

Dear recommender,
Dear reviewers,

We extend our heartfelt gratitude to the recommender and reviewers for their meticulous assessment and valuable feedback, which significantly contributed to improving this manuscript. We thank you all for your time, effort, and expertise invested in evaluating our research.

Below, please find *the reviewers' comments* in *black and italic* and **our answers** in **blue**. In the manuscript, we highlighted the modifications using **red fonts**.

MATTHIEU BOISGONTIER

Dear Authors,

Thank you for submitting your work to PCI Health & Movement Sciences. I would like to begin this decision letter by commending your commitment to good research practices, including open data and open code.

Thank you for your positive comment. We strongly believe that this type of initiative should take on greater importance and be in the researchers and public interest.

*The primary objective of your study is to assess the effect of age on movement efficiency in one upper limb task and three whole-body tasks. Movement efficiency was assessed using an index based on the activity of antigravity muscles. The results suggest that this effect of age is dependent on the type of movement. I find the study interesting because it assesses movement efficiency in two types of tasks that are often studied independently in the literature, providing an opportunity to test the generalizability of the effect of age on movement efficiency. However, a number of concerns were raised by three experts in the field of your study and one expert in machine learning. Their comments appear below and mainly relate to **readability**, the clarity of the hypotheses and key concepts, the thoroughness of the EMG analysis, and the **use of machine learning** and ANCOVA analyses on the same dataset. I share these concerns of the reviewers.*

*Regarding the latter concern, it is my understanding that the authors used the same dataset for both the selection of variables and the subsequent analysis of the differences in those variables, which could potentially have biased the results. Using the same dataset that was used to select the variables that differentiate between younger and older adults' strategies introduces the risk of overfitting the model to the dataset. A consequence of this overfitting is the possibility that the results will not be replicable in future studies. One of the options that might address this concern would be to remove the machine learning approach and to focus on **all** the antigravity muscles in the analyses (e.g., adding the T7 erector spinae and the posterior deltoid), as it makes sense from a theoretical standpoint. If the authors decide to keep the machine learning analysis, it should at least be described in more detail, the table of the results should not be in supplemental material, and the limitations should be acknowledged, as suggested by the fourth reviewer.*

We thank the recommender for pointing out this important concern. It seems that we did not properly explain our rationale.

We employed a theory-driven analysis that built upon previous results and required focusing on the activation patterns of antigravity muscles (Gaveau et al. 2021; Poirier et al. 2022; Thomas et al. 2023; Chambellant et al. 2024). Antigravity muscles are muscles that pull against the gravity vector, as defined by their position and orientation in the musculo-skeletal system. In the studied tasks, the antigravity muscles are: i) the Anterior Deltoid (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 D7 (ESD7), extending the rachis; v) the Soleus (SOL), flexing the ankle in the plantar direction. Because the Erector Spinae D7 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 does not seem appropriate to test whether the nervous system takes advantage of gravity to produce the movement. We focused on DA during arm movements and on VL and ESL1 during

movements of the entire body. We added a few lines in the manuscript to clarify this aspect (please see lines 267-280).

Here we are interested in comparing arm movement and whole-body movement control because the scientific literature has reported that whole-body movement control changes with age, while arm movement control does not (Paizis et al. 2008; Vernazza-Martin et al. 2008; Casteran et al. 2018; Poirier et al. 2020, 2023). An issue with focusing on a restrictive number of muscles is that we may probe 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 movements control. To achieve this, we employed machine learning to perform a control analysis. This analysis enabled us to quantify how much each muscle activation was altered by age, thereby ensuring that we were focusing on muscles that discriminated movement control between younger and older adults. We clarified this aspect in the new manuscript by adding a few lines (please see lines 298-326)

As regards data overfitting, we believe that there is no such issue in the present study. This is for two reasons. First, we did not use the machine learning approach to test our specific hypotheses or to choose the muscles of interest. We only used machine learning to verify that the main analyses we performed in the study, on phasic EMG negativity, were meaningful. A factual demonstration of this is that we did not include the arm movement data in the machine learning analysis. We only included the whole-body movement data, hence verifying that the muscles we picked up – based on our a-priori theory driven approach – were conveying information about the already known effect of age on whole-body movement control (from kinematic studies; Paizis et al. 2008; Vernazza-Martin et al. 2008; Casteran et al. 2018). Second, we employed a cross-validation procedure that ensured that the machine learning classification was tested on data that were unknown to the trained algorithm (please see the dedicated answer to the specific comment of Reviewer number 4).

In my own reading, the introduction and discussion put a lot of emphasis on the concept of compensation. However, I wonder whether the study is really about compensation, since it does not examine the relationship between the effect of age on movement efficiency and any age-related processes that this effect might compensate for. To me, the study is about the effect of age on movement efficiency. The variables collected in the study do not allow for the investigation of a possible compensatory effect. Following on from this comment, I think there are several cases of overstatement where the conclusions are not based on the data and should rather be presented as potential explanations or interpretations of the results that require further research to be confirmed or rejected. I think it is essential for science to avoid drawing conclusions that are not supported by evidence. Such invalid conclusions cascade through the literature, because, unfortunately, articles are most often cited for the conclusions drawn by the authors, not for the evidence supported by the data.

We thank the recommender for this comment. We agree with these constructive criticisms. Please see detailed responses in the “specific comments” section.

In the main results, the authors pooled the data from the three whole-body tasks. I think that an analysis testing the 4 tasks x 2 age groups interaction would be important: the absence of a significant interaction

in each of the 3 whole-body tasks would further support the main results, whereas a significant interaction in one of the whole-body tasks would mitigate them. In any case, this analysis would provide useful information to the reader.

We thank the recommender for this insightful request. We have now added this analysis to the results section. The analysis reveals that the age effect is similar across the different whole-body tasks. Please see page lines (397-400).

In addition to these general comments, I would like to provide specific comments that may improve the quality of the manuscript, should the authors succeed in addressing the major concerns raised at this stage of the evaluation process.

*Best regards,
Matthieu Boisgontier*

Specific Comments:

*- Line 137: Please provide the rationale for the **sample size** used in this study (e.g., Lakens, 2022).*

We had no a-priori robust data to calculate the ideal sample size. We therefore included as many participants as possible over a fixed recruitment period (given the timeline of the PhD thesis of the first author). We added this information to the manuscript. Please see lines (111-112).

- Line 143 (experimental tasks): Could the authors clarify why they chose to use a single task for upper-limb movements and 3 tasks for whole-body movements? If this study and sample population were used for another article, please mention this in the manuscript.

We appreciate the point of the reviewer. Our group and others have extensively studied how arm movements are adapted to gravity environment. Over a variety of arm movement tasks including single or multi-degree of freedom pointing movements, drawing movements, reach to grasp movements, or arm movements that transport a hand-grasped object (Papaxanthis et al., 1998, 2005; Leseac'h and McIntyre 2007; Berret et al. 2008; Crevecoeur et al. 2009; Gaveau et al. 2011; Gaveau and Papaxanthis 2011; Yamoto and Kushiro 2013), the results consensually support an optimization principle that shapes arm motor patterns to take advantage of gravity effects in order to discount muscle effort. Thus, to make the protocol doable in a single session with each participant, we only included one arm task in the present experiment. We added a few lines to clarify this aspect in the Methods section (lines 123-127). One may wonder whether the present conclusions would hold for more complex arm movements. Using multi-degree of freedom arm movements to study motor adaptation to an externally imposed force-field, other studies also reported results showing that, alike younger adults, older adults maintain the ability to produce movements that are energetically efficient (Huang et Ahmed 2014; Healy et al. 2023; Summerside et al. 2024). The present mono-articular results therefore likely generalize to other types of arm movements. Future work may test whether the present conclusions extend to more complex and functional arm movements. To clarify this aspect, we added a few lines in the new version of the manuscript (please see lines 550-564).

The three whole-body tasks were selected because they include an equilibrium constraint, they represent movements of daily life, and they have been investigated in previous studies

(Millington et al. 1992; Mourey et al. 1998; Manckoundia et al. 2006; Paizis et al. 2008; Casteran et al. 2018; Jeon et al. 2021). We clarified this aspect lines (123-127, 147-148).

- Line 146 (Figure 1A): Perhaps put the down arrow under the arm of the avatar that is on the left of the picture.

Indeed, it makes more sense, we updated the figure.

- Line 157: I would rather call it as shoulder flexion/extension. Shoulder elevation is when the shoulder moves toward the ear (involving contraction of the upper trapezius muscle).

See line 145: Indeed, it makes more sense, we modified as suggested.

- Line 158: The STS/BTS movement is not described.

See lines 150-151: we improved the description.

- Line 168: "her or his" can be replaced by "their".

See line 159: We have taken this comment into account.

- Line 187-193 (Kinematics): Please remove the capital letter in "Clavicle"; "sternum" - where exactly on the sternum?; "backs of the head" - on which bone structure?; "on the scapula" - where exactly on the scapula?; "shoulders (acromion)" - acromion is still the scapula; "forearms (lower lateral 1/3 left, 2/3 right)" - on which bone (ulna or radius)?; "fingers (second metacarp)" - metacarpals (not metacarps) are not part of fingers; "knees (flexion/extension axis)" - on the medial or lateral side of the knee?; "thighs (upper lateral 1/3 left, 2/3 right)" - please clarify, is the position different for the right and left thigh?; "calves (upper lateral 1/3 left, 2/3 right)" - please clarify.

See lines 178-189: The description indeed lacked important details. We improved it.

- Line 199: « vastus lateralis (VL) biceps femoris (BF)»: please add a comma.

We have taken this comment into account.

- Line 200: T7 (for thoracic) instead of D7 (old nomenclature)

We have taken this comment into account throughout the paper.

- Line 200: "anterior tibialis (TA)" should read "tibialis anterior (TA)"

We have taken this comment into account throughout the paper.

- Lines 236-248: "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." On what basis were these decisions made? Why not 2SD? Why not 35 ms? Please clarify.

See 283-284: We thank the recommender for his insightful question. We clarified this aspect: "This duration has been chosen after preliminary tests to avoid detecting false-positive. We kept it constant for all analyses."

- Line 251: Please clarify how the negativity index is to be interpreted. Do higher values indicate better efficiency?

See lines 288-289: Indeed, this part needed clarification: “This value is always negative or null. The lower the value, the greater the efficiency.”

- Lines 250-252: “[...] negativity index, defined as $T \times NA / TA$, 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”. Since the negativity index is central to this study, please illustrate T, NA, and TA in a figure to provide the reader with a visual explanation of what variables are included in this index.

We agree with the reviewer that the figure should be improved. We updated the figure to help the understanding.

- Line 261 (Statistics): Please clarify which tests were conducted and which variables (and covariates) were included.

See lines 329-343: We are grateful for this comment. This was indeed poorly described, please see the updated statistics section.

- Line 264 (Machine learning): Since the machine learning results appear to inform the ANCOVAs conducted, should this section not be placed before the “Statistics” section. Also, is machine learning not also a statistical analysis?

See lines 299-326: as explained in one of the above comments, the machine learning did not inform the conducted ANCOVAs. It only confirmed that our theory-driven choice of muscles was meaningful. We changed the section title to better discriminate Machine learning from the more classical inferential univariate statistics.

- Line 284: “Movement duration [...] was slightly reduced in older compared to younger participants”. Was movement duration shorter in older adults? How do the authors define “slightly”?

See lines 346-347: That’s indeed a mistake, the younger participants were faster. Slightly is now quantified: “overall older adults were 3.5% slower”.

- Line 318: Perhaps visually indicate what is green and what is blue, as in the other figures using this color code?

We thank you for this comment, we updated the figure.

- Line 319: Please also test the Age x Task interaction without combining the 3 whole-body tasks, similar to what is done in the exploratory analyses.

See lines 397-400: We added this analyze and the figure 7 is now composed of two graphs including an illustration of this analysis.

- Lines 304-312: This part might be better suited for the Methods section.

Indeed, we updated the description of the results.

- Line 314: Please include Supplementary Figure 1 in the manuscript. Please further describe the results of this table in the text.

See lines 366-376: We added the figure from the supplemental which is now figure 6 in the manuscript. We add a description of these results.

- Lines 349-350: *This information should be mentioned in the Methods section.*

See lines 427-428: It is also mentioned in detail in the methods. We believe that this short sentence helps the readability of the paper.

- Line 321: *I know it's already mentioned above, but please clarify again that the muscles that were used to compute this average muscle pattern were those selected according to the machine learning analysis.*

See 379-380: We clarified this point: *“(vastus lateralis and erector spinae in L1 were averaged for whole-body tasks and deltoid anterior was used for arm tasks)”*

- Lines 316-318: *“in the following we focus the analysis on antigravity muscles. Those muscles are the Anterior Deltoid for the arm task and the Vastus lateralis and Erector Spinae at L1 level for the tasks involving movements of the entire body (STS/BTS and WBR).” Why not the T7 erector spinae and the posterior deltoid, which also have an antigravity action?*

T7 erector spinae plays a much less antigravity role, being located higher up the spine. As its main role is to open the thoracic cage, we didn't feel it was relevant to include it in the analysis. For both groups, we observe very little negativity, and not systematically, on this muscle. For the arm pointing task, the posterior deltoid acts with gravity. It does not have an antigravity role. It did not seem appropriate to include it.

- Line 365: *“The results revealed an age-related alteration of muscle commands that differ between tasks.” Since there is no evidence of a change in the whole-body task, it might be more accurate to write that the alteration is dependent on the type of task.*

See line 442: Indeed, we have taken this comment into account.

- Lines 366-367: *“we found that a muscle marker of effort minimization was reduced during whole-body movements but not during arm movements”. The results showed no evidence that effort minimization was reduced during arm movement, not that it was absent. “Absence of evidence is not evidence of absence” (Alderson, 2004).*

See 443-444: We modified the sentence as suggested.

- Lines 372-373: *“The present results reveal that effort-minimization was downregulated in older adults compared to younger adults”. I suggest the authors clarify that this statement reflects their interpretation rather than facts. The pooled data from whole-body movement suggests that there is no such age-related downregulation.*

We are not sure that we correctly understand what the recommender means with the following sentence: *“The pooled data from whole-body movement suggests that there is no such age-related downregulation”*. As requested by the reviewer in a previous comment, we added an analysis of variance to test whether there existed an age difference between the three tasks involving movements of the entire body (The ANCOVA Age x Whole-Body-Tasks). This analysis clearly does not reveal such a difference. Given the significant interaction effect obtained with the Age x Task-Type ANCOVA (along with the confidence intervals comparing age groups for each type of Task), we believe our results reveal a downregulation of effort-minimization during whole body movements in older compared to younger adults.

- Lines 373-374: *“Overall, the present results suggest a compensation process that modulates planning strategies to maximize equilibrium in older adults.” How can the results suggest this when there was no assessment of balance in the study? To me, this conclusion is not supported by the results of the study.*

We agree with the recommender, please see comment below for a combined response.

- Line 432-434: *“In conclusion, probing a specific motor control process, the present study provides a set of behavioral results that support the interpretation of a compensatory process that counterbalances other deteriorated processes in older adults.” How can the study support the fact that the results of the study support a compensatory process that counterbalances other deteriorated processes in older adults, when the deteriorated processes were not assessed, and their relationship to the Negativity Index not tested? The results suggest that the effect of age on movement efficiency is moderated by movement type. Whether this moderation reflects a compensatory mechanism requires further research.*

We may have gone a little too far in our interpretations. We thank you again for pointing this out.

Focusing on the EMG analysis, our rationale was that the age effect on whole body movements could not be a deterioration since the older group is able to create efficient patterns when pointing with their arm. If this is not deterioration, what else could it be but compensation. We nonetheless agree that quantifying the possible beneficial effect of this supposed compensation would be a lot more convincing.

We have now calculated some simple criteria that are related to balance. These are the center-of-mass displacement and the peak center-of-mass velocity. We focused on the downward movements, as these are the ones that present the greatest negativity and the greatest challenge to balance. We tested the correlations between these different kinematic parameters and our EMG criterion. All parameters were negatively correlated to the EMG index, showing that reducing movement efficiency was associated with center-of-mass movements that were less risky (less ample and slower). Please see methods lines (213-228) and results lines (408-425).

References:

- Alderson P. *Absence of evidence is not evidence of absence. BMJ. 2004;328(7438):476-477.*
- Lakens D. *Sample size justification. Collabra: Psychology. 2022;8(1):33267.*

Reviewer #1: PIERRE MOREL

This manuscript provides a valuable contribution by addressing the discrepancies found in prior research regarding movement efficiency in younger versus older adults. Previous studies on arm movements find that efficient control of movements is maintained in older adults, while studies on whole-body movements show degradations. However these results came from different studies, using different samples and different tasks and measurements.

The strength of the current study is to compare both types of movements within the same sample of young and older adults and using the same type of measurement and analysis. For this, the authors adapted to whole-body movements a measure of the optimization of movements against gravity using phasic EMG, previously used for arm movements. The study confirms the earlier observed differences between the control of arm-only movements and whole body movements in older adults.

I however have three main concerns with the manuscript. First, since it is so central to the argument, the manuscript would benefit from a more detailed exploration of the adaptation of phasic EMG analysis to whole-body movements, taking into account potential limitations and confounds that could enrich the discussion (see point 9 below). Second, further clarification on the selection of muscles for analysis and the use of the machine learning approach is crucial to strengthen the rigor of the study (see point 10 below). Last, streamlining certain sections could improve readability and argument flow. I will provide more detailed comments and questions below, which I hope will be helpful.

[We sincerely thank the reviewer for his positive assessment of our work.](#)

Abstract / Introduction

1. The abstract could be revised for clarity and conciseness. Specifically, it should more clearly define what is meant by "behavioral compensation" and articulate the relationship between compensation and energy efficiency in the gravitational environment

[We thank the reviewer for pointing this out. We reformulated the abstract accordingly. Please see Abstract. To better convey the study rational, we also updated the title.](#)

2. The hypothesis presented in the abstract and introduction —that age-related compensatory processes may correspond to an adaptation process altering movement strategy— lacks clear differentiation among the terms "compensatory processes" "adaptation processes" and "changes in movement strategy". This ambiguity makes it challenging to conceive an alternative hypothesis.

[Given the following comment, we have largely shortened the introduction. We believe this helps reducing the ambiguity, presenting a clearer message. Our view is that “compensatory processes”, “adaptation processes” and “change in movement strategy” are equivalent. They are used separately in different literatures \(gerontology, motor control...\) but are in fact closely related. In the Introduction we hope that we clearly convey this message when writing:](#)

[- “this decreased efficiency reflects an age-related compensation that changes movement strategy \(i.e. an age-related motor adaptation process\)”, \(lines 96-98\)](#)

[and](#)

- “Here we test the hypothesis that age-related alterations in movement efficiency correspond to an adaptation process, i.e. a change in movement strategy that compensates for other deteriorated sensorimotor components”, lines (103-105).

3. The introduction's first two paragraphs makes a good point in explaining what compensation is, why it is important to study it and why it is difficult. However the rest of the intro could be refined, notably to present more clearly the literature on movement efficiency. In addition to point 2 above: The paragraph on neural mechanisms (L.72-86) could be more concise if its only point is to show that previous studies used broad measures as written L. 90.

We thank the reviewer for this comment. We agree that the introduction was too long. We shortened it (please see Introduction).

L. 95 "There is no denying": informal

We erased this informal wording.

The sentence L.108-110 makes the point that previously cited studies did not really study compensations and hints that studies cited in the following paragraph do. This could be better explained and demonstrated in both paragraphs.

In line with previous comments and responses, we've removed this paragraph because it made the introduction unnecessarily cumbersome.

The paragraph L.111-134 could benefit from a more coherent structuring to clearly present conflicts in the literature and show how the current study aims to resolve them.

We thank the reviewer for his insightful comment. We worked on the structure of this paragraph. Please see lines (86-108).

Methods

4. The Methods section would benefit from additional detail to address the following points:

The description of target placement (L. 154) should specify if it is only in front of the right shoulder, as only the right arm is used

See line 141: We corrected the text that erroneously mentioned the left shoulder. We thank the reviewer for spotting this mistake.

The spacing of targets (L. 166) needs clarification on whether two targets are used and if subjects reach with both hands.

We tried to make this aspect more explicit. Please see line 157.

The methods did not specify which motion-tracking markers are used for movement segmentation for each type of movement

We added this information. Please see lines (207-208).

L. 220: "signals were integrated...". More precisions could be added: do the authors refer to sliding-window averaging, RMS ? How does it compare/mesh with the envelope generation using low-pass filtering mentioned L. 228 ?

See line 247: We added precisions regarding the analysis of the EMG signals.

This integrated signal was then smoothed using the second low-pass filtering. The envelope is thus perfectly synchronized with the integrated signal. We made this more explicit line 430-431.

L. 227-239: All steps seem to require resampled EMG, but details are missing (resampling of slow movements, how the additional delays mentioned L221-221 are taken in account for the resampling)

See lines (259-260): We added the information.

L. 239: should "from the EMG trace of each fast movement" be "from the EMG trace of each pair of fast movements" since averages are made in pairs ?

See line 265: We corrected accordingly.

L. 264 The stated goal of the machine learning approach as described in the methods section is not as clear as in the results sections.

See line (298-326): Indeed, the machine learning approach was not properly introduced. Other reviewers also pointed this out. We improved this part of the manuscript. Please see the changes.

5. The figure 2 shows a marked decrease of the shoulder vertical position before the onset of the upward movement and after the offset of the downward movement. This raises several questions: What causes it ? Is it the subject bending forward before sitting up ?

Yes, this corresponds to participants bending forward before rising.

Why were onset/offset point definitions chosen so that these were ignored ?

This is because the present study focuses on how the motor systems interacts with gravity torque to produce movements that are prone to imbalance. During this first phase of a seat to stand movement, imbalance is weak (the participant is still seating) and gravity torque (projected in the plane of motion) is weak too because the orientation of the trunk is very close to vertical. Thus, we removed this part of the motion to focus our analyses on the part where imbalance and gravity torque effects are maximal. This choice also makes the synchronization between slow and fast movements less error-prone.

6. In figure 3 There are identifiable bumps in the fast EMG signals visible in panel A that are not visible in panel C, notably a period at around 2/3 of the movement where there is a high variability between fast traces that is not present on the phasic traces. What causes this discrepancy ? Moreover it could be useful for comprehension to represent extracted / computed values (NA, TA, etc) in figure 3.

We agree that the figure could help understand the meaning of the computed parameter. We modified the figure accordingly. Regarding the bumps that you can observe on the panel A and that do not appear on panel C, this is because integrated EMG signals from fast movements are averaged two by two. There are 12 EMG curves in panel A and 6 in panel C.

Results

7. The results section should specify that Figure 4 and lines 284-289 pertain to the fast movements only, if that is the case.

We modified the figure caption and text accordingly.

8. The authors indicate that movement duration was used as a covariate in further analyses. The manuscript would benefit from an explanation of how this was done what were the outcomes of this.

See line (228-3443): We have now slightly modified the statistics section in the methods to make this more explicit. ANCOVA compare the means of one (dependent) variable in several groups while taking into account the variability of other continuous variables (COVARIATES). ANCOVA checks for differences in 'adjusted' means (i.e. adjusted for the effects of the covariate). In our case the covariate is movement duration. The ANCOVA controls the analysis for a possible biasing effect of movement duration on Phasic EMG negativity.

9. The fact that negativities reflect the exploitation of gravity to reduce muscle efforts in arm movements is sound and well established in itself, but the jump from this to the comparison of two populations and whole body and multi-joint movements seems quite steep and doesn't explore limits and confounds. Here are a few points:

The analysis of EMG alone seems limiting, as a difference in EMG would not be interpreted in the same way when it is accompanied by a difference in kinematics or when kinematics are the same. For example in Figure 5 for ESL1 and VL in WBR downward movements some differences in the EMG phasic traces appear to be due to timing differences rather than amplitude differences. Could those be due to different timings in the movements of different segments of the body between the groups ? How would the interpretation change if this was the case ?

Relating EMG activation to limb kinematics is complex and may be the specific topic of an entirely dedicated study. We nonetheless understand the concern of the reviewer. As noted by the reviewer, muscle activations may be tuned in amplitude and duration. Seminal studies on pulse height and pulse width strategies have long demonstrated it (Gottlieb, Corcos and Agarwal 1989; Berardelli et al. 1996). In previous work on the negativity of phasic EMGs, we have reported that the temporal dimensions showed more tuning than the amplitude one (Gaveau et al. 2021; Poirier et al. 2022, 2023). This may be simply because maximal deactivation of antigravity muscles is easily achieved, whilst the precise temporal organization of the pattern is more challenging. The present results corroborate previous ones.

We have now added a supplemental analysis of center-of-mass kinematics and tested for possible links with our main EMG results. This new set of results demonstrate that the main result of the study, on phasic EMGS, is linked to differences on movement kinematics. Please see methods lines (213-228) and results lines (408-425). We believe that these results overcome the limit that the reviewer rightfully raised. We thank the reviewer for his insightful comment.

The above comment is also linked to the observation #5 about figure 2. If this is indeed the subject bending forward, could there be differences between the groups on this ?

For the reason provided above (comment #5), we did not test whether age-differences existed in the bending phase. However, whether there exists difference or not, we do not think that this would change the present conclusions.

I imagine that the way gravity acts on movements would depend on the build of the person and the way muscle and fat mass are distributed in the body and limbs. The two groups could notably differ in that respect, which could be discussed.

We generally agree with the reviewer that one should be careful when interpreting her/his results and that one should mention the limits that may affect her/his conclusions. We agree that body composition and other peripheral properties may impact EMG measures. However, because our main result is the interaction effect between Age and Task-Types, we believe our conclusion is likely independent of those factors. The age effect on body composition is likely similar across body parts. We therefore believe that adding a discussion part on this aspect would be very speculative. We prefer not to add it, but we remain open to further discussion with the reviewer if he feels there is more to say.

Negativity indices for different tasks are compared in the same statistical model. It is not immediately clear whether the normalisation process is sufficient to compare directly an index computed from two muscles in a multi-joint complex movement to an index computed from a single muscle in a single-joint simple movement.

We understand the reviewer's comment. We however do not see what specific argument would support the idea that our comparison is biased in some way. More specifically, we do not see how this concern would affect the comparisons between age-groups. We remain open to further discussion with the reviewer if he feels there is more to say.

10. L.304-318: The machine learning approach is explained more clearly here. Its goal is to confirm that that the antigravity muscles are the ones that allow the best discrimination between groups, reflecting the differences in motor strategies between groups. I find the argument and the data not convincing here, and the results raise a concern of bias in the selection of muscles:

Some non-antigravity muscles in whole body tasks, such as DP, show classification performances that are not far off the performance of the chosen muscles (VL and ESL1)

Some known antigravity muscles such as the soleus muscle yield comparatively poor scores here and are not selected for the main analysis. Was the machine learning approach then used for selection and not just for confirmation ? This raises a concern of potential "double dipping" if that was the case.

We thank the reviewer for his comment. Other reviewers also raised related concerns. The previous manuscript was clearly not clear enough on this aspect.

In the present work, we employed a theory-driven analysis that builds upon previous results and required focusing on the activation patterns of antigravity muscles (Gaveau et al. 2021; Poirier et al. 2022; Thomas et al. 2023; Chambellant et al. 2024). Antigravity muscles are muscles that pull against the gravity vector, as defined by their position and orientation in the musculo-skeletal system. In the studied tasks, the antigravity muscles are: i) the Anterior Deltoid (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 D7 (ESD7), extending the rachis; v) the Soleus (SOL), flexing the ankle in the plantar direction. Because the Erector Spinae D7 and the Soleus muscles did not play a strong focal role but a rather postural one in the present tasks, investigating, we focused our analyses on the remaining three muscles (DA, VL and ESL1). Probing the activation of a postural muscle does not seem appropriate to test whether the nervous system takes advantage of gravity to produce the movement. We focused on DA during arm

movements and on VL and ESL1 during movement of the entire body. We added a few lines in the manuscript to clarify this aspect (please see lines 267-280).

Moreover, here we are interested in comparing arm movement and whole-body movement control because the scientific literature has reported that whole-body movements control changes with age, while arm movement control does not (Paizis et al. 2008; Vernazza-Martin et al. 2008; Casteran et al. 2018; Poirier et al. 2020, 2023). An issue with focusing on a restrictive number of muscles is that we may probe 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 movements control. To this aim, we employed machine learning to perform a control analysis. This analysis enabled us to quantify how much each muscle activation was altered by age, thereby ensuring that we were focusing on muscles that discriminated movement control between younger and older adults. To summarize, the point of the machine learning analysis was not to say that we picked the muscles that best discriminate between age groups but muscles – selected based on our theory-driven hypothesis – that contained information to discriminate between age-groups. We clarified this aspect in the new manuscript by adding a few lines (please see lines 298-326)

*11. The reporting of statistical results seems incomplete. Additionally to my comment #8:
L. 320-335: Main effects of age and tasks are not reported*

See Supplemental Table 3: We did not report these effects to focus on those that specifically allow testing our hypotheses. For the sake of transparency, we now report the other effects in a dedicated table.

L. 349-360: Here the mentioned models include task direction as a covariate. Was this explored in the main analysis ?

See line (427-437) and Supplemental Table 3: Our presentation of the result was not clear enough. The direction was not used as a covariate but as a factor. We focus our analysis on the age effect and therefore we did not explore the direction effect in the main analysis (because it did not relate to our age hypothesis). We improved this section and the statistical model simplified.

12. Fig 7 is not referred to in the text. It also does not present data from the arm task. The legend mentions different panels for data from the ESL1 and VL but this does not appear in the figure.

See line 429: We thank the reviewer for pointing this out. We now refer to fig 7 (which became fig 9) in the main text. The goal of this analysis was to provide descriptive details about these newly investigated tasks (whole-body tasks), as the arm tasks have already been more deeply described. The figure has also been updated. As mentioned in the figure caption, this is the mean result of ESL1 and VL that is presented in this figure.

Discussion

13. L. 373-374: The authors mention that results suggest that the planning strategies maximise balance but this was not shown in the results L. 344

We may have gone a little too far in our interpretations. We thank you again for pointing this out. Focusing on the EMG analysis, our rationale was that the age effect on whole body movements could not be a deterioration, since the older group is able to create efficient patterns when pointing with their arm. If this is not a deterioration, what else could it be but a compensation. We nonetheless agree that quantifying the possible beneficial effect of this supposed compensation would be a lot more convincing.

We have now calculated some simple criteria that are related to balance. These are the center-of-mass displacement and the peak center-of-mass velocity. We focused on the downward movements (as these are the ones that present the greatest negativity and the greatest challenge to balance). We tested the correlations between these different kinematics parameters and our EMG criterion. All parameters were negatively correlated to the EMG index, showing that reducing movement efficiency was associated with center-of-mass movements that were less risky (less ample and slower). Please see methods lines (213-228) and results lines (408-425).

14. The similarity between paragraph L. 393-404 and the previous paragraph (same citations) should be addressed to avoid redundancy.

We thank the reviewer for his comment. We do not agree that those paragraphs are redundant. The first paragraph discusses results on arm movements efficiency whilst the second one discuss the expansion of knowledge to whole-body movements.

15. L. 426: About the non-reproduction of previous results, the authors mention that the EMG-based analysis of the current paper might yield different results from the kinematic analysis from the previous study. Since motion was recorded here, the same analyses could be repeated to check this. This is linked to my comment #9.

We understand the reviewer's concern. We should not speculate that much in a scientific paper and therefore chose to remove this sentence from the discussion.

This is not because we do not want to perform those analyses. We performed them and obtained qualitatively similar results but the distance effect (See supplementary figure 1). Those results correlate with our EMG results. For the following reasons, we believe that adding those results to the present manuscript would not improve it. 1. The metrics that were used in this previous study (Casteran et al. 2018) are hardly interpretable in term of balance control. To interpret them, one needs an optimal control model. This is an important new work that would make the paper even heavier than it already is. The simple kinematic parameters that we added in the new manuscript (about the center-of-mass movements) are a lot more straightforward to interpret. 2. The study of Casteran et al. (2018) only included 10 younger and 9 older adults. It then drew its conclusion about the effect of movement distance based on the difference between a significant (older adults) and a non-significant result (younger adults) whilst it is notoriously known that this is not a proper statistical way of testing for an interaction effect (Gellman and Stern 2006). The fact that we do not replicate their results, with more than twice their number of participants, suggest that their distance results was an epiphenomenon. In the new version of the discussion, we simply conclude that our results do not support their conclusion. Please see lines (521-525).

16. *The tasks proposed here differ not only in terms of arm versus whole-body involvement but also in their intrinsic nature, which could affect the control strategies employed. This could be discussed. Notably: Some tasks have a precision component with pointing (ARM, WBR downward D1 and D2), while others do not (STS/BTS, and WBR upward D1 and D2).*

If the WBR tasks are bimanual (see #4) this makes them also different conceptually from the ARM task.

We thank the reviewer for his comment. Based on one of the recommender's comments, we have now added a new ANCOVA analysis that compares our EMG results between whole-body tasks. This analysis reveals no interaction between age and whole-body-tasks. We believe that this result strongly dampens the bias mentioned by the reviewer, especially the one about precision, as age effects were similar between whole-body tasks. Regarding the bimanual vs unimanual comment, this analysis reveals that bimanual movement (WBR) and movements without the arms (STS/BTS) lead to the same results. We do not see what specific argument we could discuss that would possibly bias our results. Again, we remain open to further discussion with the reviewer if he feels there is more to say.

Reviewer #2: Anonymous reviewer 1

Major comments:

- The abstract needs a complete re-organization and also needs to include more information about the methods, results, and conclusions.

We thank the reviewer for this insightful comment. We have rewritten the abstract. Please see lines 18-39. To better convey the study rationale, we also updated the title.

- I think the Introduction can be shortened and focus more on the specific gap the study is investigating - compensatory mechanisms in fine movements in older adults.

We thank the reviewer for this insightful comment. We have shortened the introduction. Please see Introduction.

- It is not clear what type of adaptations are required in these simple tasks. In other words, why these tasks were chosen is not clear. This needs to be justified in the Introduction or briefly in the Methods.

We thank the reviewer for pointing this out. We added this information lines (123-127).

- The authors mentioned in the Introduction that they are investigating compensatory mechanisms at the behavioural level but they are doing the analysis based on EMG signals. The EMG signals are at the cellular level (motor units). I am not sure this is considered behaviour.

We believe this type of EMG analysis is considered behavioral in the motor control field. This is because, measuring the peripheral muscle activation with dipoles, as we performed, does not allow inferring individual cell activities.

- It is not clear why an ML analysis was needed when they could statistically compare the EMG metrics between the groups.

We did not explain our logic properly. We thank the reviewer for pointing this out. Other reviewers also questioned this aspect of the manuscript. We tried to improve it as much as possible.

In the present work, we employed a theory-driven analysis that builds upon previous results and required focusing on the activation patterns of antigravity muscles (Gaveau et al. 2021; Poirier et al. 2022; Thomas et al. 2023; Chambellant et al. 2024). Antigravity muscles are muscles that pull against the gravity vector, as defined by their position and orientation in the musculo-skeletal system. In the studied tasks, the antigravity muscles are: i) the Anterior Deltoid (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 D7 (ESD7), extending the rachis; v) the Soleus (SOL), flexing the ankle in the plantar direction. Because the Erector Spinae D7 and the Soleus muscles did not play a strong focal role but a rather postural one in the present tasks, investigating, we focused our analyses on the remaining three muscles (DA, VL and ESL1). Probing the activation of a postural muscle does not seem appropriate to test whether the nervous system takes advantage of gravity to produce the movement. We focused on DA during arm movements and on VL and ESL1 during movement of the entire body. We added a few lines in the manuscript to clarify this aspect (please see lines 267-280).

Moreover, here we are interested in comparing arm movement and whole-body movement control because the scientific literature has reported that whole-body movements control changes with age, while arm movement control does not (Paizis et al. 2008; Vernazza-Martin et al. 2008; Casteran et al. 2018; Poirier et al. 2020, 2023). An issue with focusing on a restrictive number of muscles is that we may probe 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 movements control. To this aim, we employed machine learning to perform a control analysis. This analysis enabled us to quantify how much each muscle activation was altered by age, thereby ensuring that we were focusing on muscles that discriminated movement control between younger and older adults. To summarize, the point of the machine learning analysis was not to say that we picked the muscles that best discriminate between age groups but muscles – selected based on our theory-driven hypothesis – that contained information to discriminate between age-groups. We clarified this aspect in the new manuscript by adding a few lines (please see lines 298-326)

- If the simple arm movement tasks did not show compensatory mechanism differences, then the authors' claim in the Introduction that simple task are needed to study this mechanism is not valid.

We did not write that studying simple movements was needed. We argued that experimental paradigm should try to focus on specific motor control processes to avoid mixing deterioration and compensation. In our case, this means comparing simple arm movements and more complex whole-body movement. The result that simple arm movement did not reveal any age-effect supports the hypothesis that planning efficient movements remains functional in older adults, as also supported by the results of Huang and Ahmed 2014; Poirier et al. 2020; Healy et al. 2023; Summerside et al. 2024. We believe that this result is key to the interpretation of the new correlation results between center-of-mass kinematics and muscle activation patterns. Without the arm null result, one could interpret the correlation result as demonstrating that older adults lose the ability to plan energetically efficient movement and, thus, move their whole-body less and more slowly. We added a few lines in the new manuscript to make this rationale more explicit (see lines 96-98 and 452-462).

- Overall, I am not convinced about this conclusion: "Overall, the present results suggest a compensation process that modulates planning strategies to maximize equilibrium in older adults."

We agree with the reviewer and other reviewers' comment.

Focusing on the EMG analysis, our rationale was that the age effect on whole body movements could not be a deterioration, since the older group is able to create efficient patterns when pointing with their arm. If this is not a deterioration, what else could it be but a compensation. We nonetheless agree that quantifying the possible beneficial effect of this supposed compensation would be a lot more convincing.

We have now calculated some simple criteria that are related to balance. These are the center-of-mass displacement and the peak center-of-mass velocity. We focused on the downward movements (as these are the ones that present the greatest negativity and the greatest challenge

to balance). We tested the correlations between these different kinematics parameters and our EMG criterion. All parameters were negatively correlated to the EMG index, showing that reducing movement efficiency was associated with center-of-mass movements that were less risky (less ample and slower). Please see methods lines (213-228) and results lines (408-425).

Minor comments:

- *The first four lines of the abstract can be shortened to focus more on the specific problem the study is targeting.* - *Lines 28-31: Belongs to the intro of the abstract.*

We have now reformulated the abstract. We believe the first four lines allow introducing the topic to a general audience. We prefer keeping them.

- *Only oral consent, not written?*

The French National Ethics Committee (2019-A01558-49) gave us their approval to perform this experiment using an oral informed consent only. Nonetheless, each participant was included in the study by a medical doctor.

Reviewer #3: FLORIAN MONJO

Summary:

The paper presents a thorough investigation into age-related compensation in motor control processes, focusing on how older adults adapt their movements to maintain efficiency and functionality. The study involved twenty younger adults and twenty-four older adults, comparing their muscle activation patterns during tasks involving arm and whole-body movements. By utilizing a specific analysis method, the researchers aimed to uncover whether age-related alterations in movement efficiency reflect an adaptation process or dysfunction. The findings suggest that age-related changes in whole-body movements may be interpreted as a form of compensation for deteriorated sensorimotor components, rather than simply dysfunction. The study provides valuable insights into the intricate relationship between aging and motor control, highlighting the importance of understanding compensatory mechanisms in maintaining optimal movement patterns. However, certain aspects of the paper require further clarification, particularly concerning the definition of its central concepts and certain methodological elements.

[We thank the reviewer for his positive evaluation of our work.](#)

Overall Comments:

Central Concepts of the Study: The paper could benefit from defining and clarifying central concepts such as movement efficiency, effort, effort minimization, effort minimization downregulation or upregulation and their relationship throughout the text. For instance, the authors introduce the concept of energy efficiency in the abstract; nevertheless, it remains undefined and is not revisited in the main text. It would also enhance clarity to illustrate how the various variables measured and analyzed relate to these concepts.

[We thank the reviewer for this important remark. We added a dedicated paragraph in the revised manuscript. Please see lines \(463-480\). The methodological Figure 3 has also been improved.](#)

Discussion on Potential Confounding Factors: Addressing potential confounding variables such as physical fitness levels and cognitive function would enhance the interpretation of the results.

[We thank the reviewer for this comment. We added a dedicated section in the discussion. Please see lines \(541-549\).](#)

Specific Comments:

Introduction:

Line 54: Consider clarifying the statement regarding the elementary concept of health.

Line 55: “despite normal age-related deterioration, compensatory processes enable older adults to remain in good health and continue to perform their daily activities comfortably.” It’s important to specify that this pertains to successful aging.

[See lines \(51-56\): We developed this notion to make this point more explicit. We also clarified that this pertained to successful aging.](#)

Line 75: “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 neural activation and behavioral performance in older adults”. Do you mean the consensus? Also, could

you clarify what you mean by 'neural activation' and 'spatial recruitment'? It seems vague; are you referring to the spatial recruitment of motor units and to the neural activation of muscles?

We indeed mean consensus and were writing about brain activation. To answer the comments from reviewer1 and reviewer 2, we shortened the introduction. To this aim, we suppressed this part.

Line 79: "This literature has not reached a consensus on the neural changes underlying compensatory mechanisms in older adults. Indeed, several studies reported a positive correlation, and as many reported no correlation or even a negative correlation". The intended meaning is ambiguous regarding which correlation is being referenced.

We were writing about the correlation between brain activation and behavioral performance. To answer the comments from reviewer1 and reviewer 2, we shortened the introduction. To this aim, we suppressed this part.

Line 85: "Several reasons may explain these discrepancies". If these reasons aren't elaborated upon, consider removing this sentence.

We removed this part.

Line 88: not sure 'neuronal alterations' is the appropriate term. It sounds like you are investigating the nervous system directly. I suppose it would be better to refer to sensorimotor alterations.

This part refers to references about behavioral as well as neurophysiological investigations of compensation processes in older adults. To encompass both investigation levels, we now use the term neural alteration. Please see line 76.

Line 92: In the same line, not sure it's appropriate to talk about measuring neural mechanisms, given that, as you mentioned, these studies used 'broad measures'. Rather, these studies investigate behaviors through experimental paradigms that allow inference of some neural mechanisms.

The studies referenced in these lines (the article from Krakauer et al. 2007 and the review from Poirier et al. 2021) develop their rationale based on behavioral and neurophysiological investigations during crude tasks. So, we believe that it is appropriate to talk about neural mechanisms here.

Line 96: Still in the same vein, you write 'linking the brain to behavior.' It still sounds as if you are conducting an imagery study."

The studies referenced in these lines (Krakauer et al. 2017; Pereira et al. 2020; Poirier et al. 2021; Urai et al. 2022) develop their rationale based on behavioral and neurophysiological investigations. So, we believe that it is appropriate to talk about linking the brain to behavior here.

Line 95: Avoid 'There's' and prefer 'There is'

We removed this informal wording. Please see line 82.

Line 106: "older adults favor movement efficiency over precision to compensate for their increased energetic cost". It's important to clarify what you mean by 'movement efficiency' (In my understanding, a movement is more efficient when achieving similar mechanical output with lower effort or neuromuscular

activation). Additionally, I don't understand why you oppose movement efficiency and precision here because, in my view, these are not contradictory concepts; a precise movement can indeed be efficient. As mentioned in the overall comments, the concept of movement efficiency is central to the study and requires clearer definition and its relationship with concepts such as effort minimization and neural activation needs to be established.

We thank the reviewer for this comment. The paragraph added lines (463-481) should help clarifying these aspects. The present work builds upon results of previous computational studies using the optimal control framework (Berret et al. 2008; Gaveau et al. 2011, 2014, 2016, 2021). This framework has proven relevant to explain an important body of results in the motor control domain (Franklin and Wolpert 2011). Those studies allowed identifying single motor costs (such as effort or precision) that may explain how humans adapt their movements to varied context. Within the optimal control framework, the opposition of movement efficiency and precision relates to the fact that the optimal solution to each of a set of motor cost are rarely equal. For example, the most precise movement are notoriously associated to increased co-contraction? Co-contraction is however energy consuming and is, by definition, not compatible with a pure effort minimization control law.

Line 111: Please clarify the concepts of upregulation and downregulation of effort minimization.

We have now clarified this aspect lines (230-243) and (486-489).

Methods:

Line 138: Why did participants only provide oral consent instead of written consent?

The French National Ethics Committee (2019-A01558-49) gave us their approval to perform this experiment using an oral informed consent only. Nonetheless, each participant was included in the study by a medical doctor.

Line 151: "vertical arm movements around the shoulder joint." Would it be more accurate to refer to shoulder flexion?

Indeed, it would be more accurate. We made the modifications.

Line 157: Is "shoulder elevation" the appropriate term here?

Indeed, it would be more accurate. We made the modifications.

STS/BTS task: If I am not mistaken, the rationale for using slow and fast movements is not presented.

This pertains to the methodological separation of the tonic and phasic component of muscle activations. Please see lines (253-267).

Line 171: Please use "x" instead of "".*

See line 163: We have taken this comment into account.

Trial organization: It is not stated whether slow/fast trials and tasks were randomized.

See line 120: It is stated that the blocks were randomized but not the trials.

The variables analyzed are not clearly identified, making it difficult for the reader to understand the rationale behind performing ANCOVAs in the statistics section. Further development is necessary to clarify this aspect.

See lines (328-343): We thank the reviewer for his comment. The statistical section has been improved to clarify this aspect.

Results:

Some parts appear to be more suitable for inclusion in the method section, particularly the paragraph beginning at line 304.

See lines (298-326): We thank the reviewer for his comment. We updated accordingly the Methods/Results section.

Line 348: I am unclear why these are categorized as exploratory analyses, as they seem to be testing your hypothesis.

The main analyze was on the negativity index taking the average of the antigravity muscles and comparing how age affects whole-body tasks vs arm tasks. The exploratory analyses were performed to provide additional details and to get a better understanding of the phenomenon of negativity on phasic from whole-body movements as it has never been done before. Those analyses are mostly descriptive and are not necessary to test our specific hypothesis about age differential effect on arm vs whole-body movements.

Discussion:

Line 364: "muscle patterns" does not appear to be the appropriate term; perhaps you mean "muscle activation pattern."

Indeed, it would be more accurate. We made the modifications throughout the paper.

Line 365: "Muscle command" is rather unusual and seems inappropriate given that the command is generated centrally.

See line 441: We have taken this comment into account. See "alteration of [muscle activation](#) that differ"

Line 366: It could be helpful to describe this muscle marker and to rather refer to muscle activation marker of effort minimization.

See line 471: We have taken this comment into account. See "minimization, [i.e negativity index on EMG phasic](#), was"

Line 386: "Thus, arm movements equally optimized gravity effects in younger and older adults." I do not understand the intended meaning here. Do you mean that both younger and older adults optimize gravity effects to control arm movements?

Yes, previous studies proposed that younger and older adults optimize gravity effects to the same extent. We reproduced this result.

Line 397: I would suggest placing the references at the end of the sentence.

See line 489: We have taken this comment into account.

Line 399: "Muscular patterns" – please refer to previous comments.

We have taken this comment into account.

Reviewer #4: Anonymous reviewer 2

General comments:

This was an interesting and generally well-written manuscript. My reviewing role was exclusively with respect to the application of machine learning (ML). I encourage the authors to 1) include the results from the ML analysis in the main text; 2) more clearly describe the process for splitting the training/test data and evaluating model performance; and 3) mention the limitations of the ML approach in the discussion section.

More detailed comments are provided below:

1. The inclusion of Supplemental Figure 1 in the main manuscript would help the reader evaluate the effectiveness of the classification algorithm. Otherwise, consider adding accuracy values in text to support statements such as “This analysis indeed revealed that antigavity muscles contained important information, allowing separating age-groups with some of the best success rates.” [lines 312-314]

Indeed, we thank the reviewer for this comment. The supplemental section on machine learning has been added to the manuscript and better described (see Figure 6 and lines 298-326 and 366-376).

2. The phrasing on lines 277-280 make it difficult to distinguish whether: a) the data was split into training and test-sets in the traditional ML manner (i.e., model construction/training is performed on cross-validated training dataset, and a separate test-set is withheld for model evaluation); or b) whether five-fold cross-validation was performed on the full dataset and ‘training and test sets’ refer to the four training folds and one validation fold for each subset of the data (i.e., no test set was withheld to assess the models performance and generalizability on unseen data; see below for visualization).

a) Train + test split (80/20 split as example)

Full Dataset

├ Training Data (80% of Full Dataset)
| ├ Fold 1: Train (80%) | Validate (20%)
| ├ Fold 2: Train (80%) | Validate (20%)
| ├ Fold 3: Train (80%) | Validate (20%)
| ├ Fold 4: Train (80%) | Validate (20%)
| └ Fold 5: Train (80%) | Validate (20%)
|
└ Testing Data (20% of Full Dataset) - Used for final model evaluation

OR

b) Cross-validation on full dataset

Full Dataset

├ Fold 1: Train (80%) | Validate (20%)
├ Fold 2: Train (80%) | Validate (20%)
├ Fold 3: Train (80%) | Validate (20%)
├ Fold 4: Train (80%) | Validate (20%)
└ Fold 5: Train (80%) | Validate (20%)

I have reviewed the methods papers cited in the manuscript (Chambellant et al., 2023; Thomas et

al., 2023) and, in conjunction with the present paper, my impression is that this method employs cross-validation across the full dataset and that an independent test-set was not withheld. Correct me if I am mistaken. Either way, please clarify in the manuscript whether the model was evaluated on an unseen test set.

3.If there is a rationale for not testing model performance on unseen data, please provide supporting citations in-text for readers unfamiliar with this approach to ML. Otherwise, please mention the limitations of this approach in the discussion (i.e., limited ability of the model to generalize to unseen data, possibility of data leakage, limited ability to assess model overfitting). Finally, consider rephrasing lines 276-277 "To ensure robustness and generalization of the results, we employed a five-fold cross-validation method" to address the lack of generalizability when testing on the validation set (c.f., the test set).

Answer to question 2 & 3:

We thank the reviewer for this important comment. We agree that this aspect of the manuscript indeed required clarifications. We used cross-validation over the whole dataset and did not isolate a testing set because we were not trying to tune the model. LDA with a linear kernel do not even have hyperparameters to tune in their classical form. The objective of the cross-validation here was to obtain a robust estimation of the accuracy that can be obtained with the ML model on our data, i.e. avoiding the risk of misestimating this accuracy due to an "unlucky" train/test split. We avoided the risk of overfitting since the collected accuracies were the ones from the validation sets, whose data were unknown to each trained algorithm. However, we agree with the reviewer that the word "generalization" was indeed misused here. The objective of the cross-validation was not to know if any of the algorithm used would be able to produce similar results on new participants but to quantify which muscles conveyed the most information in discriminating younger from older adults. We removed the word "generalization" from the manuscript.

Regarding the risk of data leakage, we believe it is minimal since the data preprocessing was identical on all data and erased baseline differences (as we removed the tonic component of the EMG patterns) as well as maximal amplitude differences (EMG min/max values were normalized to -1/1) before feeding the algorithm. Our data pre-processing should therefore avoid data leakage. We do not see how other aspects of the data processing could lead to data leakage in the present work.

References

- Berardelli, A., Hallett, M., Rothwell, J. C., Agostino, R., Manfredi, M., Thompson, P. D., & Marsden, C. D. (1996). Single-joint rapid arm movements in normal subjects and in patients with motor disorders. *Brain*, *119*(2), 661-674. <https://doi.org/10.1093/brain/119.2.661>
- 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>
- 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. (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>
- 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>
- Franklin, D. W., & Wolpert, D. M. (2011). Computational Mechanisms of Sensorimotor Control. *Neuron*, *72*(3), 425-442. <https://doi.org/10.1016/j.neuron.2011.10.006>
- 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>
- Gottlieb, G. L., Corcos, D. M., & Agarwal, G. C. (1989). Organizing principles for single-joint movements. I. A speed-insensitive strategy. *Journal of Neurophysiology*, *62*(2), 342-357. <https://doi.org/10.1152/jn.1989.62.2.342>
- 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>
- 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>
- 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>

- 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>
- McIntyre, J., Lipshits, M., Zaoui, M., Berthoz, A., & Gurfinkel, V. (2001). Internal reference frames for representation and storage of visual information : The role of gravity. *Acta Astronautica*, *49*(3-10), 111-121. [https://doi.org/10.1016/S0094-5765\(01\)00087-X](https://doi.org/10.1016/S0094-5765(01)00087-X)
- 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.
- Mourey, F., Pozzo, T., Rouhier-Marcet, 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>
- 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>
- 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., Gaveau, J., & Mourey, F. (2020). *La chute et la pomme ? Vieillesse et adaptation sensori-motrice à l'environnement gravitaire.*
- 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>
- 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*, e1596232024. <https://doi.org/10.1523/JNEUROSCI.1596-23.2024>
- 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>

- Urai, A. E., Doiron, B., Leifer, A. M., & Churchland, A. K. (2022). Large-scale neural recordings call for new insights to link brain and behavior. *Nature Neuroscience*, 25(1), 11-19.
<https://doi.org/10.1038/s41593-021-00980-9>
- Vernazza-Martin, S., Tricon, V., Martin, N., Mesure, S., Azulay, J. P., & Le Pellec-Muller, A. (2008). Effect of aging on the coordination between equilibrium and movement : What changes? *Experimental Brain Research*, 187(2), 255-265. <https://doi.org/10.1007/s00221-008-1301-4>
- Yamamoto, S., & Kushiro, K. (2014). Direction-dependent differences in temporal kinematics for vertical prehension movements. *Experimental Brain Research*, 232(2), 703-711.
<https://doi.org/10.1007/s00221-013-3783-y>