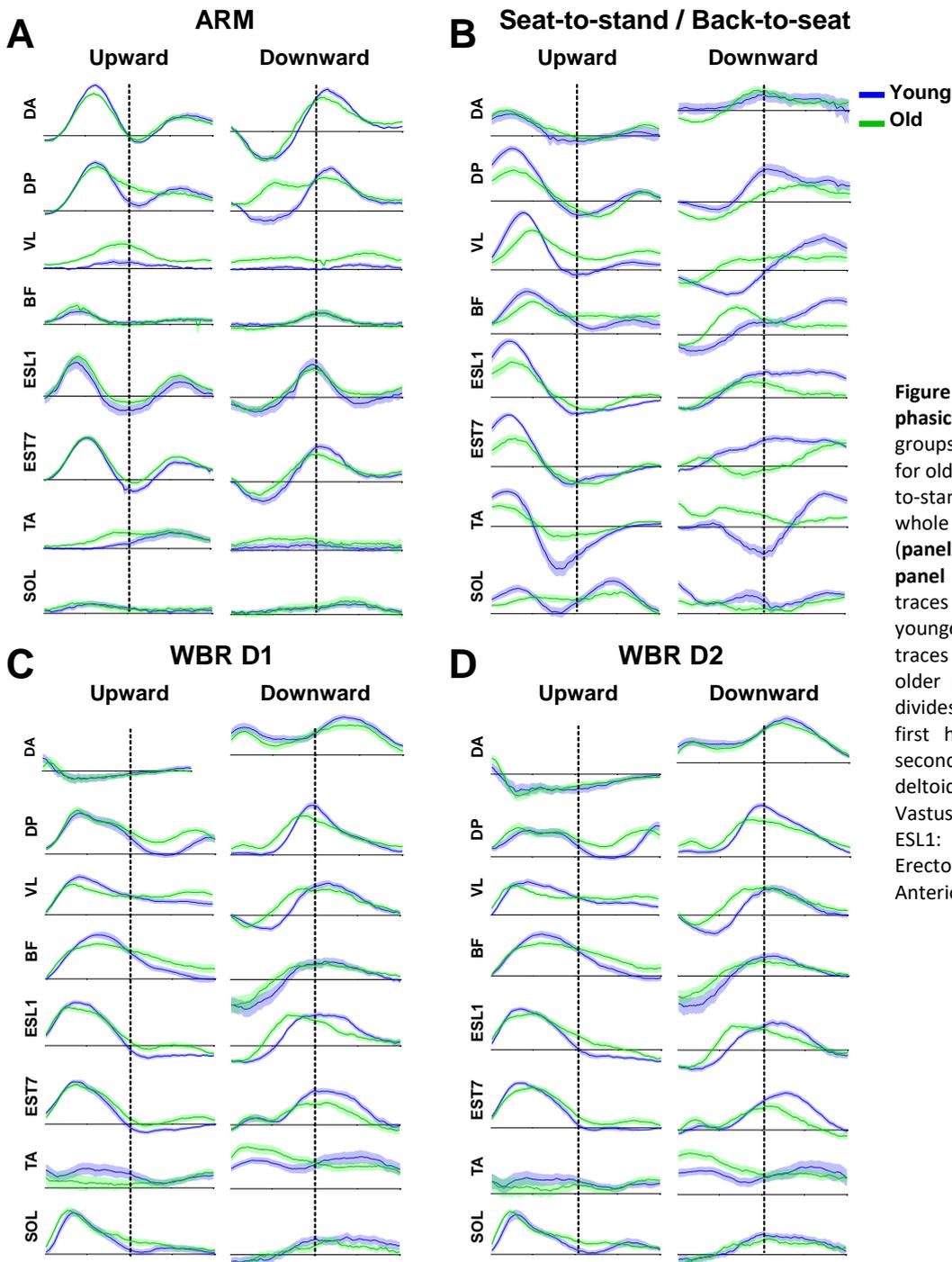

Figure 5: Mean (±SE) integrated phasic EMGs recorded for both groups (n = 20 for younger and n = 24 for older) during arm (**panel A**), Seat-to-stand/Back-to-seat (**panel B**), and whole body reaching movements (**panel C** for short distance D1 and **panel D** for long distance D2). Blue traces present EMGs recorded for younger participants, while green traces present EMGs recorded for older participants. The dotted line divides the movement in two: the first half is acceleration and the second is deceleration. (DA: Anterior deltoid, DP: Posterior deltoid, VL: Vastus Lateralis, BF: Biceps Femoris, ESL1: Erector Spinae in L1, EST7: Erector Spinae in T7, TA: Tibialis Anterior, SOL: Soleus).

359 Figure 6 displays the results of this ANCOVA analysis (Age × Task-Type), revealing a significant interaction
360 between age and task factors ($F_{(1,42)}$= 5.48, P=2.44E-02, η^2=0.120) but no Age or Tasks effect (for detailed
361 statistical results, please see Supplementary Table 3). This result demonstrates that age differently alters
362 motor strategies for arm movements vs whole-body movements. Older adults used gravity effects to a similar
363 extent as younger ones when performing arm movements (older adults, mean ± SD: -10.7 ± 5.6, 95% CI: [-8.4;-
364 13.0]; younger adults, -11.4 ± 3.6, [-9.8;-13.0]), but to a lesser extent when performing whole-body movements
365 (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
366 et al. (2024), similar arm results in younger and older adults suggest that the ability to plan movements that
367 optimally use gravity effects to save energy remains functional in older adults. The results obtained in whole-
368 body movement tasks (STS/BTS and WBR) could thus suggest that the difference observed between older and
369 younger adults does not reflect a deterioration of the ability to plan movements that are optimally adapted to
370 the gravity environment. Instead, it would suggest a change in movement strategy that compensates for other
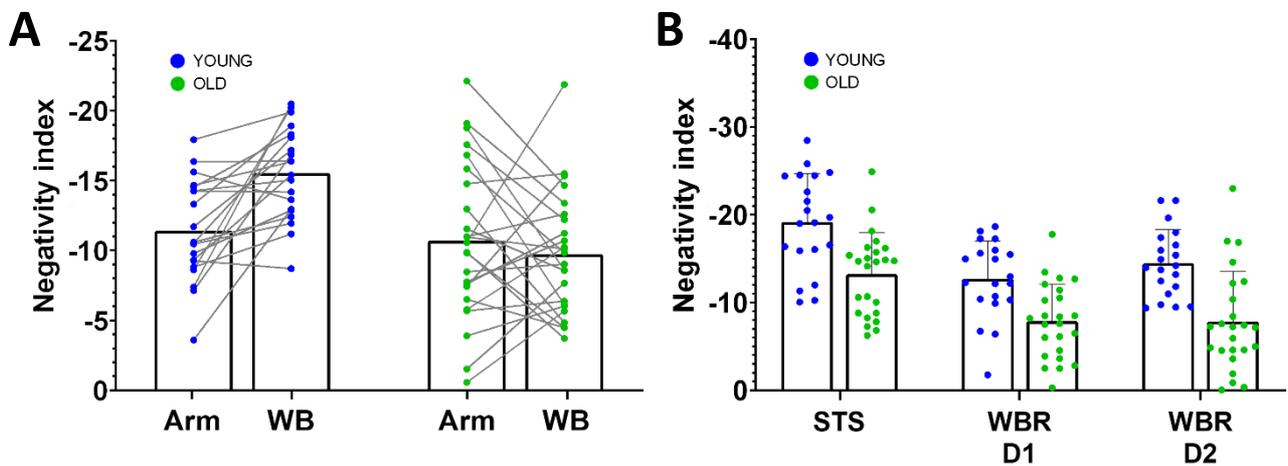371 deteriorated control processes (for example, the loss of muscle mass & force).

Figure 6. Negativity index computed for **A**. 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) and **B**. each whole-body task (STS/BTS: seat-to-stand/back-to-sit, WBR D1: whole-body reaching from D1 and WBR D2: 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 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 correspond to the older participants. Each point corresponds to the mean value of one participant (mean across trials and antigravity muscles, and/or tasks).

372 We performed a complementary analysis to determine whether every whole-body task showed the same
373 age effect (ANCOVA Age x Whole-Body Tasks). This test did not reveal any interaction effect ($F_{(2,42)}$= 0.77,
374 P=4.67E-01, η^2=0.019), further supporting the interpretation that this is the "whole body" aspect of the task
375 that impacts the motor strategy in older adults (please see Supplementary Table 3 for full analysis).
376 Previous studies have proposed that the change in kinematic strategies observed between older and
377 younger adults during whole-body movements could be explained as a strategy maximizing equilibrium
378 maintenance rather than energetic efficiency (Casteran et al., 2018; Paizis et al., 2008). Following this
379 hypothesis, one would predict increasing differences between younger and older adults when the equilibrium
380 constraint increases. In the present experiment, increased equilibrium constraint was produced by increasing
381 the target distance during whole body reaching movements (WBR D1 vs WBR D2; alike Casteran et al., 2018).
382 The Age x Whole-Body Tasks ANCOVA, however, did not reveal such a difference.

383   Last, we analyzed kinematic patterns in order to investigate whether the decreased energetic efficiency
384   observed during whole body tasks in older adults could actually be interpreted as compensation. We tested
385   whether the negativity of phasic EMGs correlated with kinematic parameters that are related to balance
386   control (the COM displacement, and COM peak velocity, see Figure 7; and see Supplementary Figure 1 for
387   detailed results of the reproduction of the tests conducted by Casteran et al., (2018) Paizis et al., (2008). The
388   EMG criterion during the Back to Seat task was found to be significantly correlated with the COM displacement
389   (Pearson correlation, P=2.2E-2, Pearson's r=-0.343) and the COM peak velocity (Pearson correlation, P=1.9E-
390   3, Pearson's r=-0.476). This same EMG criterion also turned out to be significantly correlated for the Whole-
391   Body Bending task with the COM displacement (Pearson correlation, P=3.2E-3, Pearson's r=-0.435) and with
392   the COM peak velocity (Pearson correlation, P=1.2E-7, Pearson's r=-0.700). The linear regressions revealed
393   that the more a participant used the effects of gravity, the more and the quicker she/he displaced his COM.
394   One could interpret this result as demonstrating that older adults lose the ability to plan energetically efficient
395   movement and, thus, move their whole-body less and more slowly. However, the null age effect on arm
396   movement control supports the hypothesis that planning efficient movements remains functional in older
397   adults, as also supported by recent other results (Healy et al., 2023; Huang & Ahmed, 2014; Poirier et al., 2020;
398   Summerside et al., 2024). Overall, during movements performed with the entire body, i.e., when equilibrium
399   maintenance is challenged, the present results support an age-related adaptation process that selects a less
400   energetically efficient but more stable movement strategy in healthy older adults.
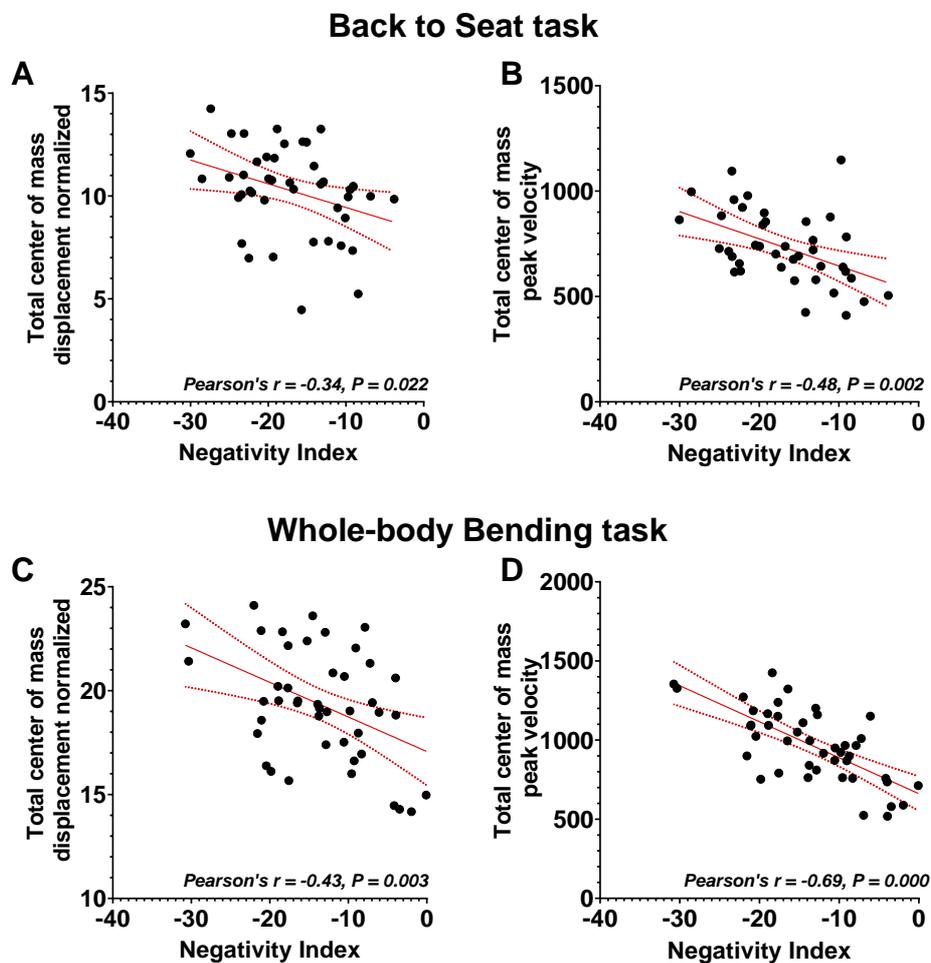

Figure 7. Center of mass analyses. Linear relationship between EMG negativity (Vastus Lateralis and Spinal Erector L1) and total displacement of the center of mass during **A**. back-to-sit movements and **B**. bending movements from the whole-body reaching tasks (averaged between distances D1 and D2).

Exploratory analyses

To provide a fine-grained analysis of the age effect on phasic EMG negativity during whole-body motion, we probed negativity duration, negativity amplitude, and negativity occurrence across tasks and age-groups (see Figure 9). Here also, the bigger the values, the bigger the use of gravity effects to produce body motion. A repeated measure ANCOVA Age x Tasks (Young/Older x STS_BTS/WBRD1/WBRD2) 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). 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). No interaction between Age and the other factors reached significance (see Supplementary Table 3 for detailed results). Overall, all variables showed qualitatively smaller negativity on phasic EMGs, thus reduced use of gravity effects, in older compared to younger adults. As already observed for arm movements (Poirier et al. 2024), it is mainly the duration of inactivation that is modulated.

Here we were interested in comparing arm movement and whole-body movement control because the scientific literature has reported that the control of whole-body movements changes with age, while the control of arm movements does not (Casteran et al., 2018; Paizis et al., 2008; Poirier et al., 2020, 2024; Vernazza-Martin et al., 2008). Focusing on a limited number of muscles is problematic, as we risk probing muscles whose activation patterns are not affected by age. To ensure that our restrictive theory-driven analysis provides meaningful results, we verified that our cherry-picked muscles truly conveyed information about age-related modifications of whole-body movement control. To this aim, we employed machine learning analyses that quantified how much each muscle activation was altered by age. This allowed controlling that we were actually focusing on muscles that discriminated movement control between younger and older adults.

Our rationale was the following: if the algorithm can successfully separate the data of younger and older adults, using antigravity muscle activation patterns, this would demonstrate that important information is contained in those muscles regarding age-related modifications of movement control. For more details on similar use and operation of machine learning algorithms on EMG signals, please see (Chambellant et al., 2024; Thomas et al., 2023; Tolambiya et al., 2011). 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).

The Machine Learning analysis indeed revealed that antigravity muscles contained important information, allowing separating age-groups with some of the best success-rates (see Figure 8 for results regarding LDA accuracy). The vastus lateralis (VL) and the spinal erectors on L1 (ESL1) achieved the best classification accuracies of 57.72% and 59.51% respectively (considering that these classifications are significantly better than chance if they are above 52.5% according to a fairness test). The main results presented here are therefore quantitatively based. They originate from analyses of the muscles that show the most information to distinguish younger from older adults during whole-body movement. Other muscles, such as DP or EST7, also exhibit reasonably good classification accuracies. This is not unexpected as humans and animals are known to control their varied muscles in a synergistic manner (Berret et al., 2009; d'Avella et al., 2006; Tresch et al., 1999), and even the slightest alteration of movement strategy may require modifying the activation of several muscles.
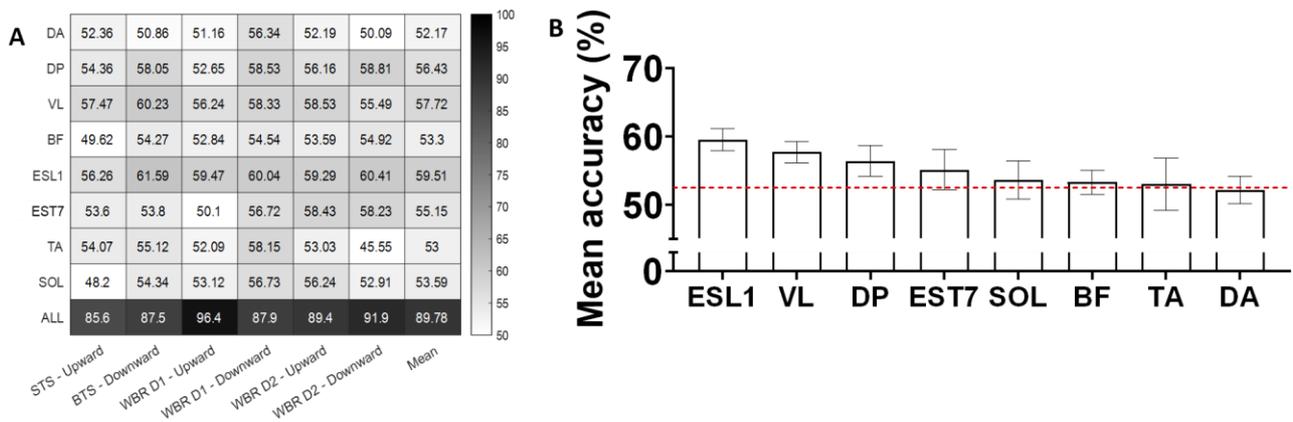
Figure 8. A. Heatmap representing the accuracy of the LDA algorithm to discriminate young from older adults using phasic EMGs recorded during the tasks mobilizing the entire body. The eight first lines correspond to the accuracy of each individual muscle. The last line corresponds to the accuracy of taking all muscles simultaneously (DA: Anterior deltoid, DP: Posterior deltoid, VL: Vastus Lateralis, BF: Biceps Femoris, ESL1: Erector Spinae in L1, EST7: Erector Spinae in T7, TA: Tibialis Anterior, SOL: Soleus). The first six columns correspond to the six whole-body tasks of the experiment (STS = Sit To Stand; BTS = Back To Sit; WBR D1 = Whole Body Reaching near target; WBR D2 = Whole body reaching far target), the last column corresponds to the average accuracy of the six tasks for each muscle. This analysis has been conducted to showcase which muscles are important for discrimination. We can see taht those antigravity muscles (muscles that act against gravity, in our case, the VL and the ESL1) contain relevant information as they reach the highest scores. **B**. Mean ± SD distance between groups representations by the LDA algorithm for each individual muscle (DA: Anterior deltoid; DP: Posterior deltoid; VL: Vastus Lateralis; BF: Biceps Femoris; ESL1: Erector Spinae in L1; EST7: Erector Spinae in T7; TA: Tibialis Anterior; SOL: Soleus). The higher the distance, the more differentiable the groups are. Values corresponds to the average distance obtain for all six tasks. We can see that those antigravity muscles (muscles that act against gravity, in our case, the VL and the ESL1) contain relevant information as they reach some of the highest values. Error bars correspond to the standard error across a five-fold cross-validation.
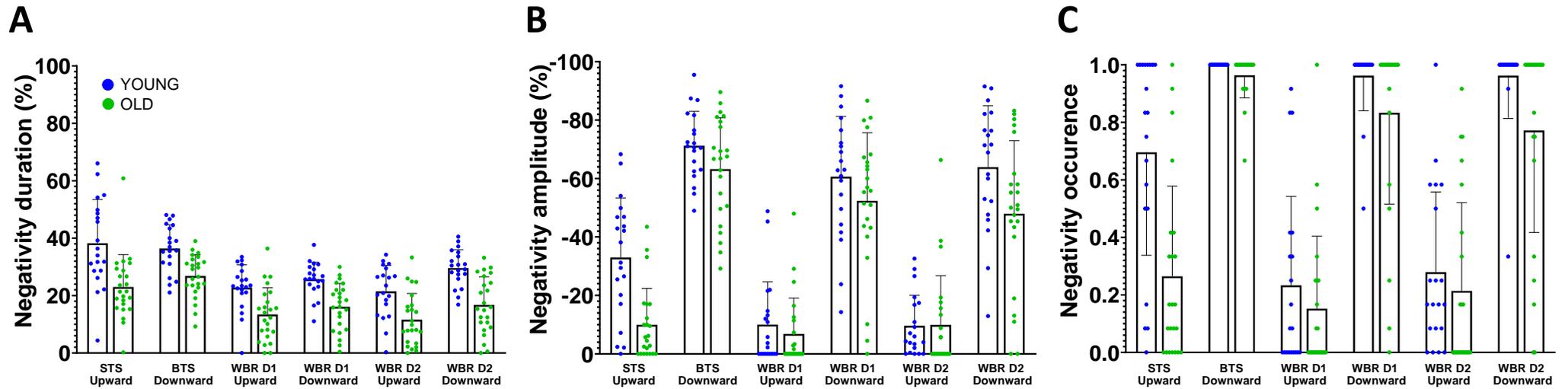
Figure 9. Mean ± SD negativity quantification for all tasks and groups (STS: Seat-to-stand, BTS: Back-to-seat, WBR: Whole-body-reaching, D1: Short distance=15% of the heighy of the subject, and D2: Long distance=30% of the heighy of the subject). Quantification was carried out using three criteria: negativity duration (panel **A**), negativity amplitude (panel **B**), and negativity occurrence (panel **C**) on the antigravity muscles (vastus lateralis and the erector spinae). The blue points correspond to the younger participants, and the green points correspond to the older participants. Each point corresponds to the mean value across trials and antigravity muscles.

Discussion

444

445   In younger and older adults, we investigated the muscle activation patterns responsible for arm and
446 whole-body movements. The results revealed an age-related alteration of muscle activation that differed
447 between the types of tasks. Comparing older adults to younger ones, we found that a muscle marker of
448 energetic efficiency was reduced during whole-body movements, but the results show no evidence that
449 this marker was reduced during arm movements. Previous works have demonstrated that this marker
450 allows quantifying the output of a sensorimotor control process that adapts human movements to gravity
451 (Gaveau et al., 2021; Poirier et al., 2022, 2024). More precisely, this marker allows for quantifying how
452 much one harvests gravity effects to save energy. Here, arm movement results reveal that this energetic-
453 efficiency process remains functional in older adults. During whole-body movements, however, the present
454 results reveal that a criteria linked to energetic-efficiency was downregulated in older adults compared to
455 younger adults. Overall, the present results suggest a compensation process that modulates planning
456 strategies to maximize equilibrium in older adults.

457   **Age-related compensatory processes in sensorimotor control**. A number of studies have proposed
458 that the differences observed between younger and older adults can be interpreted as compensations for
459 age-related deteriorations. Of particular interest are studies from the last decade that have sought to
460 investigate specific motor control processes rather than broad motor performance. For example, some of
461 these studies indirectly suggested that older adults favor feedforward rather than feedback control (Moran
462 et al., 2014; Wolpe et al., 2016) to compensate for the attenuation of sensory processing with increasing
463 age (Moran et al., 2014; Parthasharathy et al., 2022; Saenen et al., 2023). Others indirectly suggested that
464 older adults favor movement efficiency over precision (Healy et al., 2023; Poirier et al., 2020) to
465 compensate for their increased energetic cost (Didier et al., 1993; Hortobagyi et al., 2011; John et al., 2009).
466 Yet, because the focus of these studies was not on compensatory processes, they did not include dedicated
467 experimental conditions. The aim of the present study was to fill this gap.

468   **Maintained efficiency of arm movements in older adults**. The metabolic rate is known to influence
469 resource use, body size, rate of senescence, and survival probability (Brown et al., 2004; DeLong et al.,
470 2010; Strotz et al., 2018; Van Voorhies & Ward, 1999). The nervous system has therefore developed the
471 ability to design movement strategies that minimize our every-day efforts (Cheval et al., 2018; Gaveau et
472 al., 2016; Huang et al., 2012; Morel et al., 2017; Selinger et al., 2015; Shadmehr et al., 2016). The present
473 findings confirm the results of previous arm movement studies that proposed a theory according to which
474 motor control takes advantage of gravity effects to save energy (Berret et al., 2008; Crevecoeur et al., 2009;
475 Gaveau et al., 2014, 2016, 2021; Gaveau & Papaxanthis, 2011). Here, we focused on the muscle activation
476 marker of gravity-related energetic-efficiency, i.e., the negativity of phasic EMG. Previous modeling and
477 experimental work demonstrated that this phasic EMG negativity results from an optimal control process
478 that plans efficient arm movements in the gravity field (Gaveau et al., 2021). As reported by (Poirier et al.,
479 2024), we found similar phasic EMG negativity during arm movements in older and younger adults. Thus,
480 arm movements equally optimized gravity effects in younger and older adults. These results align with
481 those of studies that probed progressive motor adaptation to a new environment in older adults. Using
482 locally induced force fields in a robotic environment, these studies revealed that older adults decreased
483 their metabolic costs similarly to younger adults while adapting to new environmental dynamics (Healy et
484 al., 2023; Huang & Ahmed, 2014). Overall, results from arm movement studies advocate for the
485 maintenance of the ability to optimally integrate environmental dynamics and plan arm movements that
486 are energetically efficient in older adults.

487   **Whole-body movements also harvest gravity effects to save energy.** Current results also extend the
488 current knowledge on the planning of energetically efficient movements to more global movements, both
489 in younger and older adults. They unravel that deactivating muscles below the tonic level that would be
490 necessary to compensate for external dynamics are not only relevant to controlling focal arm movement
491 but also for whole-body movements. Using a combination of modeling and experimental work, previous
492 studies demonstrated that healthy participants move their arms following trajectories and using muscular
493 patterns that save energy in the gravity environment (Berret et al., 2008; Crevecoeur et al., 2009; Gaveau
494 et al., 2014, 2016, 2021; Gaveau & Papaxanthis, 2011). To isolate gravity effects, most studies focused on
495 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.

Decreased efficiency of whole-body movements in older adults. 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, adding 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). Previous kinematic studies suggested that older adults favor movement strategies that maximize balance maintenance rather than energy efficiency (Casteran et al., 2018; Paizis et al., 2008). However, age differences observed during whole-body movements may also be interpreted as an inability to save energy when coordinating complex movements (Goodpaster et al., 2006; Henry & Baudry, 2019; Quinlan et al., 2018; Vernazza-Martin et al., 2008). Here, contrasting results from arm and whole-body movements in the same participants, we provide support for a compensation process that adapts movement strategy in older adults, rather than a deterioration of the ability to optimally coordinate whole-body movements. Since arm movements revealed that older participants maintained the ability to plan energetically efficient movements, altered whole-body movement may be explained as an adaptation of movement strategy rather than deteriorated motor planning. More importantly, we found that decreased efficiency was associated with decreased center-of-mass displacement and speed, i.e., less instability. This further suggests that decreased efficiency in older adults is a compensation process that trades efficiency with equilibrium maintenance. This could be explained as an optimal motor planning process that minimizes a composite cost function; i.e., energy and unstability. It has been proposed that the central nervous system combines different costs – related to energy, precision, or duration, for example – when planning a movement (Berret et al., 2011; Gielen, 2009; Healy et al., 2023; Liu & Todorov, 2007; Mombaur et al., 2010; Poirier et al., 2024; Tanis et al., 2023; Vu et al., 2016). In older adults, this combination would increase the relative weighting of the instability (equilibrium) cost and decrease the relative weighting of the energetic cost. Future work may use this framework to probe age-related motor adaptation.

Effect of target distance. During the whole-body reaching task, reusing the protocol (Casteran et al., 2018), 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 (see Supplementary Table 3).

Age-related compensation in the brain. In the sensorimotor field, following the consensus that aging is associated with increased activation and increased spatial recruitment, numerous studies have attempted to establish a correlation between brain 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 the aging brain. 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). Building on the theoretical work of Krakauer et al. (2017), we recently proposed that an important reason for this lack of consensus may be that previous studies, while focusing on brain activations, used crude behavioral paradigms that likely mixed deteriorated and compensatory processes (Poirier et al., 2021). Using behavioral paradigms that focus on specific motor control processes, as performed here, could help differentiate compensatory mechanisms from deteriorative ones.

Role of physical and cognitive fitness in age-related compensation. Physical and cognitive fitness may influence how much older adults favor stability over energetic efficiency. It is well-known that physical and cognitive fitness significantly impact functional mobility in older adults (Marusic et al., 2018; Wickramarachchi et al., 2023; Zhao et al., 2014). One could speculate that physical and cognitive fitness

550 are inversely related to the level of physical and cognitive deterioration. For example, muscle force and
551 sensory integration are crucial for controlling balance. The more deteriorated they are, the greater the
552 need for compensatory processes to adapt movement control to the participant's capacities. Future
553 research should account for variations in physical and cognitive fitness to better understand their role in
554 the development of compensatory mechanisms.

555 **Simple mono-articular vs complex multi-articular arm movements**. Another aspect that needs to be
556 highlighted here is the choice of the arm task, which is not representative of all existing tasks for studying
557 upper limb motor skills. Using this very same task, the results from two previous studies also support the
558 preservation of arm movement efficiency in older adults (Poirier et al., 2020, 2024). One may wonder
559 whether the present conclusions would hold for more complex arm movements. Using multi-degree of
560 freedom arm movements to study motor adaptation to an externally imposed force-field, other studies
561 also reported results showing that, alike younger adults, older adults maintain the ability to produce
562 movements that are energetically efficient (Healy et al., 2023; Summerside et al., 2024). The present mono-
563 articular results are therefore likely to generalize to other types of arm movements. In young adults, the
564 efficient integration of gravity effects to save energy has been demonstrated with varied arm movements,
565 such as single or muti-degree of freedom pointing movements, drawing movements, reach to grasp
566 movements, or arm movements that transport a hand-grasped object (Berret et al., 2008; Crevecoeur et
567 al., 2009; Gaveau et al., 2011; Gaveau & Papaxanthis, 2011; Le Seac'h & McIntyre, 2007; Papaxanthis et al.,
568 1998, 2005; Yamamoto & Kushiro, 2014b). Future work may test whether the present conclusions extend
569 to more complex and functional arm movements.

570 In conclusion, probing a specific motor control process, the present study provides a set of behavioral
571 results that support the interpretation of a compensatory process that counterbalances other deteriorated
572 processes in older adults. Probing age effects on specific sensorimotor control processes may help
573 disentangle compensation from deterioration processes that occur through healthy aging (Poirier et al.,
574 2021). We believe that understanding compensation at a behavioral level is an important step toward
575 pinpointing its neural underpinning (Krakauer et al., 2017) and, later, preventing unhealthy aging (Baltes &
576 Baltes, 1990; Martin et al., 2015; Zhang & Radhakrishnan, 2018).

Data, scripts, code, and supplementary information availability

581 Data are available online: 10.5281/zenodo.10619701, webpage hosting the data:
582 https://doi.org/10.5281/zenodo.10619701 (*citation of the data eg* Mathieu et al, 2024);
583 Scripts and code are available online: 10.5281/zenodo.10634004, webpage hosting the scripts:
584 https://doi.org/10.5281/zenodo.10634004 (*citation of the scripts eg* Mathieu et al, 2024);
585 Supplementary information is available online: 10.5281/zenodo.10671496, webpage hosting the file:
586 https://doi.org/10.5281/zenodo.12671953 (*citation of the supplementary file eg* Mathieu et al, 2024);

Conflict of interest disclosure

588 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in
589 relation to the content of the article.
590 Jérémie Gaveau is a member of the managing board of the PCI Health & Movement Sciences.

References

Baltes, P. B. (1997). On the incomplete architecture of human ontogeny : Selection, optimization, and compensation as foundation of developmental theory. *American Psychologist*, *52*(4), 366-380. https://doi.org/10.1037/0003-066X.52.4.366

Baltes, P. B., & Baltes, M. M. (1990). Psychological perspectives on successful aging : The model of selective optimization with compensation. In P. B. Baltes & M. M. Baltes (Éds.), *Successful Aging* (1^re éd., p. 1-34). Cambridge University Press. https://doi.org/10.1017/CBO9780511665684.003

Barbero, M., Merletti, R., & Rainoldi, A. (2012). *Atlas of Muscle Innervation Zones*. Springer Milan. https://doi.org/10.1007/978-88-470-2463-2

Barulli, D., & Stern, Y. (2013). Efficiency, capacity, compensation, maintenance, plasticity : Emerging concepts in cognitive reserve. *Trends in Cognitive Sciences*, *17*(10), 502-509. https://doi.org/10.1016/j.tics.2013.08.012

Bernard, J. A., & Seidler, R. D. (2012). Evidence for motor cortex dedifferentiation in older adults. *Neurobiology of Aging*, *33*(9), 1890-1899. https://doi.org/10.1016/j.neurobiolaging.2011.06.021

Berret, B., Bonnetblanc, F., Papaxanthis, C., & Pozzo, T. (2009). Modular Control of Pointing beyond Arm's Length. *Journal of Neuroscience*, *29*(1), 191-205. https://doi.org/10.1523/JNEUROSCI.3426-08.2009

Berret, B., Chiovetto, E., Nori, F., & Pozzo, T. (2011). Evidence for Composite Cost Functions in Arm Movement Planning : An Inverse Optimal Control Approach. *PLoS Computational Biology*, *7*(10), e1002183. https://doi.org/10.1371/journal.pcbi.1002183

Berret, B., Darlot, C., Jean, F., Pozzo, T., Papaxanthis, C., & Gauthier, J. P. (2008). The Inactivation Principle : Mathematical Solutions Minimizing the Absolute Work and Biological Implications for the Planning of Arm Movements. *PLoS Computational Biology*, *4*(10), e1000194. https://doi.org/10.1371/journal.pcbi.1000194

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). TOWARD A METABOLIC THEORY OF ECOLOGY. *Ecology*, *85*(7), 1771-1789. https://doi.org/10.1890/03-9000

Buckles, V. D. (1993). Age-Related Slowing. In G. E. Stelmach & V. Hömberg (Éds.), *Sensorimotor Impairment in the Elderly* (p. 73-87). Springer Netherlands. https://doi.org/10.1007/978-94-011-1976-4_6

Buneo, C. A., Soechting, J. F., & Flanders, M. (1994). Muscle activation patterns for reaching : The representation of distance and time. *Journal of Neurophysiology*, *71*(4), 1546-1558. https://doi.org/10.1152/jn.1994.71.4.1546

Bunzeck, N., Steiger, T. K., Krämer, U. M., Luedtke, K., Marshall, L., Obleser, J., & Tune, S. (2024). Trajectories and contributing factors of neural compensation in healthy and pathological aging. *Neuroscience & Biobehavioral Reviews*, *156*, 105489. https://doi.org/10.1016/j.neubiorev.2023.105489

Cassady, K., Gagnon, H., Freiburger, E., Lalwani, P., Simmonite, M., Park, D. C., Peltier, S. J., Taylor, S. F., Weissman, D. H., Seidler, R. D., & Polk, T. A. (2020). Network segregation varies with neural distinctiveness in sensorimotor cortex. *NeuroImage*, *212*, 116663. https://doi.org/10.1016/j.neuroimage.2020.116663

Cassady, K., Gagnon, H., Lalwani, P., Simmonite, M., Foerster, B., Park, D., Peltier, S. J., Petrou, M., Taylor, S. F., Weissman, D. H., Seidler, R. D., & Polk, T. A. (2019). Sensorimotor network segregation declines with age and is linked to GABA and to sensorimotor performance. *NeuroImage*, *186*, 234-244. https://doi.org/10.1016/j.neuroimage.2018.11.008

Cassady, K., Ruitenberg, M. F. L., Reuter-Lorenz, P. A., Tommerdahl, M., & Seidler, R. D. (2020). Neural Dedifferentiation across the Lifespan in the Motor and Somatosensory Systems. *Cerebral Cortex*, *30*(6), 3704-3716. https://doi.org/10.1093/cercor/bhz336

Casteran, M., Hilt, P. M., Mourey, F., Manckoundia, P., French, R., & Thomas, E. (2018). Shifts in Key Time Points and Strategies for a Multisegment Motor Task in Healthy Aging Subjects. *The Journals of Gerontology: Series A*, *73*(12), 1609-1617. https://doi.org/10.1093/gerona/gly066

Chambellant, F., Gaveau, J., Papaxanthis, C., & Thomas, E. (2023). *Deactivation and Collective Phasic Muscular Tuning for Pointing Direction : Insights from Machine Learning* [Preprint]. Neuroscience. https://doi.org/10.1101/2023.03.15.532800

Chambellant, F., Gaveau, J., Papaxanthis, C., & Thomas, E. (2024). Deactivation and Collective Phasic Muscular Tuning for Pointing Direction : Insights from Machine Learning. *Heliyon*, e33461. https://doi.org/10.1016/j.heliyon.2024.e33461

Cheval, B., Tipura, E., Burra, N., Frossard, J., Chanal, J., Orsholits, D., Radel, R., & Boisgontier, M. P. (2018). Avoiding sedentary behaviors requires more cortical resources than avoiding physical activity : An EEG study. *Neuropsychologia*, *119*, 68-80. https://doi.org/10.1016/j.neuropsychologia.2018.07.029

Clark, D. J., Christou, E. A., Ring, S. A., Williamson, J. B., & Doty, L. (2014). Enhanced Somatosensory Feedback Reduces Prefrontal Cortical Activity During Walking in Older Adults. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *69*(11), 1422-1428. https://doi.org/10.1093/gerona/glu125

Cover, T. M. (1965). Geometrical and Statistical Properties of Systems of Linear Inequalities with Applications in Pattern Recognition. *IEEE Transactions on Electronic Computers*, *EC-14*(3), 326-334. https://doi.org/10.1109/PGEC.1965.264137

Crevecoeur, F., Thonnard, J.-L., & Lefèvre, P. (2009). Optimal Integration of Gravity in Trajectory Planning of Vertical Pointing Movements. *Journal of Neurophysiology*, *102*(2), 786-796. https://doi.org/10.1152/jn.00113.2009

Darling, W. G., Cooke, J. D., & Brown, S. H. (1989). Control of simple arm movements in elderly humans. *Neurobiology of Aging*, *10*(2), 149-157. https://doi.org/10.1016/0197-4580(89)90024-9

d'Avella, A., Fernandez, L., Portone, A., & Lacquaniti, F. (2008). Modulation of Phasic and Tonic Muscle Synergies With Reaching Direction and Speed. *Journal of Neurophysiology*, *100*(3), 1433-1454. https://doi.org/10.1152/jn.01377.2007

d'Avella, A., Portone, A., Fernandez, L., & Lacquaniti, F. (2006). Control of Fast-Reaching Movements by Muscle Synergy Combinations. *Journal of Neuroscience*, *26*(30), 7791-7810. https://doi.org/10.1523/JNEUROSCI.0830-06.2006

DeLong, J. P., Okie, J. G., Moses, M. E., Sibly, R. M., & Brown, J. H. (2010). Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. *Proceedings of the National Academy of Sciences*, *107*(29), 12941-12945. https://doi.org/10.1073/pnas.1007783107

Didier, J. P., Mourey, F., Brondel, L., Marcer, I., Milan, C., Casillas, J. M., Verges, B., & Winsland, J. K. D. (1993). The Energetic Cost of Some Daily Activities : A Comparison in a Young and Old Population. *Age and Ageing*, *22*(2), 90-96. https://doi.org/10.1093/ageing/22.2.90

Fernandez, N. B., Hars, M., Trombetti, A., & Vuilleumier, P. (2019). Age-related changes in attention control and their relationship with gait performance in older adults with high risk of falls. *NeuroImage*, *189*, 551-559. https://doi.org/10.1016/j.neuroimage.2019.01.030

Fettrow, T., Hupfeld, K., Reimann, H., Choi, J., Hass, C., & Seidler, R. (2021). Age differences in adaptation of medial-lateral gait parameters during split-belt treadmill walking. *Scientific Reports*, *11*(1), 21148. https://doi.org/10.1038/s41598-021-00515-z

Flanders, M., & Herrmann, U. (1992). Two components of muscle activation : Scaling with the speed of arm movement. *Journal of Neurophysiology*, *67*(4), 931-943. https://doi.org/10.1152/jn.1992.67.4.931

Flanders, M., Pellegrini, J. J., & Soechting, J. F. (1994). Spatial/temporal characteristics of a motor pattern for reaching. *Journal of Neurophysiology*, *71*(2), 811-813. https://doi.org/10.1152/jn.1994.71.2.811

Gaveau, J., Berret, B., Angelaki, D. E., & Papaxanthis, C. (2016). Direction-dependent arm kinematics reveal optimal integration of gravity cues. *eLife*, *5*, e16394. https://doi.org/10.7554/eLife.16394

Gaveau, J., Berret, B., Demougeot, L., Fadiga, L., Pozzo, T., & Papaxanthis, C. (2014). Energy-related optimal control accounts for gravitational load : Comparing shoulder, elbow, and wrist rotations. *Journal of Neurophysiology*, *111*(1), 4-16. https://doi.org/10.1152/jn.01029.2012

Gaveau, J., Grospretre, S., Berret, B., Angelaki, D. E., & Papaxanthis, C. (2021). A cross-species neural integration of gravity for motor optimization. *Science Advances*, *7*(15), eabf7800. https://doi.org/10.1126/sciadv.abf7800

Gaveau, J., Paizis, C., Berret, B., Pozzo, T., & Papaxanthis, C. (2011). Sensorimotor adaptation of point-to-point arm movements after spaceflight : The role of internal representation of gravity force in trajectory planning. *Journal of Neurophysiology*, *106*(2), 620-629. https://doi.org/10.1152/jn.00081.2011

Gaveau, J., & Papaxanthis, C. (2011). The Temporal Structure of Vertical Arm Movements. *PLoS ONE*, *6*(7), e22045. https://doi.org/10.1371/journal.pone.0022045

Gentili, R., Cahouet, V., & Papaxanthis, C. (2007). Motor planning of arm movements is direction-dependent in the gravity field. *Neuroscience*, *145*(1), 20-32. https://doi.org/10.1016/j.neuroscience.2006.11.035

Gielen, S. (2009). Review of Models for the Generation of Multi-Joint Movements in 3-D. In D. Sternad (Éd.), *Progress in Motor Control* (Vol. 629, p. 523-550). Springer US. https://doi.org/10.1007/978-0-387-77064-2_28

Goble, D. J., Coxon, J. P., Wenderoth, N., Van Impe, A., & Swinnen, S. P. (2009). Proprioceptive sensibility in the elderly : Degeneration, functional consequences and plastic-adaptive processes. *Neuroscience & Biobehavioral Reviews*, *33*(3), 271-278. https://doi.org/10.1016/j.neubiorev.2008.08.012

Goodpaster, B. H., Park, S. W., Harris, T. B., Kritchevsky, S. B., Nevitt, M., Schwartz, A. V., Simonsick, E. M., Tylavsky, F. A., Visser, M., Newman, A. B., & for the Health ABC Study. (2006). The Loss of Skeletal Muscle Strength, Mass, and Quality in Older Adults : The Health, Aging and Body Composition Study. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *61*(10), 1059-1064. https://doi.org/10.1093/gerona/61.10.1059

Gueugneau, N., Martin, A., Gaveau, J., & Papaxanthis, C. (2023). Gravity-efficient motor control is associated with contraction-dependent intracortical inhibition. *iScience*, *26*(7), 107150. https://doi.org/10.1016/j.isci.2023.107150

Harada, T., Miyai, I., Suzuki, M., & Kubota, K. (2009). Gait capacity affects cortical activation patterns related to speed control in the elderly. *Experimental Brain Research*, *193*(3), 445-454. https://doi.org/10.1007/s00221-008-1643-y

Hawkins, K. A., Fox, E. J., Daly, J. J., Rose, D. K., Christou, E. A., McGuirk, T. E., Otzel, D. M., Butera, K. A., Chatterjee, S. A., & Clark, D. J. (2018). Prefrontal over-activation during walking in people with mobility deficits : Interpretation and functional implications. *Human Movement Science*, *59*, 46-55. https://doi.org/10.1016/j.humov.2018.03.010

Healy, C. M., Berniker, M., & Ahmed, A. A. (2023). Learning vs. minding : How subjective costs can mask motor learning. *PLOS ONE*, *18*(3), e0282693. https://doi.org/10.1371/journal.pone.0282693

Henry, M., & Baudry, S. (2019). Age-related changes in leg proprioception : Implications for postural control. *Journal of Neurophysiology*, *122*(2), 525-538. https://doi.org/10.1152/jn.00067.2019

Heuninckx, S., Wenderoth, N., & Swinnen, S. P. (2008). Systems Neuroplasticity in the Aging Brain : Recruiting Additional Neural Resources for Successful Motor Performance in Elderly Persons. *The Journal of Neuroscience*, *28*(1), 91-99. https://doi.org/10.1523/JNEUROSCI.3300-07.2008

Hoffstaedter, F., Grefkes, C., Roski, C., Caspers, S., Zilles, K., & Eickhoff, S. B. (2015). Age-related decrease of functional connectivity additional to gray matter atrophy in a network for movement initiation. *Brain Structure and Function*, *220*(2), 999-1012. https://doi.org/10.1007/s00429-013-0696-2

Holtzer, R., Mahoney, J. R., Izzetoglu, M., Wang, C., England, S., & Verghese, J. (2015). Online fronto-cortical control of simple and attention-demanding locomotion in humans. *NeuroImage*, *112*, 152-159. https://doi.org/10.1016/j.neuroimage.2015.03.002

Holtzer, R., Verghese, J., Allali, G., Izzetoglu, M., Wang, C., & Mahoney, J. R. (2016). Neurological Gait Abnormalities Moderate the Functional Brain Signature of the Posture First Hypothesis. *Brain Topography*, *29*(2), 334-343. https://doi.org/10.1007/s10548-015-0465-z

Hondzinski, J. M., Soebbing, C. M., French, A. E., & Winges, S. A. (2016). Different damping responses explain vertical endpoint error differences between visual conditions. *Experimental Brain Research*, *234*(6), 1575-1587. https://doi.org/10.1007/s00221-015-4546-8

Hortobagyi, T., Finch, A., Solnik, S., Rider, P., & DeVita, P. (2011). Association Between Muscle Activation and Metabolic Cost of Walking in Young and Old Adults. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *66A*(5), 541-547. https://doi.org/10.1093/gerona/glr008

Hortobagyi, T., Mizelle, C., Beam, S., & DeVita, P. (2003). Old Adults Perform Activities of Daily Living Near Their Maximal Capabilities. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *58*(5), M453-M460. https://doi.org/10.1093/gerona/58.5.M453

Huang, H. J., & Ahmed, A. A. (2014). Older adults learn less, but still reduce metabolic cost, during motor adaptation. *Journal of Neurophysiology*, *111*(1), 135-144. https://doi.org/10.1152/jn.00401.2013

Huang, H. J., Kram, R., & Ahmed, A. A. (2012). Reduction of Metabolic Cost during Motor Learning of Arm Reaching Dynamics. *Journal of Neuroscience*, *32*(6), 2182-2190. https://doi.org/10.1523/JNEUROSCI.4003-11.2012

Huber, M., Knottnerus, J. A., Green, L., Horst, H. V. D., Jadad, A. R., Kromhout, D., Leonard, B., Lorig, K., Loureiro, M. I., Meer, J. W. M. V. D., Schnabel, P., Smith, R., Weel, C. V., & Smid, H. (2011). How should we define health? *BMJ*, *343*(jul26 2), d4163-d4163. https://doi.org/10.1136/bmj.d4163

Jeon, W., Hsiao, H.-Y., & Griffin, L. (2021). Effects of different initial foot positions on kinematics, muscle activation patterns, and postural control during a sit-to-stand in younger and older adults. *Journal of Biomechanics*, *117*, 110251. https://doi.org/10.1016/j.jbiomech.2021.110251

John, E. B., Liu, W., & Gregory, R. W. (2009). Biomechanics of Muscular Effort : Age-Related Changes. *Medicine & Science in Sports & Exercise*, *41*(2), 418-425. https://doi.org/10.1249/MSS.0b013e3181884480

Johnson, R. A., & Wichern, D. W. (1988). *Applied multivariate statistical analysis* (2. ed). Prentice Hall.

Jor'dan, A. J., Poole, V. N., Iloputaife, I., Milberg, W., Manor, B., Esterman, M., & Lipsitz, L. A. (2017). Executive Network Activation is Linked to Walking Speed in Older Adults : Functional MRI and TCD Ultrasound Evidence From the MOBILIZE Boston Study. *The Journals of Gerontology: Series A*, *72*(12), 1669-1675. https://doi.org/10.1093/gerona/glx063

Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., & Poeppel, D. (2017). Neuroscience Needs Behavior : Correcting a Reductionist Bias. *Neuron*, *93*(3), 480-490. https://doi.org/10.1016/j.neuron.2016.12.041

Larivière, S., Xifra-Porxas, A., Kassinopoulos, M., Niso, G., Baillet, S., Mitsis, G. D., & Boudrias, M. (2019). Functional and effective reorganization of the aging brain during unimanual and bimanual hand movements. *Human Brain Mapping*, *40*(10), 3027-3040. https://doi.org/10.1002/hbm.24578

Larsson, L., Degens, H., Li, M., Salviati, L., Lee, Y. I., Thompson, W., Kirkland, J. L., & Sandri, M. (2019). Sarcopenia : Aging-Related Loss of Muscle Mass and Function. *Physiological Reviews*, *99*(1), 427-511. https://doi.org/10.1152/physrev.00061.2017

Le Seac'h, A. B., & McIntyre, J. (2007). Multimodal reference frame for the planning of vertical arms movements. *Neuroscience Letters*, *423*(3), 211-215. https://doi.org/10.1016/j.neulet.2007.07.034

Liu, D., & Todorov, E. (2007). Evidence for the Flexible Sensorimotor Strategies Predicted by Optimal Feedback Control. *The Journal of Neuroscience*, *27*(35), 9354-9368. https://doi.org/10.1523/JNEUROSCI.1110-06.2007

Loibl, M., Beutling, W., Kaza, E., & Lotze, M. (2011). Non-effective increase of fMRI-activation for motor performance in elder individuals. *Behavioural Brain Research*, *223*(2), 280-286. https://doi.org/10.1016/j.bbr.2011.04.040

Manckoundia, P., Mourey, F., Pfitzenmeyer, P., & Papaxanthis, C. (2006). Comparison of motor strategies in sit-to-stand and back-to-sit motions between healthy and Alzheimer's disease elderly subjects. *Neuroscience*, *137*(2), 385-392. https://doi.org/10.1016/j.neuroscience.2005.08.079

Martin, P., Kelly, N., Kahana, B., Kahana, E., Willcox, B. J., Willcox, D. C., & Poon, L. W. (2015). Defining Successful Aging : A Tangible or Elusive Concept? *The Gerontologist*, *55*(1), 14-25. https://doi.org/10.1093/geront/gnu044

Marusic, U., Verghese, J., & Mahoney, J. R. (2018). Cognitive-Based Interventions to Improve Mobility : A Systematic Review and Meta-analysis. *Journal of the American Medical Directors Association*, *19*(6), 484-491.e3. https://doi.org/10.1016/j.jamda.2018.02.002

Mattay, V. S., Fera, F., Tessitore, A., Hariri, A. R., Das, S., Callicott, J. H., & Weinberger, D. R. (2002). Neurophysiological correlates of age-related changes in human motor function. *Neurology*, *58*(4), 630-635. https://doi.org/10.1212/WNL.58.4.630

Millington, P. J., Myklebust, B. M., & Shambes, G. M. (1992). Biomechanical analysis of the sit-to-stand motion in elderly persons. *Archives of Physical Medicine and Rehabilitation*, *73*(7), 609-617.

Mombaur, K., Truong, A., & Laumond, J.-P. (2010). From human to humanoid locomotion—An inverse optimal control approach. *Autonomous Robots*, *28*(3), 369-383. https://doi.org/10.1007/s10514-009-9170-7

Moran, R. J., Symmonds, M., Dolan, R. J., & Friston, K. J. (2014). The Brain Ages Optimally to Model Its Environment : Evidence from Sensory Learning over the Adult Lifespan. *PLoS Computational Biology*, *10*(1), e1003422. https://doi.org/10.1371/journal.pcbi.1003422

Morel, L., Chiang, M. S. R., Higashimori, H., Shoneye, T., Iyer, L. K., Yelick, J., Tai, A., & Yang, Y. (2017). Molecular and Functional Properties of Regional Astrocytes in the Adult Brain. *The Journal of Neuroscience*, *37*(36), 8706-8717. https://doi.org/10.1523/JNEUROSCI.3956-16.2017

Mourey, F., Pozzo, T., Rouhier-Marcer, I., & Didier, J.-P. (1998). A kinematic comparison between elderly and young subjects standing up from and sitting down in a chair. *Age and Ageing*, *27*(2), 137-146. https://doi.org/10.1093/ageing/27.2.137

Ouwehand, C., De Ridder, D. T. D., & Bensing, J. M. (2007). A review of successful aging models : Proposing proactive coping as an important additional strategy. *Clinical Psychology Review*, *27*(8), 873-884. https://doi.org/10.1016/j.cpr.2006.11.003

Paizis, C., Papaxanthis, C., Berret, B., & Pozzo, T. (2008). Reaching beyond arm length in normal aging : Adaptation of hand trajectory and dynamic equilibrium. *Behavioral Neuroscience*, *122*(6), 1361-1370. https://doi.org/10.1037/a0013280

Papaxanthis, C., Pozzo, T., & McIntyre, J. (2005). Kinematic and dynamic processes for the control of pointing movements in humans revealed by short-term exposure to microgravity. *Neuroscience*, *135*(2), 371-383. https://doi.org/10.1016/j.neuroscience.2005.06.063

Papaxanthis, C., Pozzo, T., Vinter, A., & Grishin, A. (1998). The representation of gravitational force during drawing movements of the arm. *Experimental Brain Research*, *120*(2), 233-242. https://doi.org/10.1007/s002210050397

Parthasharathy, M., Mantini, D., & Orban De Xivry, J.-J. (2022). Increased upper-limb sensory attenuation with age. *Journal of Neurophysiology*, *127*(2), 474-492. https://doi.org/10.1152/jn.00558.2020

Pereira, T. D., Shaevitz, J. W., & Murthy, M. (2020). Quantifying behavior to understand the brain. *Nature Neuroscience*, *23*(12), 1537-1549. https://doi.org/10.1038/s41593-020-00734-z

Poirier, G., Mourey, F., Sirandre, C., Papaxanthis, C., & Gaveau, J. (2023). *Speed-dependent optimization of gravity effects for motor control*. https://doi.org/10.1101/2023.03.14.532654

Poirier, G., Ohayon, A., Juranville, A., Mourey, F., & Gaveau, J. (2021). Deterioration, Compensation and Motor Control Processes in Healthy Aging, Mild Cognitive Impairment and Alzheimer's Disease. *Geriatrics*, *6*(1), 33. https://doi.org/10.3390/geriatrics6010033

Poirier, G., Papaxanthis, C., Lebigre, M., Juranville, A., Mathieu, R., Savoye-Laurens, T., Manckoundia, P., Mourey, F., & Gaveau, J. (2024). *Aging decreases the lateralization of gravity-related effort minimization during vertical arm movements*. https://doi.org/10.1101/2021.10.26.465988

Poirier, G., Papaxanthis, C., Mourey, F., & Gaveau, J. (2020). Motor Planning of Vertical Arm Movements in Healthy Older Adults : Does Effort Minimization Persist With Aging? *Frontiers in Aging Neuroscience*, *12*, 37. https://doi.org/10.3389/fnagi.2020.00037

Poirier, G., Papaxanthis, C., Mourey, F., Lebigre, M., & Gaveau, J. (2022). Muscle effort is best minimized by the right-dominant arm in the gravity field. *Journal of Neurophysiology*, jn.00324.2021. https://doi.org/10.1152/jn.00324.2021

Pousson, M., Lepers, R., & Van Hoecke, J. (2001). Changes in isokinetic torque and muscular activity of elbow flexors muscles with age. *Experimental Gerontology*, *36*(10), 1687-1698. https://doi.org/10.1016/S0531-5565(01)00143-7

Quinlan, J. I., Maganaris, C. N., Franchi, M. V., Smith, K., Atherton, P. J., Szewczyk, N. J., Greenhaff, P. L., Phillips, B. E., Blackwell, J. I., Boereboom, C., Williams, J. P., Lund, J., & Narici, M. V. (2018). Muscle and Tendon Contributions to Reduced Rate of Torque Development in Healthy Older Males. *The Journals of Gerontology: Series A*, *73*(4), 539-545. https://doi.org/10.1093/gerona/glx149

Riecker, A., Gröschel, K., Ackermann, H., Steinbrink, C., Witte, O., & Kastrup, A. (2006). Functional significance of age-related differences in motor activation patterns. *NeuroImage*, *32*(3), 1345-1354. https://doi.org/10.1016/j.neuroimage.2006.05.021

Rudnicka, E., Napierała, P., Podfigurna, A., Męczekalski, B., Smolarczyk, R., & Grymowicz, M. (2020). The World Health Organization (WHO) approach to healthy ageing. *Maturitas*, *139*, 6-11. https://doi.org/10.1016/j.maturitas.2020.05.018

Saenen, L., Verheyden, G., & Orban De Xivry, J.-J. (2023). The differential effect of age on upper limb sensory processing, proprioception, and motor function. *Journal of Neurophysiology*, *130*(5), 1183-1193. https://doi.org/10.1152/jn.00364.2022

Saftari, L. N., & Kwon, O.-S. (2018). Ageing vision and falls : A review. *Journal of Physiological Anthropology*, *37*(1), 11. https://doi.org/10.1186/s40101-018-0170-1

Salat, D. H. (2004). Thinning of the Cerebral Cortex in Aging. *Cerebral Cortex*, *14*(7), 721-730. https://doi.org/10.1093/cercor/bhh032

Seidler, R., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., Kwak, Y., & Lipps, D. B. (2010). Motor control and aging : Links to age-related brain structural, functional, and biochemical effects. *Neuroscience & Biobehavioral Reviews*, *34*(5), 721-733. https://doi.org/10.1016/j.neubiorev.2009.10.005

Selinger, J. C., O'Connor, S. M., Wong, J. D., & Donelan, J. M. (2015). Humans Can Continuously Optimize Energetic Cost during Walking. *Current Biology*, *25*(18), 2452-2456. https://doi.org/10.1016/j.cub.2015.08.016

Shadmehr, R., Huang, H. J., & Ahmed, A. A. (2016). A Representation of Effort in Decision-Making and Motor Control. *Current Biology*, *26*(14), 1929-1934. https://doi.org/10.1016/j.cub.2016.05.065

Spedden, M. E., Choi, J. T., Nielsen, J. B., & Geertsen, S. S. (2019). Corticospinal control of normal and visually guided gait in healthy older and younger adults. *Neurobiology of Aging*, *78*, 29-41. https://doi.org/10.1016/j.neurobiolaging.2019.02.005

Stapley, P., Pozzo, T., Cheron, G., & Grishin, A. (1999). Does the coordination between posture and movement during human whole-body reaching ensure center of mass stabilization? *Experimental Brain Research*, *129*(1), 134-146. https://doi.org/10.1007/s002210050944

Strotz, L. C., Saupe, E. E., Kimmig, J., & Lieberman, B. S. (2018). Metabolic rates, climate and macroevolution : A case study using Neogene molluscs. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1885), 20181292. https://doi.org/10.1098/rspb.2018.1292

Summerside, E. M., Courter, R. J., Shadmehr, R., & Ahmed, A. A. (2024). Slowing of Movements in Healthy Aging as a Rational Economic Response to an Elevated Effort Landscape. *The Journal of Neuroscience*, *44*(15), e1596232024. https://doi.org/10.1523/JNEUROSCI.1596-23.2024

Tanis, D., Calalo, J. A., Cashaback, J. G. A., & Kurtzer, I. L. (2023). Accuracy and effort costs together lead to temporal asynchrony of multiple motor commands. *Journal of Neurophysiology*, *129*(1), 1-6. https://doi.org/10.1152/jn.00435.2022

The Lancet. (2009). What is health? The ability to adapt. *The Lancet*, *373*(9666), 781. https://doi.org/10.1016/S0140-6736(09)60456-6

Thomas, E., Ali, F. B., Tolambiya, A., Chambellant, F., & Gaveau, J. (2023). Too much information is no information : How machine learning and feature selection could help in understanding the motor control of pointing. *Frontiers in Big Data*, *6*, 921355. https://doi.org/10.3389/fdata.2023.921355

916 Tolambiya, A., Thomas, E., Chiovetto, E., Berret, B., & Pozzo, T. (2011). An Ensemble Analysis of
917   Electromyographic Activity during Whole Body Pointing with the Use of Support Vector
918   Machines. *PLoS ONE*, *6*(7), e20732. https://doi.org/10.1371/journal.pone.0020732
919 Tresch, M. C., Saltiel, P., & Bizzi, E. (1999). The construction of movement by the spinal cord. *Nature*
920   *Neuroscience*, *2*(2), 162-167. https://doi.org/10.1038/5721
921 Urai, A. E., Doiron, B., Leifer, A. M., & Churchland, A. K. (2022). Large-scale neural recordings call
922   for new insights to link brain and behavior. *Nature Neuroscience*, *25*(1), 11-19.
923   https://doi.org/10.1038/s41593-021-00980-9
924 Van Voorhies, W. A., & Ward, S. (1999). Genetic and environmental conditions that increase longevity
925   in *Caenorhabditis elegans* decrease metabolic rate. *Proceedings of the National Academy of*
926   *Sciences*, *96*(20), 11399-11403. https://doi.org/10.1073/pnas.96.20.11399
927 Vernazza-Martin, S., Tricon, V., Martin, N., Mesure, S., Azulay, J. P., & Le Pellec-Muller, A. (2008).
928   Effect of aging on the coordination between equilibrium and movement : What changes?
929   *Experimental Brain Research*, *187*(2), 255-265. https://doi.org/10.1007/s00221-008-1301-4
930 Vu, V. H., Isableu, B., & Berret, B. (2016). On the nature of motor planning variables during arm
931   pointing movement : Compositeness and speed dependence. *Neuroscience*, *328*, 127-146.
932   https://doi.org/10.1016/j.neuroscience.2016.04.027
933 Ward, N. S. (2006). Compensatory mechanisms in the aging motor system. *Ageing Research Reviews*,
934   *5*(3), 239-254. https://doi.org/10.1016/j.arr.2006.04.003
935 Ward, N. S., Swayne, O. B. C., & Newton, J. M. (2008). Age-dependent changes in the neural correlates
936   of force modulation : An fMRI study. *Neurobiology of Aging*, *29*(9), 1434-1446.
937   https://doi.org/10.1016/j.neurobiolaging.2007.04.017
938 White, O., Gaveau, J., Bringoux, L., & Crevecoeur, F. (2020). The gravitational imprint on
939   sensorimotor planning and control. *Journal of Neurophysiology*, *124*(1), 4-19.
940   https://doi.org/10.1152/jn.00381.2019
941 Wickramarachchi, B., Torabi, M. R., & Perera, B. (2023). Effects of Physical Activity on Physical
942   Fitness and Functional Ability in Older Adults. *Gerontology & Geriatric Medicine*, *9*,
943   23337214231158476. https://doi.org/10.1177/23337214231158476
944 Winter, D. (2009). *Biomechanics and Motor Control of Human Movement*. John Wiley & Sons, Inc.
945   https://doi.org/10.1002/9780470549148
946 Wolpe, N., Ingram, J. N., Tsvetanov, K. A., Kievit, R. A., Henson, R. N., Wolpert, D. M., Cam-CAN,
947   Brayne, C., Bullmore, E., Calder, A., Cusack, R., Dalgleish, T., Duncan, J., Matthews, F. E.,
948   Marslen-Wilson, W., Shafto, M. A., Campbell, K., Cheung, T., Davis, S., … Rowe, J. B.
949   (2016). Ageing increases reliance on sensorimotor prediction through structural and functional
950   differences in frontostriatal circuits. *Nature Communications*, *7*(1), 13034.
951   https://doi.org/10.1038/ncomms13034
952 Yamamoto, S., & Kushiro, K. (2014a). Direction-dependent differences in temporal kinematics for
953   vertical prehension movements. *Experimental Brain Research*, *232*(2), 703-711.
954   https://doi.org/10.1007/s00221-013-3783-y
955 Yamamoto, S., & Kushiro, K. (2014b). Direction-dependent differences in temporal kinematics for
956   vertical prehension movements. *Experimental Brain Research*, *232*(2), 703-711.
957   https://doi.org/10.1007/s00221-013-3783-y
958 Zalewski, C. (2015). Aging of the Human Vestibular System. *Seminars in Hearing*, *36*(03), 175-196.
959   https://doi.org/10.1055/s-0035-1555120
960 Zhang, W., & Radhakrishnan, K. (2018). Evidence on selection, optimization, and compensation
961   strategies to optimize aging with multiple chronic conditions : A literature review. *Geriatric*
962   *Nursing*, *39*(5), 534-542. https://doi.org/10.1016/j.gerinurse.2018.02.013
963 Zhao, E., Tranovich, M. J., & Wright, V. J. (2014). The role of mobility as a protective factor of
964   cognitive functioning in aging adults : A review. *Sports Health*, *6*(1), 63-69.
965   https://doi.org/10.1177/1941738113477832
966