

University of Groningen

Preservation of motor flexibility in healthy aging

Greve, Christian

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:
2018

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Greve, C. (2018). *Preservation of motor flexibility in healthy aging: Flexibility in joint coordination is unaffected by age and task constraints in two fundamental activities of daily living*. [Thesis fully internal (DIV), University of Groningen]. Rijksuniversiteit Groningen.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

6

General Discussion

6.1. MAIN FINDINGS

When humans perform voluntary movements such as reaching for a target or sit-to-stand, the abundant joint motions provide the neuromuscular system with a large range of movement possibilities [1–4]. Young and old adults make use of this rich movement repertoire to perform daily life reaching and sit-to-stand movements under different intrinsic and task constraints. The current thesis provides evidence that this key feature of human motor behavior, motor flexibility, is retained with aging during even challenging reaching and sit-to-stand tasks. The results of the thesis challenge the generally accepted view that healthy aging leads to a universal loss of motor performance and joint coordination in particular. Based on the principle of motor abundance [2,5] and the constraints to movement hypothesis [6,7] the general discussion focuses on the possibility that flexibility in joint coordination might actually increase with aging in compensation for deficits in task relevant neuromuscular functions.

6.2. THE UCM METHOD AS A FRAMEWORK TO STUDY AGE-DIFFERENCES IN MOTOR FLEXIBILITY

6 To establish age-differences in motor flexibility the uncontrolled manifold approach was used. The UCM method follows the principle of motor abundance and assumes that the available degrees of freedom (e.g., joints) co-vary to stabilize the task variable of primary importance (e.g. end-effector position during reaching or COM position during sit-to-stand) [4,5]. The extent to which co-variation among the available joint motions stabilizes task performance can be quantified by decomposing trial-to-trial variability in joint motions into coordination patterns stabilizing (GEV) and de-stabilizing (NGEV) the task variable of primary importance [4,5]. GEV and NGEV emerge during performance based on how the actual constraints imposed by the neuromuscular system interact with the requirements of the motor task [5–13]. High values of GEV imply that the neuromuscular system uses a larger range of different but equivalent coordination patterns to guarantee task stability. Allowing a larger range of motor solutions to emerge during performance improves the neuromuscular systems' capacity to adapt to unexpected changes in movement constraints or external and internal perturbations [5,14–16]. This form of performance stability through motor flexibility is essential for everyday motor performance since the actual constraints to movement are poorly predictable and frequently change in daily life. In addition internal sources of noise during perception and movement preparation [17], task execution [18] and feedback processing [19] require flexible adjustments in joint coordination to guarantee task success.

Age-related deficits in intrinsic constraints change the way old as compared to young adults move their joints during reaching and sit-to-stand movements. For example, old as compared to young adults perform reaching movements slower and employ larger trunk flexion when

rising from a chair [20,21]. These adaptations in joint coordination strategies allow old adults to lower the accuracy and strength requirements of reaching and sit-to-stand movements [22–24]. This thesis aimed to establish whether old as compared to young adults differently use the range of movement possibilities to perform challenging reaching and sit-to-stand movements. Following the framework of motor abundance and the constraints to movement concept it was hypothesized that the age-related decline in intrinsic constraints interacts with the requirements of challenging reaching and sit-to-stand tasks leading to an increase in motor flexibility. This age related increase in motor flexibility with aging would allow old adults to guarantee stability of daily life reaching and sit-to-stand movements despite neuromuscular deficits.

6.3. AGE AND TASK CONSTRAINTS DO NOT AFFECT FLEXIBILITY IN JOINT COORDINATION

6.3.1. Effects of task constraints on motor flexibility during sit-to-stand

In line with the hypothesis healthy old adults with strength deficits employed larger GEV when repeatedly standing up from low (100% lower leg length) chair heights (Chapter 2, Figure 3). We argued that this increase in motor flexibility was a compensation for age-related muscle weakness. When old adults with strength deficits stand up from a low chair they use 80 – 100% of the available knee extensor muscle strength compared to 40–60% in healthy young adults [23,25]. Operating at the limits of the available force capacities requires old adults to coordinate the COM more accurately and closer to the knee at lift-off not to exceed the available muscle strength. Using a larger range of equivalent motor solutions for the same COM position at lift-off would allow old adults to safely rise from low chair heights despite deficits in muscle strength.

Based on the idea that flexibility in joint coordination underlies COM stability it was expected that healthy old and young adults would employ larger GEV during repeated sit-to-stand performance under high force and balance constraints (Chapter 5). The force constraint was manipulated during the second sit-to-stand experiment by adding weight with a weight vest to the trunk (30% MVC of the right knee extensor strength). The balance constraint was increased by decreasing the size of the support surface (0.27 * European shoe size). The rationale was that increasing force constraints and decreasing the support surface size would require a more accurate coordination of the COM position at lift-off. In compensation for this higher stability requirement old and young adults might employ larger GEV to guarantee sit-to-stand stability. Contrary to this expectation, UCM analysis revealed that GEV and NGEV were similar between age groups and remained unchanged by increases in the force or balance constraints (Chapter 5.3.2). These results showed that old and young adults did not employ a larger range of the available motor solutions to guarantee sit-to-stand stability under challenging force and balance constraints.

Instead of using a larger range of the same movement patterns old and young adults adapted to the higher force and balance constraints by moving slower and increasing trunk flexion at lift-off (Chapter 5, Table 2 – 3). Slowing down movement and bringing the COM closer to the knee at lift-off are effective strategies to minimize force requirements and improve COM stability [21,23,24]. Hence, these adaptations in movement kinematics might have been sufficient to guarantee safe sit-to-stand performance under high force and balance constraints. Motor flexibility might be used in compensation for neuromuscular deficits only when old adults operate at the limits of the available muscle strength or balance abilities.

In chapter 2 as compared to 5 the old and young adults stood up from lower chair heights (100 vs 110% of lower leg length) and employed significantly higher peak knee extension moments at lift-off (Chapter 5, Table 4; Chapter 2, Table 2). Especially low chair heights impose high force constraints because the knee extensor muscles are at an unfavorable force-length relationship. In addition, during the second sit-to-stand experiment, the old and young adults had good balance and overall physical performance capacities (Chapter 5, Table 1). Therefore the possibility exists, that old adults during the first but not the second sit-to-stand experiment operated at the limits of their intrinsic strength and maybe balance capacities requiring compensatory increase in motor flexibility.

6

6.3.2. Effects of task constraints on motor flexibility during reaching

Healthy young and old adults adapt movement kinematics but not motor flexibility to guarantee accurate end-effector positions when reaching to small targets under high accuracy constraints (Chapter 3 and 4). During the reaching experiments, the accuracy constraint was manipulated by decreasing the target size. The idea was that old and young adults would employ a larger range of equivalent coordination patterns to guarantee accurate end-effector positions when reaching to smaller targets. However, GEV did not increase with an increase in accuracy constraints. Instead of employing a larger range of equivalent coordination patterns old and young adults moved slower and used lower peak end-effector velocities to adapt to the higher accuracy constraints (Chapter 4, Table 2 and 4). These findings on motor flexibility and reaching kinematics were reproduced in an experiment where healthy young adults moved at their comfortable instead of maximal speed (Chapter 4, Table 4; Chapter 4.3.8).

The observed adaptations in movement kinematics were more pronounced in old as compared to young adults and similar to observations reported in previous studies [20,22,26]. It is assumed that using more time to bring the end effector to the target provides the neuromuscular system with more time to process visual information. This sensory information can be used to improve accuracy of the end-effector when reaching to smaller targets [22]. Therefore, adaptations in movement kinematics might have been sufficient to guarantee reaching success under higher accuracy constraints not requiring the use of alternative motor solutions through increases in motor flexibility.

When force constraints increased during the reaching task both variability components, GEV and NGEV proportionally increased with the force requirements (Chapter 4, Figure 3; Chapter 3, Figure 4). The proportional increase in GEV and NGEV with higher force constraints was initially interpreted in the context of previous studies showing that higher muscle forces are associated with more noise in the neuromuscular system (Chapter 3.4.1) [27–29]. Assuming that the larger GEV and NGEV resulted from larger noise, one would expect a similar change in motor flexibility when force requirements increased during the sit-to-stand experiment. However, GEV and NGEV remained unaffected by increases in force requirements during the second sit-to-stand experiment not confirming our initial hypothesis. As an alternative explanation I propose that increasing the resistance to the reaching movement through a pulley system introduced an additional coordinative task constraint. Pulling on the end-effector in the opposite direction of the movement trajectory might have required larger compensatory adjustments among the available joints leading to an increase in overall variability (GEV and NGEV). Stability of task performance was maintained because GEV and NGEV increased proportionally with the force constraint.

Overall, the data suggest that healthy aging does not seem to affect flexibility in joint coordination during challenging reaching and sit-to-stand tasks. It remains inconclusive whether and if so how variations in force, accuracy and balance constraints during reaching and sit-to-stand movements lead to adaptations in motor flexibility in young and old adults. The possibility exists that flexibility in joint coordination might serve in compensation for neuromuscular deficits only when old adults operate at the limits of intrinsic force, balance and coordinative capacities. As long as the neuromuscular system performs within a safe range of intrinsic capacities adaptations in movement kinematics might be sufficient to guarantee safe and accurate sit-to-stand and reaching performance. To further the understanding of how age-related deficits in neuromuscular functions interact with flexibility in joint coordination, future studies should aim to maximize task constraints in such a way that old and young adults can operate at the limits of their intrinsic capacities. In the following chapter I will discuss additional conceptual, experimental and methodological limitations possibly affecting the analysis and interpretation of UCM measures in the study of age-differences in motor flexibility.

6.4. LIMITATIONS AND RECOMMENDATIONS FOR FUTURE STUDIES

6.4.1. Classification of GEV and NGEV in motor flexibility research

Traditional UCM analysis assumes that NGEV reflects bad or unwanted variability and GEV good or wanted variability [4,5,14,30]. The constraints to movement hypothesis and our data and previous studies question the existence of such a strict categorization of the variability components [6,31]. The main issue with UCM analysis is that the decomposition of trial-

to-trial variability into GEV and NGEV is based on the value of a pre-defined, single task variable of primary importance (e.g. end-effector position during reaching) [4,5]. The extent to what joint coordination patterns lie within the solution space of that task variable defines the amount of GEV and NGEV. However, during any motor task there are multiple intrinsic and task constraints which interact with each other and the emerging coordination patterns need to satisfy all constraints to movement. For example, during fast, goal-directed reaching movements in addition to end-effector accuracy, energetic costs impose an intrinsic constraint to the movement [32,33]. To satisfy both accuracy and energetic constraints the emerging coordination patterns do not entirely lie within the solution space of the end-effector position but also some NGEV will emerge [6,7,34]. However, this NGEV is not bad but reflects the requirement to minimize energetic costs. Hence, NGEV does not simply reflect a measure of performance instability but shows how other than the task constraint of primary importance interact with the characteristics of the neuromuscular system. In the following paragraph I will review two examples to elaborate on this idea.

As a first example, Park et al (2012) reported during a multi-finger force coordination task that co-variation among individual finger forces increased when the agonist muscles were fatigued [35]. This increase in multi finger co-variation was reflected by a larger increases in GEV as compared to NGEV. The authors concluded that increasing co-variation among individual finger forces guaranteed accurate force control despite deficits in agonist muscle strength [35–37]. However, when the fatigued muscles were less relevant for accurate force control (operated as antagonist and not agonist muscles) NGEV increased while GEV declined without a change in total performance error [35]. This finding was unexpected and the authors did not provide an interpretation of the larger NGEV and drop in GEV when the antagonist muscles were fatigued. It is likely that the larger NGEV reflected those coordination patterns which required less antagonist muscle force. These coordination patterns emerged to better satisfy the deficit in intrinsic strength constraints. Because the agonist muscles were not fatigued accurate force control could be maintained despite higher NGEV.

Similarly, motor learning studies showed that depending on the details of the new motor task and the stage of the learning process, GEV or NGEV might be employed to facilitate the learning process [31,38–51]. For example if the task variable of primary importance of a new motor task is unknown the learner benefits from larger amounts of NGEV [43,49,51,52]. It is assumed that employing those coordination patterns which lead to variable task performance allows the learner to discover the task relevant information and the range of successful motor solutions [43,49,52]. Once the solution space is known NGEV would gradually decrease and GEV would increase or remain the same to guarantee performance stability [42,43,49–51,53]. On the other hand when the goal of the task is known and the new motor task requires adaptation to an external perturbation (e.g. force field) larger GEV guides the learning process. Employing a larger range of equivalent motor solutions would allow the neuromuscular system

to adapt to the external perturbations and stabilize task important variables at the desired value [38,46,49]. Interestingly this relation between flexibility in joint coordination and motor learning seems to account only for naturally emerging motor variability. A recent study showed that experimentally induced variability in either the goal-equivalent or non- goal equivalent subspace does not improve but might impair motor learning abilities [39].

Summarizing, a simple categorization of GEV and NGEV into good and bad variability is inadequate considering the complex interactions between intrinsic and task constraints in even standardized experimental environments. Future studies should therefore analyze and interpret changes in both variability components independently and always in the context of how changes in intrinsic and task constraints interact with performance stability. Future studies should also consider performing UCM analysis on multiple task variables of primary importance to establish potential change in the most important task variables. Furthermore, to detect expected or unexpected learning effects during repeated task performance future studies should aim to analyze changes in UCM measures across repetitions. Until now UCM analysis is only performed within block of trials.

6.4.2. Effect of cognition on motor flexibility

Healthy aging is associated with deficits in cognition and cognitive deficits can interfere with motor performance [54–63]. For example, old as compared to young adults show decrements in lower limb coordination when performing a cognitive task while walking [60–63]. Studies using UCM measures require a high number of repetitions and detailed standardization of the start and end positions of the participants joint positions. Following the detailed experimental instructions over a high number of repetitions and positioning the joints into a specific posture prior to movement initiation might have imposed an attentional task constraint during our experiments. This attentional task constraint could interact with age-related deficits in cognition leading to changes in joint coordination and measures of motor flexibility. To account for this possibility future studies should clinically assess age-differences in cognition (e.g. clinical assessment tools such as the mini mental state assessment [64]) and relate possible age-differences to the obtained UCM measures. Furthermore increasing the cognitive load during a given motor task (e.g. counting backwards) might reveal further information on how cognition interacts with measures of motor flexibility in old and young adults.

6.4.3. Individual joint variability

A methodological limitation of current UCM analyses is that it does not allow to distinguish between trial-to-trial variability originating from multi-joint co-variation and individual joint variability [65–67]. Therefore, individual joint variability might confound UCM measures leading to incorrect classification of trial-to-trial variability in joint coordination patterns into GEV and NGEV. Future studies should aim to establish methods allowing to correct for the confounding effect of individual joint variability in traditional UCM measures.

6.5. CONCLUSION

The present thesis examined how healthy old as compared to young adults make use of the abundant joint motions to stabilize task important variables during reaching and sit-to-stand movements. Taken current and past data together it seems that there is not a universal decline or increase in motor flexibility with aging as measured with UCM analysis. It remains inconclusive whether and if so how age-related changes in intrinsic constraints or changes in task constraints affect flexibility in joint coordination during reaching and sit-to-stand movements. Flexibility in joint coordination might serve in compensation for neuromuscular deficits only when old or young adults operate at the limits of their force, balance or coordinative capacities. As long as the neuromuscular system does not operate at the limits of the available intrinsic capacities, adaptations in movement kinematics might be sufficient to guarantee safe and accurate reaching and sit-to-stand performance.

The inconclusiveness in results on age-differences in motor flexibility might imply that complex and individual specific interactions between intrinsic and task constraints define the extent to what flexibility in joint coordination is used during voluntary movements. To improve the understanding of how healthy aging affects motor flexibility future studies should perform analyses on an individual rather than a group level. Furthermore future studies should investigate trial-to-trial changes in UCM measures to detect possible learning or adaptation effects which remain undetected with block analyses.

REFERENCES

1. Bernstein N (1967) *The co-ordination and regulation of movements*. Pergamon Press, London.
2. Gelfand IM, Latash ML (1998) On the Problem of Adequate Language in Motor Control. *Motor Control* **2**: 306–313.
3. Domkin D, Laczko J, Jaric S, Johansson H, Latash ML (2002) Structure of joint variability in bimanual pointing tasks. *Exp brain Res* **143**: 11–23.
4. Scholz JP, Schöner G (1999) The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp brain Res* **126**: 289–306.
5. Latash ML, Scholz JP, Schöner G (2007) Toward a new theory of motor synergies. *Motor Control* **11**: 276–308.
6. Newell KM (1986) Constraints on the development of coordination. In Wade MG, Whiting HT (eds.), *Motor development in children: aspects of coordination and control* pp 341–360. Springer, Berlin.
7. Hu X, Newell KM (2011) Modeling constraints to redundancy in bimanual force coordination. *J Neurophysiol* **105**: 2169–2180.
8. Yang J-F, Scholz JP, Latash ML (2007) The role of kinematic redundancy in adaptation of reaching. *Exp brain Res* **176**: 54–69.
9. Mattos DJS, Latash ML, Park E, Kuhl J, Scholz JP (2011) Unpredictable elbow joint perturbation during reaching results in multijoint motor equivalence. *J Neurophysiol* **106**: 1424–1436.
10. Gera G, Freitas S, Latash M, Monahan K, Schoener G, Scholz J (2010) Motor Abundance Contributes to Resolving Multiple Kinematic Task Constraints. *Motor Control* **14**: 83–115.
11. Klous M, Danna-dos-Santos A, Latash ML (2010) Multi-muscle synergies in a dual postural task: evidence for the principle of superposition. *Exp brain Res* **202**: 457–471.
12. Reisman DS, Scholz JP, Schöner G (2002) Coordination underlying the control of whole body momentum during sit-to-stand. *Gait Posture* **15**: 45–55.
13. de Freitas SMSF, Scholz JP, Stehman AJ (2007) Effect of motor planning on use of motor abundance. *Neurosci Lett* **417**: 66–71.
14. Latash ML (2012) The bliss (not the problem) of motor abundance (not redundancy). *Exp brain Res* **217**: 1–5.
15. Latash ML (2016) Biomechanics as a Window Into the Neural Control of Movement by. **52**: 7–20.
16. Ambike S, Mattos D, Zatsiorsky VM, Latash ML (2016) Synergies in the space of control variables within the equilibrium-point hypothesis. *Neuroscience* **315**: 150–161.
17. Churchland MM, Afshar A, Shenoy K V (2006) A central source of movement variability. *Neuron* **52**: 1085–1096.
18. van Beers RJ, Haggard P, Wolpert DM (2004) The Role of Execution Noise in Movement Variability. *J Neurophysiol* **91**: 1050–1063.
19. Lisberger SG, Medina JF (2015) How and why neural and motor variation are related. *Curr Opin Neurobiol* **33**: 110–116.
20. Sleimen-Malkoun R, Temprado J-J, Berton E (2013) Age-related changes of movement patterns in discrete Fitts' task. *BMC Neurosci* **14**: 145.
21. Hughes M a, Weiner DK, Schenkman ML, Long RM, Studenski S a (1994) Chair rise strategies in the elderly. *Clin Biomech (Bristol, Avon)* **9**: 187–192.
22. Van Halewyck F, Lavrysen A, Levin O, Boisgontier MP, Elliott D, Helsen WF (2015) Factors underlying age-related changes in discrete aiming. *Exp brain Res* **233**: 1733–1744.
23. Hughes M a, Myers BS, Schenkman ML (1996) The role of strength in rising from a chair in the functionally impaired elderly. *J Biomech* **29**: 1509–1513.
24. Lindemann U, Mucbe R, Stuber M, Zijlstra W, Hauer K, Becker C (2007) Coordination of strength exertion during the chair-rise movement in very old people. *J Gerontol A Biol Sci Med Sci* **62**: 636–640.
25. Lindemann U, Mucbe R, Stuber M, Zijlstra W, Hauer K, Becker C (2007) Coordination of strength exertion during the chair-rise movement in very old people. *J Gerontol A Biol Sci Med Sci* **62**: 636–640.
26. Sleimen-Malkoun R, Temprado J-J, Berton E (2013) Age-related changes of movement patterns in discrete Fitts' task. *BMC Neurosci* **14**: 145.
27. Bays PM, Wolpert DM (2007) Computational principles of sensorimotor control that minimize uncertainty and variability. *J Physiol* **578**: 387–396.
28. Schmidt RA (1979) Motor-output variability: A theory for the accuracy of rapid motor acts. *Psychol Rev* **86**: 415–451.
29. Faisal a A, Selen LPJ, Wolpert DM (2008) Noise in the nervous system. *Nat Rev Neurosci* **9**: 292–303.
30. Latash ML (2016) Biological Movement and Laws of Physics. *Motor Control* **1–29**.
31. Hu X, Newell KM (2011) Modeling constraints to redundancy in bimanual force coordination. 2169–2180.
32. Shadmehr R, Huang HJ, Ahmed AA (2016) A Representation of Effort in Decision-Making and Motor Control. *Curr Biol* **26**: 1929–1934.
33. Shadmehr R, Mussa-Ivaldi S (2012) *Biological Learning and Control*.

34. Newell KM, Liu Y-T, Mayer-Kress G (2001) Time scales in motor learning and development. *Psychol Rev* **108**: 57–82.
35. Park J, Singh T, Zatsiorsky VM, Latash ML (2012) Optimality versus variability: effect of fatigue in multi-finger redundant tasks. *Exp Brain Res* **216**: 591–607.
36. Singh T, Skm V, Zatsiorsky VM, Latash ML (2010) Fatigue and Motor Redundancy: Adaptive Increase in Finger Force Variance in Multi-Finger Tasks. 2990–3000.
37. Singh T, S K M V, Zatsiorsky VM, Latash ML (2010) Adaptive increase in force variance during fatigue in tasks with low redundancy. *Neurosci Lett* **485**: 204–207.
38. Singh P, Jana S, Ghosal A, Murthy A (2016) Exploration of joint redundancy but not task space variability facilitates supervised motor learning. *Proc Natl Acad Sci* **113**: 14414–14419.
39. Cardis M, Casadio M, Ranganathan R (2017) High variability impairs motor learning regardless of whether it affects task performance. *J Neurophysiol* **119**: jn.00158.2017.
40. Yang JF, Scholz JP (2005) Learning a throwing task is associated with differential changes in the use of motor abundance. *Exp Brain Res* **163**: 137–158.
41. Yang J-F, Scholz JP, Latash ML (2007) The role of kinematic redundancy in adaptation of reaching. *Exp Brain Res* **176**: 54–69.
42. Pacheco MM, Newell KM (2018) Search strategies in practice: Influence of information and task constraints. *Acta Psychol (Amst)* **182**: 9–20.
43. Pacheco MM, Newell KM (2015) Transfer as a function of exploration and stabilization in original practice. *Hum Mov Sci* **44**: 258–269.
44. Wu HG, Miyamoto YR, Gonzalez Castro LN, Ölveczky BP, Smith M a (2014) Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. *Nat Neurosci* **17**: 312–321.
45. Tuitert I, Bootsma RJ, Schoemaker MM, Otten E, Mouton LJ, Bongers RM (2017) Does practicing a wide range of joint angle configurations lead to higher flexibility in a manual obstacle-avoidance target-pointing task? *PLoS One* **12**: e0181041.
46. He K, Liang Y, Abdollahi F, Fisher Bittmann M, Kording K, Wei K (2016) The Statistical Determinants of the Speed of Motor Learning. *PLoS Comput Biol* **12**: e1005023.
47. Ranganathan R, Wieser J, Mosier KM, Mussa-Ivaldi FA, Scheidt RA (2014) Learning redundant motor tasks with and without overlapping dimensions: facilitation and interference effects. *J Neurosci* **34**: 8289–8299.
48. Wu Y-H, Pazin N, Zatsiorsky VM, Latash ML (2012) Practicing elements versus practicing coordination: Changes in the structure of variance. *J Mot Behav* **44**: 471–478.
49. Dhawale AK, Smith MA, Ölveczky BP (2017) The Role of Variability in Motor Learning. *Annu Rev Neurosci* **40**: 479–498.
50. Ranganathan R, Newell KM (2010) Emergent flexibility in motor learning. *Exp Brain Res* **202**: 755–764.
51. Ranganathan R, Newell KM (2010) Influence of motor learning on utilizing path redundancy. *Neurosci Lett* **469**: 416–420.
52. Zhou T, Wu Y-H, Bartsch A, Cuadra C, Zatsiorsky VM, Latash ML (2013) Anticipatory synergy adjustments: preparing a quick action in an unknown direction. *Exp Brain Res* **226**: 565–573.
53. Newell KM, Liu YT, Mayer-Kress G (2001) Time scales in motor learning and development. *Psychol Rev* **108**: 57–82.
54. Seidler RD, Bernard JA, Burutolu TB, Fling BW, Gordon MT, Gwin JT, Kwak Y, Lipps DB (2011) Motor control and Aging: Links to age-related brain structural, functional and biomechanical effects. *Neurosci Biobehav Rev* **34**: 721–733.
55. Bernard JA, Seidler RD (2014) Moving forward: age effects on the cerebellum underlie cognitive and motor declines. *Neurosci Biobehav Rev* **42**: 193–207.
56. Morris R, Lord S, Bunce J, Burn D, Rochester L (2016) Gait and cognition: Mapping the global and discrete relationships in ageing and neurodegenerative disease. *Neurosci Biobehav Rev* **64**: 326–345.
57. Mirelman A, Maidan I, Bernad-Elazari H, Shustack S, Giladi N, Hausdorff JM (2017) Effects of aging on prefrontal brain activation during challenging walking conditions. *Brain Cogn* **115**: 41–46.
58. Dumurgier J, Artaud F, Touraine C, Rouaud O, Tavernier B, Dufouil C, Singh-Manoux A, Tzourio C, Elbaz A (2017) Gait speed and decline in gait speed as predictors of incident dementia. *Journals Gerontol - Ser A Biol Sci Med Sci* **72**: 655–661.
59. Mullick AA, Subramanian SK, Levin MF (2015) Emerging evidence of the association between cognitive deficits and arm motor recovery after stroke: A meta-analysis. *Restor Neurol Neurosci* **33**: 389–403.
60. Beurskens R, Bock O (2012) Age-related deficits of dual-task walking: a review. *Neural Plast* **2012**: 131608.
61. Belghali M, Chastan N, Cignetti F, Davenne D, Decker LM (2017) Loss of gait control assessed by cognitive-motor dual-tasks: pros and cons in detecting people at risk of developing Alzheimer's and Parkinson's diseases. *GeroScience* **39**: 305–329.
62. LaRoche DP, Greenleaf BL, Croce R V, McGaughy JA (2014) Interaction of age, cognitive function, and gait performance in 50-80-year-olds. *Age (Dordr)* **36**: 9693.

63. Chu Y-H, Tang P-F, Peng Y-C, Chen H-Y (2013) Meta-analysis of type and complexity of a secondary task during walking on the prediction of elderly falls. *Geriatr Gerontol Int* **13**: 289–297.
64. Lin JS, O'Connor E, Rossom RC, Perdue LA, Eckstrom E (2013) Screening for Cognitive Impairment in Older Adults: A Systematic Review for the U.S. Preventive Services Task Force. *Ann Intern Med* **159**: 601–612.
65. Verrel J (2011) A formal and data-based comparison of measures of motor-equivalent covariation. *J Neurosci Methods* **200**: 199–206.
66. Auyang AG, Yen JT, Chang Y-H (2009) Neuromechanical stabilization of leg length and orientation through interjoint compensation during human hopping. *Exp brain Res* **192**: 253–264.
67. Cluff T, Manos A, Lee TD, Balasubramaniam R (2012) Multijoint error compensation mediates unstable object control. *J Neurophysiol* **108**: 1167–1175.

