Normal aging reduces motor synergies in manual pointing

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Abstract

Depending upon its organization, movement variability may reflect poor or flexible control of a motor task. We studied adult age-related differences in the structure of postural variability in manual pointing using the uncontrolled manifold (UCM) method. Participants from 2 age groups (younger: 20–30 years; older: 70–80 years; 12 subjects per group) completed a total of 120 pointing trials to 2 different targets presented according to 3 schedules: blocked, alternating, and random. The age groups were similar with respect to basic kinematic variables, end point precision, as well as the accuracy of the biomechanical forward model of the arm. Following the uncontrolled manifold approach, goal-equivalent and nongoal-equivalent components of postural variability (goal-equivalent variability [GEV] and nongoal-equivalent variability [NGEV]) were determined for 5 time points of the movements (start, 10%, 50%, 90%, and end) and used to define a synergy index reflecting the flexibility/stability aspect of motor synergies. Toward the end of the movement, younger adults showed higher synergy indexes than older adults. Effects of target schedule were not reliable. We conclude that normal aging alters the organization of common multidegree-of-freedom movements, with older adults making less flexible use of motor abundance than younger adults.
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1. Introduction

Normal adult aging has been hypothesized to lower individuals' ability to adapt their behavior to environmental and task requirements (Newell et al., 2006; Vaillancourt and Newell, 2002), possibly caused by changes in system "complexity", such as a reduction of the number of independent components, their coupling strength, or both (Lipsitz, 2004). In a similar vein and inspired by cybernetics, Thaler (2002) proposed that age-related changes in sensorimotor performance may be due to a reduction in the system's variety of perceptual states and available responses. Most of the empirical evidence for this general theoretical position stems from nonlinear time series analyses of "system output", such as physiological measures (Lipsitz and Goldberger, 1992), postural sway (Thurner et al., 2002), or step patterns (Hausdorff et al., 1997), addressing the temporal structure of variability ("dynamical degrees of freedom"). In contrast, potential age-related changes in the functional organization of variability across multiple biomechanical degrees of freedom have found only limited attention.

Adult aging affects motor performance at different levels, ranging from physiological mechanisms to coordinative skills (Spirduso et al., 2005). Studies on rapid goal-directed arm movements found older adults to show slower and more variable arm movements than younger adults (Darling et al., 1989; Yan et al., 1998, 2000) and higher levels of muscle coactivation (Seidler-Dobrin et al., 1998). Moreover, age-related impairments in movement smoothness and end-point accuracy are generally more pronounced for movements requiring shoulder-elbow coordination than for single-joint actions (Seidler et al., 2002), suggesting a selective deficit in multijoint coordination among the elderly.

Motor synergies, defined as task-specific organization of movement variability across the effector system (Latash et al., 2007), may play an important role for the efficiency of

motor control processes and their adaptation to environmental and organismic constraints (Latash and Anson, 2006; Latash, 2008), such as senescence-related skeletal, muscular, and neuronal changes. Here, we investigate adult age-related differences in motor synergies in a manual pointing task, using the uncontrolled manifold (UCM) approach (Latash et al., 2007; Latash, 2008; Scholz and Schöner, 1999).

According to the UCM hypothesis (Scholz and Schöner, 1999), variability in motor tasks involving abundant degrees of freedom (DOF) is structured in a way that takes advantage of motor equivalence, that is, of the fact that a variety of configurations of elemental variables (e.g., joint angles) can lead to the same motor output in a task variable (e.g., the position of an end effector). It is hypothesized that stabilization of a task variable by the central nervous system is achieved by selectively constraining variability along dimensions affecting that task variable while allowing for variability along "goal-equivalent" dimensions. A task variable is said to be synergistically controlled when higher amounts of goal-equivalent variability (GEV, exploiting motor abundance) are present compared with nongoal-equivalent variability (NGEV, affecting the task variable).

If this condition is met, then the strength of the synergy can be quantified by a synergy index, for instance as the relative proportion of GEV (Latash et al., 2007). Thus, higher synergy indexes indicate more flexible exploitation of motor abundance. It has to be noted that this definition of motor synergy differs from the terminology often used in clinical research and by some movement scientists (e.g., diPietro et al., 2007), where it usually refers to a relatively invariant temporal coupling among system components. In contrast, the operationalization of motor synergies used here emphasizes both the accuracy and flexibility aspect of motor coordination, by analyzing motor-equivalent stabilization of a task variable (Latash et al., 2007). Note that this is a functional rather than a data-driven definition, in the sense that a synergy is always defined with respect to a specific task variable.

Previous studies using the UCM approach have found age-related differences in the structure of variability in multifinger force production (Olafsdottir et al., 2007; Shim et al., 2004; Shinohara et al., 2004), with weaker synergies in older compared with younger adults. Latash (2008) argued that constraining the use of motor abundance (leading to lower synergy indexes) may be an adaptive strategy to cope with age-related decline in sensorimotor processing and increasing neuromuscular noise (Enoka et al., 2003). This view is partly compatible with results from simulation studies in a stochastic optimal control framework (Todorov and Jordan, 2002), in which motor behavior is modeled based on the assumption that biological controllers minimize variation in elemental variables mainly along dimensions that affect the task outcome ("minimal intervention principle"). These simulation results indicated that constraining motor abundance may be adaptive in a system with increased sensory noise or higher movement correction costs.

Pointing movements lend themselves well to a UCM analysis, due to the clearly defined goal and the motor abundance of the task, and have been studied in detail using the UCM method (e.g., Reisman and Scholz, 2003; Tseng et al., 2002, 2003). However, to our knowledge, age group differences in motor synergies in pointing attributable to normal aging have not yet been investigated. As pointing is part of our everyday movement repertoire, little or no age-related differences are expected in terms of basic performance measures, such as end point accuracy, at least under self-paced (nonspeeded) conditions. In contrast, based on previous empirical and theoretical results discussed above, we hypothesized that older adults would differ from younger adults regarding the strength of motor synergies.

Constraining abundant degrees of freedom (reducing GEV) may be particularly adaptive for immediate repetitions of the very same action (e.g., pointing to a single target), where little variation is introduced externally by the task. According to this reasoning, the use of motor abundance should be lower in uniform and predictable target schedules, compared with mixed or unpredictable ones, and uniform schedules should enhance existing age differences.

The present study examines potential adult age differences in the structure of variability in manual pointing, using the UCM approach (Scholz and Schöner, 1999). Postural variability was decomposed with respect to finger tip position control. Based on the preceding considerations, we predicted that older adults would show reduced relative amounts of GEV (and lower synergy indexes) than younger adults. To assess sequence effects, 2 targets were used, which had to be pointed at according to 3 different target schedules: blocked, alternating, and random. Our goal was to explore influences of target schedule on the structure of movement variability and potential interactions with adult age, hypothesizing that age-differences would be most pronounced in the blocked condition.

2. Methods

2.1. Participants

Twelve younger (mean age $\pm$ SD: 25.5 $\pm$ 2.2 years; 6 women) and 12 older adults (73.4 $\pm$ 2.0 years; 5 women) were recruited via telephone interviews from the participant pool of the Max Planck Institute for Human Development, Berlin, Germany. All participants were healthy, in particular free from pain or other constraints related to arm, hand and shoulder movements, according to self-report. Based on self-report and a short questionnaire on daily activities, all participants were classified as right-handed.

Participants provided written consent prior to the experiment and received 10 Euro as reimbursement. The study was approved by the Ethics Committee of the Max Planck
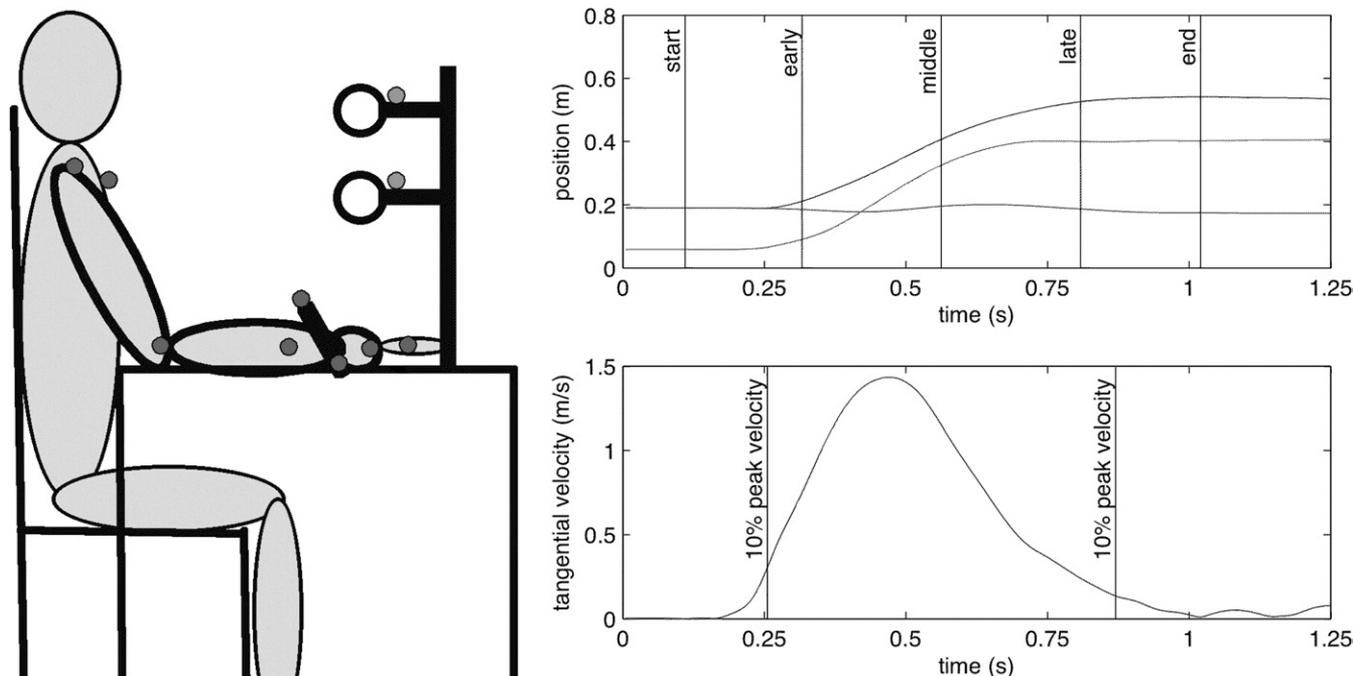
Fig. 1. Left: Setup and marker placement in start position. Note that the targets were placed in front of the left shoulder, thus the required movement trajectory was diagonally left and upward. Right: Illustration of the segmentation procedure. Cartesian 3-dimensional position data (top) and tangential velocity (bottom) of the finger tip. First, the main section of the pointing movement was determined as the interval during which the tangential velocity was above 10% of the peak velocity. Based on this, 5 time points of the movement (start, early, middle, late, and end) were determined. See text for more details.

Institute for Human Development and conducted in compliance with the declaration of Helsinki.

2.2. Setup and procedure

During the experiment, participants were comfortably seated on a chair at a height-adjusted table, with the left hand in the lap and the right hand resting on a cushion made of rubber foam, the lower arm pointing forward, and the tip of the index finger touching a small tactile marker, to ensure a consistent starting position. The experimenter continuously visually monitored the position of the right arm and index finger and intervened whenever the position was not appropriate.

Two pointing targets were mounted on a stand that was placed on the table (see Fig. 1). The position was individually adjusted for each participant, such that the target centers were in front of the left shoulder, displaced about 10 cm in upward and downward direction. The horizontal distance was chosen such that the participant could just reach (with extended arm) the target rings with the knuckles of his or her right hand. The orientation of the target rings was chosen to allow a comfortable pointing trajectory. To each target ring, a green light-emitting diode (LED) was attached that signaled the pointing target for the current trial.

The task consisted of moving the tip of the right index finger to the center of the target circle and holding it there for about half a second. Participants were told that it was not

required to react quickly but to produce smooth and precise pointing movements at a fast but comfortable speed. Moreover, participants were encouraged to lean into the chairback and instructed not to move their trunk when pointing to the target.

After instruction, participants were given practice trials (typically between 5 and 10) to become familiar with the task and to determine an appropriate movement speed. The actual experiment started immediately thereafter. Each participant completed 40 pointing trials (20 to each target) in each of 3 schedules: blocked (consecutive movements to the same target), alternating (switching between the 2 targets), and random order (pseudorandom sequence of upper and lower targets). After each of these blocks of 40 trials, a short break was taken. To avoid sequence effects, the order of schedule conditions, and the starting target (upper/lower) for the blocked and alternating schedules was counterbalanced across participants and within the 2 age groups.

2.3. Data collection and biomechanical model

Arm movements were recorded with an 8-camera VICON motion capture system (Vicon, Ltd, Oxford, UK), at a sampling rate of 200 Hz. Six reflective markers were attached with double-sided adhesives to the skin overlying the following bony landmarks on trunk and right arm: (1) sternal notch (STRN); (2) distal part of the acromioclavicular joint (ACR); (3) lateral epicondyle of the humerus

Table 1
Definitions of local coordinate systems (LCS)

Body part	LCS origin	Primary axis	Secondary axis	Relative markers
Trunk	STRN	X	Z	STRN
Shoulder	STRN	STRN–SJC	Z	STRN, ACR
Upper arm	SJC	SJC–EJC	EJC–WJC	ELB
Lower arm	EJC	EJC–WJC	LA2-LA3	LA1, LA2, LA3
Hand	WJC	WJC–HND	LA2-LA3	HND
Finger	HND	HND–FTIP	LA2-LA3	FNG, FTIP

X and Z refer to the global horizontal and vertical (pointing forward and upward relative to the subject's position). The primary axis defines the first axis of the LCS. The second and third axes of the LCS are defined by consecutive cross-products with the secondary axis to yield an orthogonal right-handed coordinate system. Note that the secondary axis is not necessarily constant with respect to the LCS.
Key: ACR, acromioclavicular joint; EJC, elbow joint center; ELB, lateral epicondyle of the humerus; FNG, head of the proximal phalanx of the index finger; FTIP, finger tip; HND, head of second metacarpal; LA1-LA3, lower arm; SJC, shoulder joint center; STRN, sternal notch; WJC, wrist joint center.

(ELB); (4) dorsal side of the lower arm, about 2 thirds of the distance from elbow to wrist (LA1); (5) just proximal to the head of second metacarpal (HND); (6) head of the proximal phalanx of the index finger (FNG). Two additional markers (LA2, LA3) were attached at the lower arm, to both ends of a 10-cm stick attached in mediolateral orientation at the wrist (see Fig. 1). The index finger was splinted in order to constrain motion to the metacarpophalangeal (MCP) joint. To estimate finger tip position (by linear extrapolation from the markers HND and FNG), the distance from the finger tip to the HND-marker was measured. Care was taken to ensure that finger tip and the HND- and FNG-markers were aligned. A (virtual) finger tip marker (FTIP) was defined based on this information.

Joint centers of the shoulder (glenohumeral joint), elbow, and wrist were estimated using a functional approach, based on calibration movements prior to the experiment. The center of the metacarpophalangeal joint was approximated by the position of the FNG marker. Calibration movements consisted of 5 repetitions of flexion/extension and abduction/adduction (for the shoulder), flexion/extension and supination/pronation (elbow), and flexion/extension and abduction/adduction (wrist), respectively. Joint center positions were determined relative to temporary local coordinate systems (LCS), using the least square regression described by Gamage and Lasenby (2002).

The shoulder joint center (SJC) was estimated from the motion of the ELB during calibration movements relative to a temporary shoulder LCS defined by the STRN-ACR axis and the global vertical (Z). This definition of the shoulder LCS is based on the assumption that motion at the sterno-clavicular joint occurs mainly in the protraction/retraction and elevation/depression directions, with no axial rotation around the clavicular axis. Due to this assumption, a single marker on the shoulder complex is sufficient to determine its orientation relative to the trunk. Thus, kinematic data of the ELB marker were transformed to the temporary shoulder LCS and used to estimate the center of rotation, that is the SJC. Similarly, the elbow and wrist joint centers (EJC, WJC) were determined relative to an LCS defined by the 3 lower-arm markers (LA1, LA2, LA3), based on the relative

motion of the SJC and HND, respectively. The accuracy of the least square regression can be assessed by the standard deviation of the distance between the estimated center of rotation and the moving landmark (ELB, SJC, HND). The error was small for each of the estimated joint centers (mean $\pm$ SD, SJC: 2.06 $\pm$ 0.74 mm; EJC: 2.46 $\pm$ 0.95 mm; WJC: 1.47 $\pm$ 1.77 mm), and did not differ between the age groups ($p > 0.1$).

Based on these computations, virtual markers (SJC, EJC, WJC) were added to the data. The actual LCS used for the angle computations were defined using this extended marker set, according to Table 1. As above, the definition of the shoulder LCS excludes axial rotation around the clavicular axis. Note that defining the upper arm LCS based on the orientation of the lower arm is only possible when the elbow is not fully extended. This was ensured during the experiment by the choice of target position, as described above.

The biomechanical model consists of the skeletal chain starting at the sternal notch (stern) and ending at the finger tip (FTIP). In total, 11 biomechanical degrees of freedom were modeled (names of the corresponding model angles are indicated in brackets): scapular abduction/adduction (SC1), elevation/depression (SC2), glenohumeral flexion/extension (SJ1), abduction/adduction (SJ2), and internal/external rotation (SJ3), elbow flexion/extension (EJ1) and forearm supination/pronation (EJ2), wrist flexion/extension (WJ1) and abduction/adduction (WJ2), finger flexion/extension (FJ1) and abduction/adduction (FJ2). The joint angles were determined by computing Euler angles from the rotation matrices describing relative orientation of proximal and distal LCS of the corresponding joint. The forward model was defined by reversing this computation, starting from the trunk as the base segment.

2.4. Data processing and analysis

Raw data were preprocessed and labeled using Vicon Nexus 1.1 (Vicon, Ltd, Oxford, UK). The experimenter (JV) manually checked all trials. Further processing was accomplished using custom-written MATLAB (Version 7.5, The MathWorks Inc., Natick, MA, USA) routines. Kinematic

data were interpolated (up to 5 missing samples, or 25 ms) using piecewise cubic splines and low-pass filtered at 10 Hz with a 2-pass third order Butterworth filter.

Calibration trials were processed to define the biomechanical model, as described above. Experimental trials were segmented according to the following procedure (see Fig. 1). The main movement was determined using a tangential velocity criterion, as the interval in which velocity was above 10% of the peak velocity of that trial. This interval was time-normalized to 0%–100% using cubic spline interpolation, to define 3 characteristic time points of the movement (early: 10%; middle: 50%; late: 90%). In addition, start and end position were determined as the minima of the tangential velocity up to 250 ms (50 samples) before and after the main movement.

Despite the instructions, all participants produced small trunk motion in the pointing movement. Therefore, to improve model accuracy, motion of the stern marker was averaged across trials within schedule and target conditions, to create an average trajectory serving as basis for the forward model. Subsequently, the model joint angles were computed. Accuracy of the forward model was assessed by comparing actual with reconstructed finger tip position. The average mean deviation was 6.25 mm (SD 2.62 mm) for younger adults, and 6.29 mm (SD 1.39 mm) for the older adults. The age groups did not differ significantly with respect to model accuracy ($t[16.7] = -0.06$, $p = 0.96$). This is important, because the quality of the forward model determines the accuracy of the decomposition into GEV and NGEV in the UCM analysis (de Freitas and Scholz, 2010).

2.5. Dependent variables

Trials were excluded from the analysis when quality of the raw data were insufficient or when the maximal deviation between actual and reconstructed finger tip position in that trial was higher than 30 mm. At least 15 trials per person and condition (schedule and target) entered the analysis, and there were no systematic differences between the age groups regarding the number of valid trials (on average 19.8, in both age groups).

2.5.1. Kinematic measures

As indexes of movement kinematics, movement duration, peak velocity, and time to peak velocity (expressed as percent of movement duration) were determined. To quantify trajectory variability, we computed, for each of the 5 characteristic time points (start, early, middle, late, end) the positional variability (average absolute deviation from mean trajectory) in finger tip position. Moreover, to assess motion at individual joints, joint angle excursions (maximal minus minimal value of a joint angle) over the pointing movement were determined for each trial.

2.5.2. Uncontrolled manifold analysis

The structure of variability was analyzed with the uncontrolled manifold (UCM) method (Scholz and Schöner, 1999). The UCM approach allows to partition postural variability in tasks exhibiting motor equivalence into goal-equivalent and nongoal-equivalent components. This is done based on a forward model, that is, a mapping from "posture space" to task space, $f: P \rightarrow T$. In the present case, the posture space P is 11-dimensional, representing the joint angles of the biomechanical model, and the task space T is 3-dimensional, representing the position of the finger tip. The forward model is defined as described above (section 2.3).

Postures (i.e., joint angle configurations) that project to the same point in task space form an 8-dimensional submanifold U of posture space (dimU + dimT = dimP), the so-called uncontrolled manifold (UCM). Postural deviations within U do not lead to deviations in task space, while deviations orthogonal to it do. Technically, the decomposition of variability into GEV and NGEV is achieved by locally approximating the forward model f by a linear mapping, the Jacobian $J = Df$ (estimated from f by numerical differentiation), and projecting postural deviations to the null-space of J (parallel to the UCM) and to its orthogonal complement (orthogonal to the UCM). The amount of total variance (trace of the covariance matrix) in each of these subspaces, normalized by the number of dimensions (8 and 3, respectively), is termed goal-equivalent and nongoal equivalent variability (GEV and NGEV), respectively.

The UCM analysis was performed across trials within each condition (specified by schedule and target) for each of the characteristic time points determined above (start, early, middle, late, and end). The variance components were computed as follows. Let N denote the orthogonal projection to the null space of J, C the projection to the orthogonal complement of the null space, and let $x_i \in P$ ($i = 1, \ldots, 20$) represent the postural deviations observed at the time point and under the condition under consideration. Then

$$GEV = \text{trace}(\text{cov}(Nx_i))/8$$
$$NGEV = \text{trace}(\text{cov}(Cx_i))/3$$

Here, cov denotes the covariance matrix and trace the matrix trace (sum of the diagonal entries). Based on the computation of GEV and NGEV, a synergy index $\alpha = GEV/NGEV$ was computed (e.g., Latash et al., 2007).

2.6. Statistical analysis

The dependent variables were determined either for each trial (movement duration, peak velocity, time to peak velocity, joint angle excursions) or for each of the characteristic time points for all trials of the same task schedule condition and target (model accuracy, variability of the trajectory, synergy index). The synergy index was log-transformed to correct for nonnormality (e.g., Hsu et al., 2007).

Table 2
Kinematic measures (mean $\pm$ SD, and t tests)

Measure	Younger	Older	Statistics
Movement duration (s)	0.66 $\pm$ 0.12	0.67 $\pm$ 0.10	$t(21.0) = -0.32$, $p = 0.75$
Peak velocity (m/s)	1.24 $\pm$ 0.20	1.36 $\pm$ 0.18	$t(21.7) = -1.59$, $p = 0.13$
Time to peak velocity (%)	35.44 $\pm$ 2.64	30.88 $\pm$ 3.85	$t(19.5) = 3.38$, $p < 0.01$
End point accuracy (mm)	4.55 $\pm$ 0.83	4.77 $\pm$ 0.64	$t(20.7) = -0.74$, $p = 0.46$

Dependent variables were submitted to a 2 (age group) $\times$ (sex) $\times$ 3 (schedule: blocked, alternating, random) analysis of variance (ANOVA), with schedule as within-subject factor. The factor target (upper, lower) was not included in the model because it was not of primary interest, and preliminary analyses did not show any relevant interactions with the other factors. For model accuracy, variability of the trajectory, and synergy index, this ANOVA was run separately for each of the 5 time points.

The critical level for statistical significance was set to 0.05 for dependent variables analyzed per trial, and to 0.01 for dependent variables analyzed for each of the 5 time points, to correct for multiple comparisons. Effect sizes are reported as (classical) $\eta^2 = SS_{explained}/SS_{total}$.

3. Results

3.1. Movement kinematics and model accuracy

Kinematic variables and the respective age group comparisons are summarized in Table 2. No significant effects were found for movement duration and peak velocity. Time to peak velocity showed a main effect of age group ($F[1,20] = 12.2$, $p < 0.005$, $\eta^2 = 0.29$), with smaller values in older adults. Model accuracy did not show significant effects at any of the characteristic time points. Variability of the finger tip trajectory did not show significant effects for start, middle, late, and end time points. For the early time point, an age group by sex interaction was found ($F[1,20] = 11.7$, $p < 0.005$, $\eta^2 = 0.21$). Importantly, the age groups did not differ in end point accuracy (see also Table 2), demonstrating that task performance was not affected by age at this level of analysis.

Joint angle excursions during the pointing movement are plotted in Fig. 2. Only EJ1 (elbow flexion/extension) showed a significant age effect ($F[1,20] = 33.0$, $p < 0.001$, $\eta^2 = 0.58$), with older adults on average exhibiting a larger elbow flexion over the course of the pointing movement. Additional analyses of starting and end postures showed that younger and older adults adopted similar starting positions for the elbow joints (mean $\pm$ SD, younger adults: 130.7 $\pm$ 9.2°; older adults: 132.6 $\pm$ 8.3°), but older adults ended the movement with a more flexed posture (younger adults: 126.4 $\pm$ 4.6°; older adults: 116.8 $\pm$ 10.8°; $F[1,20] = 10.0$, $p < 0.005$. $\eta^2 = 0.28$). Potential effects of this age difference on the UCM analysis were addressed by a separate analysis (see below).

3.2. Uncontrolled manifold analysis

For all participants and across schedules, targets, and time points, GEV was higher than NGEV (Fig. 3A). Thus the "control hypothesis" with respect to finger tip position (Latash et al., 2007) was satisfied. Summary statistics showed that the ratio between GEV and NGEV (the synergy index) had a median of 9.03, with first and third quartile at 4.27 and 18.54, respectively.

Statistical analysis of the log-transformed synergy index (see Fig. 3B) was done by time point. No significant effects were present for start, early, and middle time points. For the late time point, a main effect of age group was found ($F[1,20] = 26.9$, $p < 0.0001$, $\eta^2 = 0.36$). For the end point, a main effect of age group ($F[1,20] = 50.1$, $p < 0.0001$, $\eta^2 = 0.43$), and a marginally significant effect of sex ($F[1,20] = 7.49$, $p = 0.013$, $\eta^2 = 0.06$) were found. Higher synergy indexes were found in younger than in older adults, and a tendency for higher synergy indexes in women than in men. Target schedule did not have a reliable effect on the synergy index ($F[2,40] = 0.66$, $p = 0.52$, $\eta^2 = 0.006$).

3.3. Are age differences in motor synergies due to differences in movement kinematics or joint angle excursions?

Since statistically reliable differences between the age groups were found for 2 of the kinematic measures, time to peak velocity and elbow (EJ1) excursion, the question arises
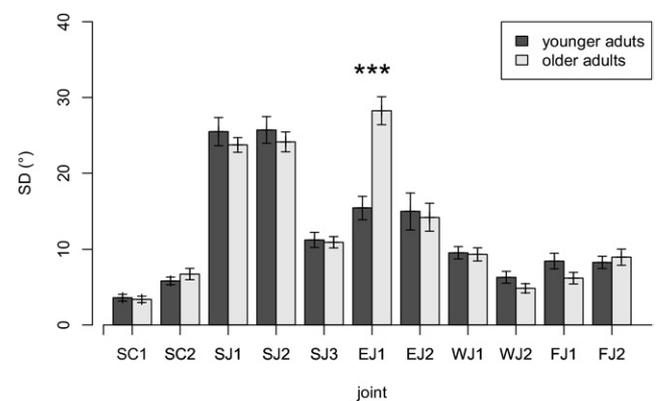

Fig. 2. Joint angle excursions (maximum minus minimum) during the pointing movement, for each joint angle and the 2 age groups. Significant differences between the age groups are indicated by stars (Welch's 2-sample t test; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Error bars represent standard error of the mean (SEM).
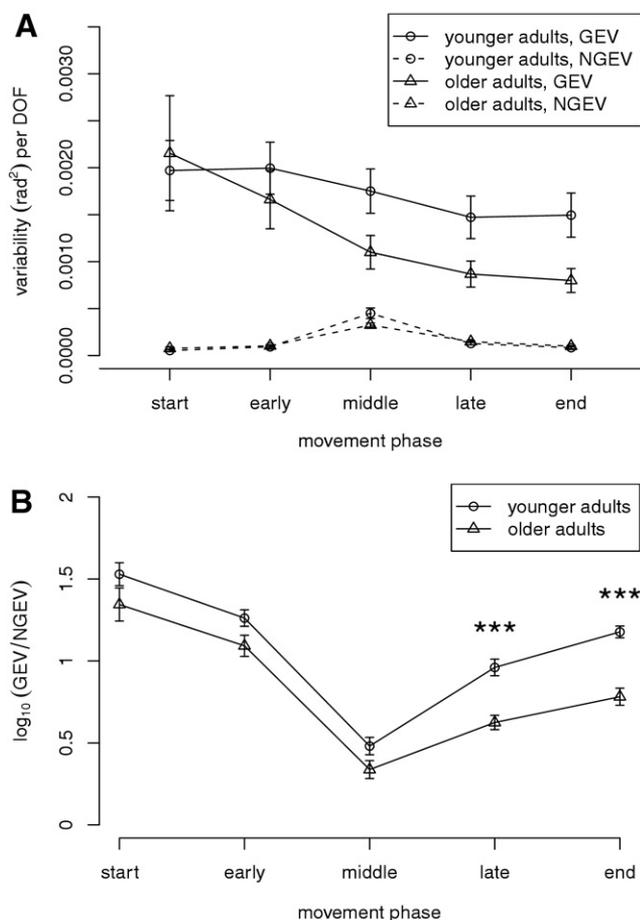
Fig. 3. Results of the uncontrolled manifold (UCM) analysis as a function of movement phase and age group. (A) Goal-equivalent and nongoal-equivalent variability (GEV, NGEV). (B) UCM index (log₁₀[GEV/NGEV]; see text). In (B) significant differences between the age groups are indicated by stars (Welch's 2-sample *t* test; *$p < 0.01$, **$p < 0.001$, ***$p < 0.0001$). Error bars represent standard error of the mean (SEM).

whether age differences in synergy indexes at the late and end time point may be due to age differences in task kinematics. This question was addressed in 2 ways. First, the ANOVAs for the synergy index were repeated with the 2 kinematic measures as covariates. In this analysis, elbow joint excursion showed a significant effect on the synergy index for the "late" and "end" time points (late: $F[1,17] = 12.6, p < 0.05, \eta^2 = 0.19$; end: $F[1,17] = 26.0, p < 0.0001, \eta^2 = 0.21$), but did not eliminate the age group effect (late: $F[1,17] = 13.7, p < 0.005, \eta^2 = 0.21$; end: $F[1,17] = 23.5, p < 0.0005, \eta^2 = 0.19$). The time to peak velocity did not show a significant effect in this analysis. To more directly test for potential influences of these 2 kinematic measures on the synergy index, we correlated each of the measures within age groups with the synergy index. Elbow excursion did not correlate significantly with the synergy index ($p > 0.3$ for all time points). Time to peak velocity correlated negatively with the synergy index for the older adults for the "late" and "end" time points (late: $\rho = -0.62, p < 0.0001$;

end: $\rho = -0.51, p < 0.005$), but not for the younger adults ($p > 0.2$ in all cases). Thus, in the older (but not in the younger) adults, a shorter relative time to peak velocity was associated with a higher synergy index.

4. Discussion

4.1. Main results

We investigated adult age-related age differences in the structure of variability in a manual pointing task, predicting that older adults would show weaker motor synergies, that is, less flexible use of motor abundance than younger adults. This main hypothesis of the present study was confirmed: at the end of the pointing movement, younger adults showed higher synergy indexes (defined as the ratio between goal-equivalent and nongoal-equivalent variability, GEV and NGEV) than older adults. Because age differences in the structure of movement variability were hypothesized to be due to constraining abundant degrees of freedom in active movement (as opposed to a passive resting position before the movement), it is plausible that age effects should be most pronounced toward the end of the movement.

The observed age-related differences in motor synergies are not explained by differences in model accuracy or basic kinematic variables. Model accuracy did not differ between age groups, which is an important control measure because inaccuracies in the biomechanical model may affect the partition of variability into goal-equivalent and nongoal-equivalent components (de Freitas and Scholz, 2010). Likewise, no age-related differences were found for movement duration, peak velocity, or end point accuracy. However, relative time to peak velocity was shorter in older adults. This may reflect a prolonged "homing in" phase of the movement in the older adults, indicating increased reliance on visual feedback (Seidler-Dobrin and Stelmach, 1998). The influence of such an altered control strategy on the structure of movement variability is difficult to estimate. Performing a larger portion of the movement under visual feedback control may be hypothesized to either decrease the amount of NGEV (as it improves accuracy) and/or to increase the amount of GEV (as such a control scheme prioritizes end-point position rather than overall posture), and would hence bias the results in a direction opposite to the observed age differences. In accordance with the latter line of reasoning, a negative correlation was found in the older adults between time to peak velocity and synergy index at the end of the movement. In addition, temporal normalization of movements with different velocity profile may lead to a comparison of functionally different time points. Note however that the significant age differences in synergy indexes were found at the late and end time points, that is at time points with low rate of position change (see Fig. 1, right panel), suggesting that the age effects are not artifacts of time normalization. Age differences were also present concerning joint angle excursion of the elbow (flexion/

extension). Additional statistical analyses (analysis of covariance [ANCOVA], correlation) confirmed that this did not explain the observed age differences in synergy indexes.

Contrary to our second, more exploratory hypothesis, target schedule (blocked, alternating, random) did not influence the synergy index. It is possible that potential effects of target schedule would only be apparent under more challenging (for instance speeded) conditions; in the present design, all conditions were very simple for all participants (according to informal self-report). Synergy indexes tended to be higher in women than in men, but this effect did not interact with age group. Given that the sex effect was only marginally significant and did not interact with age, the target dimension of this study, we refrain from interpreting it.

4.2. Discussion

The results of this study extend previous findings of adult age-related differences in the structure of movement variability from tasks of multifinger force coordination (Olafsdottir et al., 2007; Shim et al., 2004; Shinohara et al., 2004) to the task of manual pointing. Taken together, the previous studies as well as the present study provide converging evidence that normal aging affects the organization of variability in multidegree of freedom movements, with older adults making less flexible use of motor abundance. Note that the overall postural variability was lower in older relative to younger adults in the present study, indicating that the relationship between neuromuscular noise and the amount and structure of movement variability is not straightforward, but is likely be mediated by adaptation processes (Latash and Anson, 1996). We propose that in the present study, older adults may have achieved similar levels of end point accuracy by using lower amounts of motor abundance. This will be discussed in more detail below.

Converging evidence for age-related reductions in the use of motor abundance, based on methods other than the UCM approach, comes from studies investigating age-related differences in quiet standing. A direct comparison to the present study is not possible as these studies did not formally analyze motor equivalence, but their results point in the same direction. For instance, elevated levels of muscular cocontraction were observed in older relative to younger adults (Benjuya et al., 2004), which was interpreted as a strategy of stiffening/freezing the lower extremities. Moreover, older adults were found to differ from younger adults in intersegmental coordination as assessed by accelerometers along the central body axis (Accornero et al., 1997), with older adults tending to sway in an "en bloc" pattern. In line with this, (Gariépy et al. (2008) (found higher positive cross-correlations between body sway at the shoulder and hip level in older adults than in younger adults. In the same study, constraining biomechanical DOFs by means of a wooden backboard led to a pronounced increase in body sway in younger but not in older adults, suggesting that the latter were not using the available DOFs for stabilizing their balance in the first place.

At a more general level, our findings are compatible with the reduced complexity/adaptability hypothesis of physiological aging (Lipsitz, 2004; Thaler, 2002; Vaillancourt and Newell, 2002). According to the proposal by Thaler (2002), normal aging is associated with a decline in the variety of available system states and responses. In multi-DOF movements such a decline would entail a reduced ability to appropriately organize variability across the effector system in a task-specific motor-equivalent way, predicted to lead either directly to increased task variability (not observed in the present study, probably due to the simplicity of the task), or more indirectly to reduced variability in elemental variables (found in the present study), possibly reflecting a compensatory strategy of constraining motor abundance.

Recently, Latash (2008, section 6.4) proposed that constraining motor abundance may be an adaptive "choice" for a system faced with sensorimotor decline and increased neuromuscular noise (Enoka et al., 2003), a view partly supported by earlier modeling results (Todorov and Jordan, 2002). In the present study, older participants may have perceived the task as more challenging or may have been operating closer to their performance limits than the younger participants, and this may have influenced them to rely on a more conservative control strategy of constraining motor abundance. In line with this reasoning, in a study manipulating accuracy constraints in manual pointing (Tseng et al., 2003) in young adults, participants used lower amounts of GEV when pointing to targets with higher indexes of difficulty. On the other hand, the ability for fast online movement corrections, which seems to be impaired in older adults (Sarlegna, 2006), was found to be related to the availability and use of motor abundance (de Freitas et al., 2007; Robertson and Miall, 1997). Potential interactions between a strategy of restraining motor abundance at the level biomechanical degrees of freedom and age-related changes in response flexibility at other behavioral levels remain to be investigated.

Little is known about the neural representations underlying motor-equivalent control of task-related variables and potential age-related changes therein. The dedifferentiation hypothesis holds that neural structure-function relationship become less precise with age (Seidler et al., 2009). In the cognitive domain, a neurocomputational model has been proposed that links age-related changes in neuromodulatory mechanisms to less distinct of neural representations (Li et al., 2001) implicated in working memory or attention. This reduction in representational variety is hypothesized to underlie behavioral manifestations of age-related deficits in the cognitive domain, an explanatory approach that parallels that of Thaler (2002). Thus, reduction in the distinctness of sensorimotor representations in the central nervous system may be underlie age-related difference in the use of motor abundance. This explanatory approach is speculative at

present, but worthy of investigation in future empirical or modeling work.

4.3. Conclusion

In this study, we found that the use of motor abundance in a simple manual pointing task was reduced in older adults relative to younger adults, in the absence of marked differences in pointing accuracy or speed. Future research should investigate whether and in which way age-related differences in the structure of movement variability are related to performance differences in more complex and challenging motor tasks.

Disclosure statement

The authors declare that there are no actual or potential conflicts of interest.

The study was approved by the Ethics Committee of the Max Planck Institute for Human Development, Berlin, and conducted in compliance with the declaration of Helsinki.

Acknowledgements

Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: 10.1016/j.neurobiolaging.2010.07.006.

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