

EFFECTS OF AGING ON INTERLIMB COORDINATION - KINEMATICS AND KINETICS ANALYSIS OF ARM REACHING

Leia B. Bagesteiro, leia.bagesteiro@ufabc.edu.br

CECS, Universidade Federal do ABC, Santo Andre, SP, Brazil.
Laboratorio de NeuroMecanica, UNICID, Sao Paulo, SP, Brazil.

Robert L. Sainburg, rls45@psu.edu

Kinesiology, Penn State University, University Park, PA, USA.

Abstract. *Previous findings in elderly adults suggest that numerous aspects of motor control are affected by aging. There seem to be fundamental differences in motor control strategies between young and old adults. Prior research has demonstrated significant interlimb differences in the control of unilateral reaching movements, implying that movement trajectory and final position are specified and controlled differentially by the dominant and nondominant limb/hemisphere systems. Our goal in the present study was to determine whether interjoint coordination remains lateralized for older subjects. To test this hypothesis we analyzed and quantified the kinematics and kinetics of reaching movements. Joint torques were calculated for shoulder and elbow assuming that the upper extremity was two interconnected rigid links (upper arm and forearm) with frictionless joints at the shoulder and elbow. The shoulder was allowed to move freely, and the torques resulting from linear accelerations of the shoulder were included in the equations of motion for each joint. Three subject age groups were examined: young (19-24 years), older (65+ years), and oldest-old (80+ years). We used a virtual reality environment and presented two targets that required 15cm-long movements (target 1 oriented 135° relative to the horizontal axis and target 2 oriented at 45°). Each subject was given a practice session (40 trials) to familiarize themselves with the task, followed by another 40-trial experimental session. Consecutive planar reaching movements were alternated between the two targets. In addition, subjects were to match their hand velocity within a 0.4 to 0.7m/s range. Eight measures were computed to investigate group interlimb differences: shoulder and elbow torque impulses, distance error at final position, hand-path trajectory direction deviation, movement distance, movement duration, peak hand acceleration, and acceleration duration. Preliminary data analysis showed differences between left and right performance for the very old group. Our initial results indicate that interlimb (right/left difference) peak acceleration ($3.62 \pm 1.45\text{m/s}^2$) and acceleration duration ($0.36 \pm 0.08\text{s}$) were equivalent as compared to the young and elderly groups. They also showed a trend in joint torques and trajectory deviations for the right arm advantage in movement trajectory performance. The mean hand velocity was 0.50m/s (± 0.08) for all groups. As expected elderly subjects (old: $0.82 \pm 0.12\text{s}$; and oldest-old: $0.85 \pm 0.14\text{s}$) required more time than young ($0.67 \pm 0.06\text{s}$) subjects to reach the target. These results suggest that elderly subjects show a reduction in lateralization in interjoint coordination although aging differences could be manifested by greater dependency on slower feedback processes instead of rapid on-line feedforward sensory processes.*

Keywords: visuomotor rotation, inertial load, adaptation, aging.

1. INTRODUCTION

Age related deficits in motor coordination have been well documented; yet the cause of these deficits remains incompletely understood. Whereas aging results in decrements in sensory resolution and muscle strength (Cole et al. 1999, 1998; Grabiner and Enoka 1995) as well as reductions in muscle mass (Larsson et al. 1979, Schultz 1992), and force production (Cole 1991), these factors alone have been unable to account for functional coordination deficits in the elderly (Cole et al. 1998; Ketcham et al. 2002; Seidler et al. 2002). This suggests that age related changes in coordination might also result from deficits in neural control factors. Cabeza and colleagues (Cabeza 2002; Cabeza et al. 2002; Cabeza et al. 2003; Dolcos et al. 2002) have reported substantial evidence that neural lateralization for cognitive factors becomes substantially reduced in people who are older than 65 years of age. These findings, based on neural imaging, have led to the model of Hemispheric Asymmetry Reduction in Older adults (HAROLD model). Whether lateralization of motor processes also becomes reduced during aging remains unknown. It is plausible that a significant source of coordination deficits in the elderly arise from reductions in hemispheric asymmetry. Previous work have consistently demonstrated dominant arm advantages in interjoint coordination, as reflected by more efficient control of intersegmental dynamics (Bagesteiro and Sainburg 2002; Sainburg 2002; Sainburg and Kalakanis 2000). These studies have also proposed that trajectory and position control mechanisms have been specialized to the dominant and nondominant hemisphere/limb systems, respectively. Based on these earlier researches, we hypothesized that age related effects in motor lateralization would produce deficits in intersegmental coordination, when comparing the performance in three different age groups. Movements were made to two different visual targets, with different joint excursion requirements, and performed with both, dominant and nondominant arms, one at a time. To minimize velocity effects we imposed a peak velocity range to be matched by the participants. We were, thus, able to examine

how subjects from different age groups coordinated multidirectional reaching movements in the horizontal plane, and investigate if the dominant arm advantage in trajectory control persists, as individuals grow older. In order to analyze movement coordination we selected specific features of the movements such as: trajectory deviation from linearity, final position error, movement distance, movement duration, peak tangential hand acceleration, acceleration duration, and joint (elbow and shoulder) muscle torques.

2. METHODOLOGY

2.1. Participants

Thirty-four unpaid women participated in the experiment performing fast point-to-point arm reaching movements. Three subject groups were examined: young, older, and oldest-old. All participants were right-handed, as indicated by laterality scores on a 34-item modified version of the Edinburgh Inventory (Oldfield, 1971), and were naïve to the purpose of the experiment. No subject reported any history of neurological or musculoskeletal disease. All participants performed the Mini-Mental State Examination score (MMSE; Folstein et al. 1975); and had normal visual acuity (uncorrected or corrected with lenses), as evaluated by the Snellen eye chart (Schwiegerling, 2004). Maximal grip strength was measured using a Jamar dynamometer (Asimow Engineering). Table 1 summarizes the characteristics of each subject group. A brief explanation of the experiment was given to all volunteers and a signed consent form was acquired in accordance with human subject policies. The study was approved by the ethical committee of the local university.

Table 1. Summary of participants' information.

Variable (mean ± SD)	Young	Older	Oldest-old
N	12	12	10
Age (years)	24 ± 5	69 ± 4	83 ± 3
Weight (kg)	59.5 ± 9.4	62.1 ± 8.7	67.4 ± 6.3
Height (m)	1.61 ± 0.04	1.53 ± 0.05	1.52 ± 0.05
MMSE score	29 ± 1	27 ± 2	27 ± 2
Visual acuity (metric scale)	8.2 ± 1.0	5.6 ± 1.8	5.2 ± 1.3
Hand grip (N)	283 ± 62	197 ± 42	159 ± 41

2.2. Experimental setup

Figure 1 illustrates the experiment setup. Subjects sat facing a table with both arms supported over the horizontal surface, positioned just below shoulder height (adjusted to subjects' comfort), by separated air-jets system, which reduces the effects of gravity and friction. A cursor representing finger position, a start circle, and a target were projected on a horizontal back-projection screen positioned above the arm. A mirror, positioned parallel and below this screen, reflected the visual display, so as to give the illusion that the display was in the same horizontal plane as the fingertip. Calibration of the display assured that this projection was veridical. All joints distal to the elbow were immobilized using an adjustable brace. Position and orientation of each arm segment was sampled using a Flock of birds® (Ascension-Technology) magnetic 6-DOF movement recording system. Four 6-DOF sensors were used to monitor arm movements. Each arm had a single sensor attached to the upper-arm segment via an adjustable plastic cuff, while another sensor was fixed to the air sled where the forearm was fitted. The sensors were positioned approximately at the center of the limb.

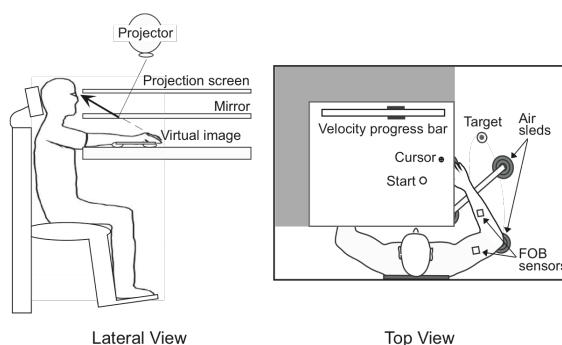


Figure 1. Experimental apparatus (lateral and top view).

Digital data was collected at 103Hz using a Macintosh computer, which controlled the sensors through separated serial ports, and stored on disk for further analysis. Custom computer algorithms for experiment control and data analysis were written in REAL BASIC™ (REAL Software, Inc.) and IgorPro™ (Wavemetrics, Inc.).

2.3. Experimental task

Throughout the experiment, the index finger position was displayed in real time as a screen cursor. We presented two targets that required 15-cm-long movements, “target 1” oriented 135° relative to the horizontal axis (i.e. requiring shoulder and elbow joints movements), and “target 2” oriented at 45° (i.e. requiring mostly elbow joint movement). Prior to movement, one of the two targets was randomly displayed. Participants were to hold the cursor within the starting circle for 0.3 seconds to initiate each trial. They were instructed to move the finger to the target using a single, uncorrected, rapid motion in response to an audiovisual “go” signal. Feedback regarding peak velocity was provided as a progress-bar display. Participants were trained to produce peak velocities ranging from 0.4 to 0.7m/s during the familiarization session (40 trials). Visual feedback of the cursor was provided during the entire session, and points were awarded for final position accuracy when the movement also satisfied the peak velocity requirement. Final position errors of less than 1cm were awarded 10 points, while errors between 1cm and 2cm were awarded 3 points, and errors between 2cm and 3cm were awarded 1 point. Points were displayed following each trial. Each subject was given a practice session (40 trials) to familiarize themselves with the task, followed by another 40-trials experimental session.

2.4. Kinematic data analysis

The 3-D position of the hand point, and elbow were calculated from sensor position and orientation data. Then joint angle was calculated from these data. All kinematic data was low pass filtered at 8 Hz (3rd order, no-lag, dual pass Butterworth), and differentiated to yield velocity and acceleration values. Each trial usually started with the hand at zero velocity, but small oscillations of the hand sometimes occurred within the start circle. In this case, the onset of movement was defined by the last minimum (below 6% maximum tangential velocity) prior to the maximum in the index finger’s tangential velocity profile. Movement termination was defined as the first minimum (below 6% maximum tangential hand velocity) following the peak in tangential hand velocity. Hand paths were calculated from joint angle data by using the measured length of the upper arm and the distance from the elbow to the index finger tip. The angular data was transformed to a Cartesian coordinate system with origin at the shoulder. Visual inspection was performed on every single trial to ensure that movement onset, peak acceleration, peak velocity, and movement termination were correctly determined.

Two measures of movement accuracy were calculated from the hand path: final position error, and hand-path deviation from linearity. Final position error was calculated as the distance between the index finger location at movement end and the target position. Deviation from linearity was assessed as the minor axis divided by the major axis of the hand path. The major axis was defined as the largest distance between any two points in the path, while the minor axis was defined as the largest distance, perpendicular to the major axis, between any two points in the path (Sainburg *et al.* 1993; Sainburg, 2002). This measure reflects interjoint coordination, as differences in linearity necessarily result from differences in coordination between the segments during movement. We also analyzed: peak tangential hand velocity, peak tangential hand acceleration, movement duration (defined as the elapsed time from movement start to movement end), acceleration duration (defined as the elapsed time from movement start to the time of peak hand velocity), and total distance traveled (calculated as the 2D distance between the start and the final location of the hand).

2.5. Kinetic data analysis

Shoulder and elbow torques were calculated using equations that model the upper arm and forearm as rigid interconnected units with frictionless joints at the shoulder and elbow. The shoulder was allowed to move freely, and the torques resulting from linear accelerations of the shoulder were included in the equations of motion for each joint. To separately analyze the effects of intersegmental forces and muscle forces on arm motion, we partitioned the terms of the equations of motion at the joint into three main components: interaction torque, muscle torque, and net torque (Sainburg *et al.* 1995, 1999). At each joint, interaction torque represents the rotational effect of the forces caused by the rotation and linear motion of the other segment. The muscle torque predominantly represents the rotational effect of muscle forces acting on the segment. However, muscle joint torque also includes the passive effects of soft tissue deformation and does not distinguish muscle forces that counter one another during co-contraction. Finally, the net torque is equal to the combined muscle and interaction torques, which is directly proportional to the joint acceleration.

Torques were computed and analyzed for the shoulder and elbow joint as detailed in the equations below. The mass of the forearm support is 0.58 kg, whereas the inertia is 0.0247 kg/m². Arm segment inertia, center of mass, and mass were computed from regression equations using subjects’ body mass and measured arm segment lengths (Winter 1990).

Elbow joint torques:

$$T_{e_I} = m_e r_e \sin(\theta_s + \theta_e) \ddot{x} - m_e r_e \cos(\theta_s + \theta_e) \ddot{y} - l_s m_e r_e \sin(\theta_e) \dot{\theta}_s^2 - (I_e + m_e r_e (r_e + l_s \cos(\theta_e))) \ddot{\theta}_s$$

$$T_{e_N} = (I_e + m_e r_e^2) \ddot{\theta}_e$$

$$T_{e_M} = T_{e_N} - T_{e_I}$$

Shoulder joint torques:

$$T_{s_I} = (m_s r_s \sin(\theta_s) + m_e l_s \sin(\theta_s)) \ddot{x} - (m_s r_s \cos(\theta_s) + m_e l_s \cos(\theta_s)) \ddot{y}$$

$$- (m_e r_e (l_e \cos(\theta_e) \ddot{\theta}_e + l_s \sin(\theta_e) \dot{\theta}_e^2 + 2l_s \sin(\theta_e) \dot{\theta}_s \dot{\theta}_e + l_s \sin(\theta_e) \dot{\theta}_s^2))$$

$$T_{s_N} = (I_s + m_s r_s^2 + m_e l_s^2 + m_e l_s r_e \cos(\theta_e)) \ddot{\theta}_s$$

$$T_{s_M} = T_{s_N} - T_{s_I} + T_{e_M}$$

where: m is mass of segment, r is center of mass of segment, l is length of segment, I is inertia of segment, θ_s is shoulder angle, θ_e is angle between center of mass of lower arm segment and upper arm, x is shoulder position along x direction, y is shoulder position along y direction, T_{e_I} is Elbow Interaction torque, T_{e_M} is Elbow Muscle torque, T_{e_N} is Elbow Net torque, T_{s_I} is Shoulder Interaction torque, T_{s_M} is Shoulder Muscle torque, T_{s_N} is Shoulder Net torque. The subscripts are defined as follows: s is upper arm segment, e is lower arm segment (including support and air sled device).

Shoulder and elbow torque impulse was calculated by integrating the absolute values of the torque profiles at each joint over the interval corresponding to the segment (movement initiation to movement end). Total torque impulse for each segment was calculated as the sum of the torque impulses.

2.6. Statistical analysis

Means of the individual dependent measures of task performance were analyzed using repeated-measures ANOVA (3 (Age) x 2 (Target) x 2 (Arm)) with one between-subject factor (Age: Young, Older and Oldest-old) and two within-subject factors (Target direction: 45° and 135°; and Arm: Dominant and Non-dominant). Subjects were treated as a random factor. For all analysis, statistical significance was tested using an alpha value of 0.05 and Tukey-Kramer honestly significantly different (HSD) tests were used for post-hoc analysis.

3. RESULTS

3.1. Task performance – hand path trajectory

Typical non-dominant and dominant hand trajectories for representative subjects, relative to each target are illustrated in Figure 2. Whereas the starting circles were in the midline position for the two movements, the positions were mirror reversed in a right-hand coordinate system for the non-dominant hand paths for clarity. While the dominant hand path is directed toward the target at movement initiation, the non-dominant path is initially directed laterally, hooking back towards the target at the end of motion. Non-dominant arm was consistently less linear to directions requiring greater interjoint coordination, regardless of age group.

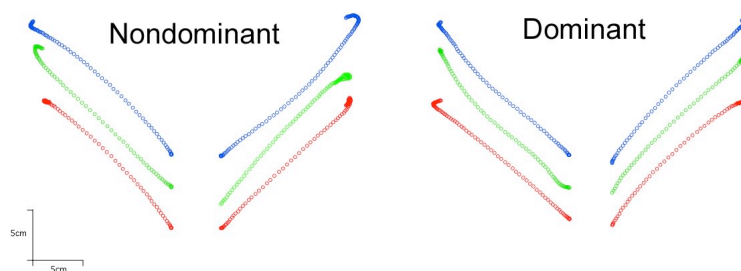


Figure 2. Hand path trajectories for movements toward the two different targets (45° and 135°) are displayed for a representative subject from each experimental group (young = red, old = green, and oldest-old = blue).

Figure 3 shows the means and standard errors (SE) for the final position error and deviation from linearity of the dominant and nondominant arms for each age group. Final positions of the elderly groups were less accurate and more variable than the young group for both hands. Thus, there was significant difference between groups for final position error [$P = 0.048$] (Fig. 3A). There was a significant interaction between hand and group for trajectory deviation from linearity [$P = 0.040$] (Fig. 3B). Interestingly, both elderly groups increased deviation from linearity, as more intersegmental coordination was necessary to perform movements toward the 135° target, presenting as much deviation as the dominant hand of the young subjects. Also, elderly groups showed similar performance between the hands indicating decrease in lateralization with age.

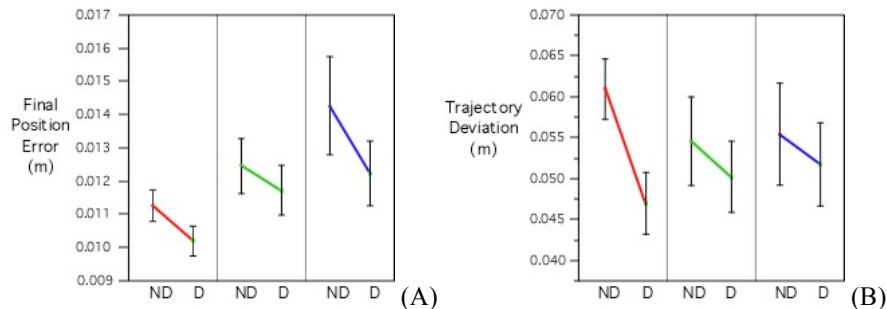


Figure 3. Means and SE for final position error (A) and deviation from linearity (B) for each experimental group (ND = nondominant, D = dominant; young = red, old = green, and oldest-old = blue).

Movement duration was systematically longer for the elderly than for the young subjects, irrespective of arm [$P = 0.001$]. Thus, regardless of the arm performing the movement, elderly subjects showed prolonged movement durations as compared to the young subjects. There was no significant difference on movement distance.

3.2. Hand kinematics – velocity and acceleration

Figure 4A shows hand velocity profiles from representative subjects, relative to each age group. As anticipated by the velocity controlled experimental task, there was no significant difference in peak hand velocity among groups. For all subjects, velocity profiles tended to be unimodal. Also there was no difference between hands and targets, with peak hand velocity ranging in average from 0.52 to 0.55m/s (young group: 0.55m/s \pm 0.05; older group: 0.55m/s \pm 0.06; oldest-old group: 0.52m/s \pm 0.06 - Mean \pm SD) (see Fig. 4B).

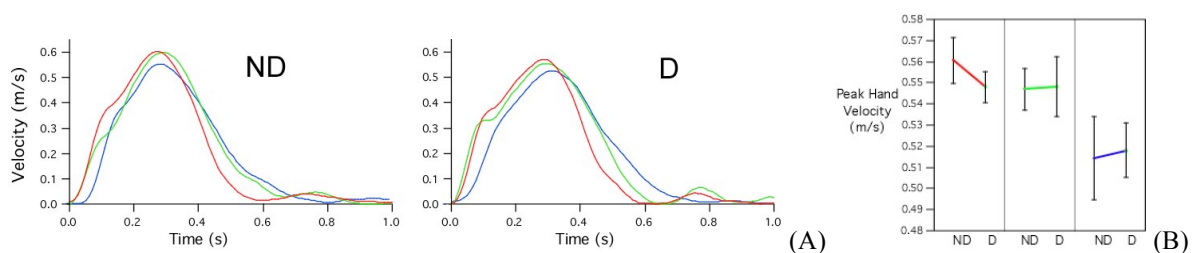


Figure 4. (A) Tangential velocity profiles for representative adults from each age group. (B) Means and SE for peak hand velocity of the three age groups. (ND = nondominant, D = dominant; young = red, old = green, and oldest-old = blue).

Figure 5A shows the acceleration profiles that correspond to the velocity profiles (Fig. 4A). The characteristic unimodal velocity profiles were produced by biphasic acceleration profiles. The initial peak in tangential acceleration is nearly constant across all age groups, so was the duration of the first acceleration pulse. However, the elderly groups generated lower peak accelerations, and achieve similar velocities by extending the duration of accelerations. Thus, there was no significant difference between groups, hands or targets, with peak hand acceleration averaging from 4.15 and 4.79m/s² (young group: 4.79m/s² \pm 1.71; older group: 4.38m/s² \pm 1.49; oldest-old group: 4.15m/s² \pm 1.53 - Mean \pm SD) (see Fig. 5B).

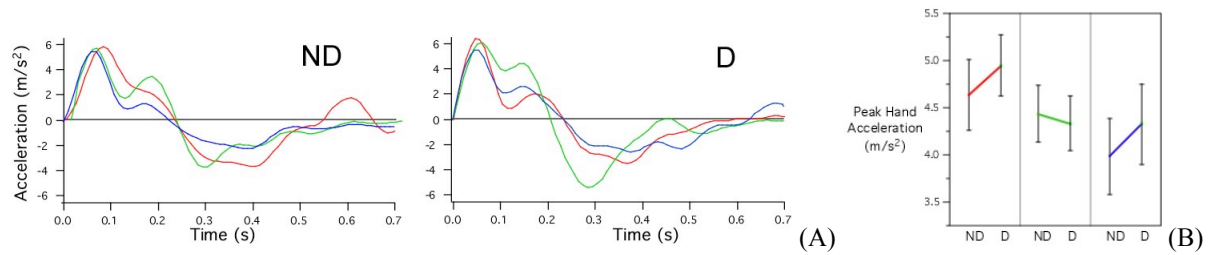


Figure 5. (A) Tangential acceleration profiles for representative adults from each age group. (B) Means and SE for peak hand acceleration of the three age groups. (ND = nondominant, D = dominant; young = red, old = green, and oldest-old = blue).

3.3. Hand kinetics – elbow and shoulder torques

The joint torque profiles representing the three different age groups are shown in Figs. 6A and 7A. Elbow and shoulder muscle torque profiles are shown from 10ms preceding movement initiation to 500 ms following movement initiation. At the elbow (Fig. 6A), muscle torque showed similar extensor phases for both elderly groups regardless of the hand performing the movement, whereas the young group showed significant higher extensor torque for the nondominant hand as compared to the dominant hand. This smaller torque output of dominant arm muscles was associated with equal speed and final position accuracy to that of the nondominant arm, suggesting a more torque-efficient strategy. These findings were confirmed with the measures of extensor muscle torque impulse, calculated over the entire movement, for all groups shown in Fig. 6B. Both elderly groups showed no significant difference between hands or target direction, which also indicate a decrease in lateralization for these subjects.

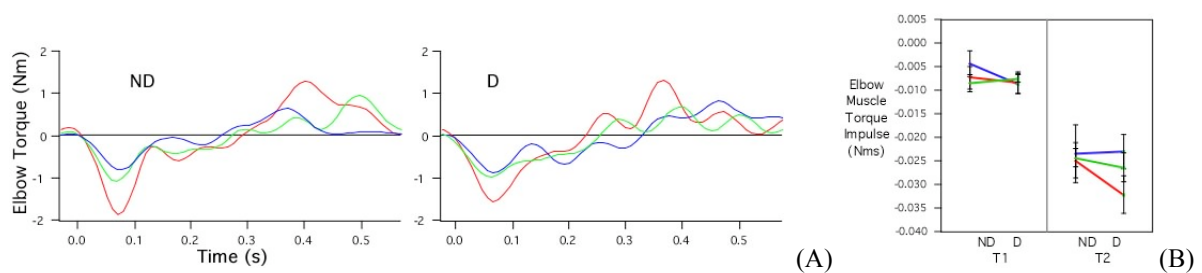


Figure 6. (A) Elbow muscle torque profiles for representative adults from each age group. (B) Means and SE for elbow muscle torque impulse of the three age groups by targets. (ND = nondominant, D = dominant; young = red, old = green, and oldest-old = blue; T1 = target 135°, T2 = target 45°).

Shoulder muscle torque profiles (Fig. 7A) showed similar initial extensor phase for dominant arm in all subjects, whereas the nondominant arm presented slightly different results, particularly at the flexor phase of movement. Shoulder extensor muscle torque counters the effects of elbow muscle actions on the upper arm that primarily results from motion of the forearm, thereby stabilizing the shoulder. As illustrated in Fig. 7B muscle torque impulse was systematically similar across all elderly subjects and for both target direction. Again, it seemed clear the effect of lateralization decrease for these subjects.

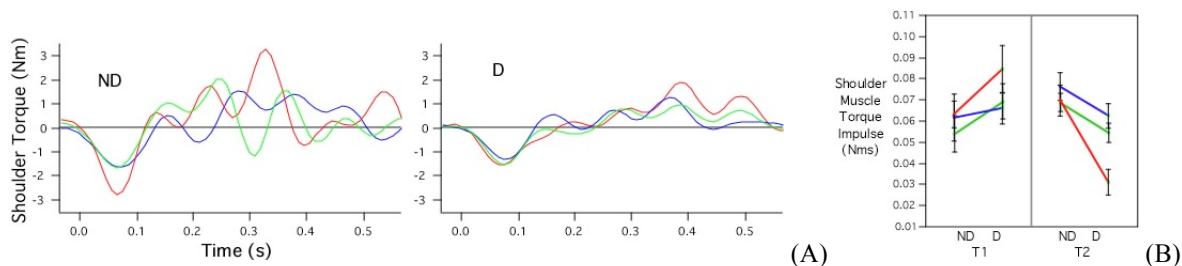


Figure 7. (A) Shoulder muscle torque profiles for representative adults from each age group. (B) Means and SE for shoulder muscle torque impulse of the three age groups by targets. (ND = nondominant, D = dominant; young = red, old = green, and oldest-old = blue; T1 = target 135°, T2 = target 45°).

4. DISCUSSION

The purpose of this study was to investigate if aging reduces asymmetries in intersegmental coordination. We were thus mainly interested in assessing the age-related changes in controlling targeted reaching movements in elderly adults, and exploring interlimb differences, which might be associated with changes in interjoint coordination. Our findings were consistent with previous studies indicating that aging results in slower movements and also becoming more symmetric with respect to speed. Nevertheless, contrary to other studies, we showed preservation in intersegmental coordination, indicating no reduced lateralization for motor coordination in the elderly group.

The idea that neural lateralization for cognitive processes is reduced in elderly subjects has been well documented. Previous studies have shown that normal aging is associated with a variable decline of performance in both cognitive and motor tasks (Cole and Rotella 2001; Spirduso et al. 2004; D'Esposito et al., 1999; Pohl et al. 1996; Grady et al., 1994; Harrington and Haaland 1992; Shimoyama et al., 1990; Smith et al., 1999). Most predominantly are morphological and neurochemical changes (Morrison and Hof, 1997; Grachev and Apkarian, 2001), with extensive changes in gray matter and white matter (Cook et al., 2002; Anderson and Rutledge, 1996; Good et al., 2001; Liu et al., 2003), particularly in frontal and temporal lobes (Head et al., 2004; Raz et al., 1997; Scahill et al., 2003), and regarding the motor system, different patterns in association with increasing age in the primary motor cortex (Kaiser et al., 2005). Functional neuro-imaging in normal aging tends to show a similar pattern of age-related changes in brain activity during both motor (Calautti et al., 2001; Hutchinson et al., 2002; Mattay et al., 2002; Ward and Frackowiak, 2003) and cognitive tasks, consisting in an increase and bilateralization of activation in older as compared to young subjects, especially when the task involves similar performance levels as in younger subjects (Cabeza et al., 2002). These changes have been widely interpreted as amplified neural recruitment by the brain to compensate for the neurobiological effects of aging. However, the cause of these changes remains elusive, and cannot be completely attributed to reductions in strength or sensory resolution. Additional evidence from functional neuroimaging studies suggests that hemispheric asymmetry is reduced in older adults as compared to younger adults during cognitive tasks, such as visual perception (Grady et al. 2000), episodic memory encoding and retrieval (Cabeza et al. 2004; Cabeza et al. 1997; Grady et al. 1995), and implicit and working memory (Jonides et al. 2000; Reuter-Lorenz et al. 2000). This suggestion is based on the consistent finding of increased bilateral activation in older adults, primarily in prefrontal cortex, during a variety of memory encoding and retrieval tasks. In young adults, the left prefrontal cortex appears to be specialized for encoding of episodic memories, whereas the right hemisphere is more specialized for memory retrieval (Nyberg et al. 2002; Tulving et al. 1994). This pattern is known as Hemispheric Encoding/Retrieval Asymmetry (HERA), and has been observed in both verbal and nonverbal contexts. On the other hand, this asymmetry seems to be reduced in older adults. More specifically, older adults present minimal prefrontal cortex activation during encoding, yet bilateral prefrontal cortex activation during recall (Cabeza et al. 1997). The general finding that prefrontal cortex activity during cognitive tasks is less lateralized in older adults as compared to younger adults has given rise to the Hemispheric Asymmetry Reduction in the Old, or the HAROLD model (Cabeza 2002). Yet, the HERA and HAROLD models have only been used with cognitive functions and related to prefrontal cortex activity.

Our results indicate significant interlimb differences between the age groups. Elderly subjects showed reduced movement velocities as compared to the young subjects. Furthermore, coordination as reflected by hand path deviation from linearity indicates a decrease in laterality, especially for the targets requiring intersegmental coordination. These findings indicate that interlimb differences in motor coordination that are presented at younger ages diminish its asymmetric pattern in advanced age, which suggests that the fundamental age-related alterations in brain systems reported by reduced bilateral asymmetry activation might be associated with an increase in ipsilateral neural activation. Some possible factors contributing to the age-related change in premotor cortex activation may include additional recruitment of premotor cortex to support neuronal processing in other areas to maintain task performance despite possible degeneration within the gray or white matter components of the distributed motor network. Our results indicate a general loss of lateralization of hemisphere/limb system specialization as evidenced in the HAROLD model (Cabeza, 2002) and from earlier studies supporting generalized loss of integration of a distributed motor network with age (Cabeza et al., 2002). Moreover, our findings support the idea proposed by Rowe et al. (2006) that older subjects showed enhanced local effective connectivity, centered on the left premotor cortex, but reduced effective connectivity between distant motor related cortical areas. This enhanced local effective connectivity suggested that not all the changes associated with aging should be considered as disadvantageous decline and degeneration, and might represent continuing maturation of local neural networks. These differences may be explicable in terms of age-related differential effects of degeneration and plasticity on local and distant connections in the network mediating voluntary action.

5. ACKNOWLEDGEMENTS

We wish to thank Ludmila C. T. Oliveira, for assistance with recruitment and data collection. This research was supported by Fapesp/Brazil (Proc. # 2005/00161-8).

6. REFERENCES

Anderson, B., Rutledge, V., 1996. Age and hemisphere effects on dendritic structure. *Brain* 119 (Pt 6), 1983–1990.

- Bagesteiro LB, Sainburg RL. Handedness: dominant arm advantages in control of limb dynamics. *Journal of Neurophysiology* 88 (5): 2408-21, 2002.
- Cabeza R, Anderson ND, Locantore JK, and McIntosh AR. (2002) Aging gracefully: Compensatory brain activity in high-performing older adults. *Neuroimage* 17: 1394-1402.
- Cabeza R, Daselaar SM, Dolcos F, Prince SE, Budde M, and Nyberg L. (2004) Task-independent and task-specific age effects on brain activity during working memory, visual attention and episodic retrieval. *Cereb Cortex* 14: 364-375
- Cabeza R, Grady CL, Nyberg L, McIntosh AR, Tulving E, Kapur S, Jennings JM, Houle S, and Craik FIM. (1997) Age-related differences in neural activity during memory encoding and retrieval: A positron emission tomography study. *J Neuroscience* 17: 391-400.
- Cabeza R, Locantore JK, and Anderson ND. (2003) Lateralization of prefrontal activity during episodic memory retrieval: Evidence for the production-monitoring hypothesis. *J Cogn Neurosci* 15: 249-259.
- Cabeza R. (2002) Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychol Aging* 17: 85-100.
- Calautti, C., Serrati, C., Baron, J.C., 2001. Effects of age on brain activation during auditory-cued thumb-to-index opposition: a positron emission tomography study. *Stroke* 32, 139–146.
- Cole KJ and Rotella DL. Old age affects fingertip forces when restraining an unpredictably loaded object. *Exp Brain Res* 136: 535-542, 2001.
- Cole KJ, Rotella DL, and Harper JG. (1999) Mechanisms for age-related changes of fingertip forces during precision gripping and lifting in adults. *J Neurosci* 19: 3238-3247.
- Cole KJ. (1991) Grasp force control in older adults. *J Mot Behav* 23(4): 251-8.
- Cole, K. J., D. L. Rotella, et al. (1998). "Tactile impairments cannot explain the effect of age on a grasp and lift task." *Exp Brain Res* 121(3): 263-9.
- Cook, I.A., Leuchter, A.F., Morgan, M.L., Conlee, E.W., David, S., Lufkin, R., Babaie, A., Dunkin, J.J., O'Hara, R., Simon, S., et al., 2002. Cognitive and physiologic correlates of subclinical structural brain disease in elderly healthy control subjects. *Arch. Neurol.* 59 (10),
- D'Esposito, M., Zarahn, E., Aguirre, G.K., Rypma, B., 1999. The effect of normal aging on the coupling of neural activity to the bold hemodynamic response. *NeuroImage* 10, 6–14.
- Dolcos F, Rice HJ, and Cabeza R. (2002) Hemispheric asymmetry and aging: right hemisphere decline or asymmetry reduction. *Neurosci Biobehav Rev* 26: 819-825.
- Folstein MF, Folstein SE, McHugh PR. (1975) "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *J Psychiatr Res.* 12(3): 189-98
- Good, C.D., Johnsrude, I.S., Ashburner, J., Henson, R.N., Friston, K.J., Frackowiak, R.S., 2001. A voxel-based morphometric study of ageing in 465 normal adult human brains. *NeuroImage* 14, 21– 36.
- Grabiner MD and Enoka RM. (1995) Changes in movement capabilities with aging. *Exerc Sport Sci Rev* 23: 65-104
- Grachev, I.D., Apkarian, A.V., 2001. Chemical network of the living human brain. Evidence of reorganization with aging. *Brain Res. Cogn. Brain Res.* 11 (2), 185–197.
- Grady CL, McIntosh AR, Horwitz B, and Rapoport SI. Age-related changes in the neural correlates of degraded and nondegraded face processing. *Cognitive Neuropsychology* 17: 165-186, 2000.
- Grady CL, McIntosh AR, Horwitz B, Maisog JM, Ungerleider LG, Mentis MJ, Pietrini P, Schapiro MB, and Haxby JV. Age-Related Reductions in Human Recognition Memory Due to Impaired Encoding. *Science* 269: 218-221, 1995.
- Grady, C.L., Maisog, J.M., Horwitz, B., Ungerleider, L.G., Mentis, M.J., Salerno, J.A., et al., 1994. Age-related changes in cortical blood flow activation during visual processing of faces and location. *J. Neurosci.* 14, 1450–1462.
- Harrington DL and Haaland KY. Skill learning in the elderly: diminished implicit and explicit memory for a motor sequence. *Psychology & Aging* 7: 425-434, 1992.
- Head, D., Buckner, R.L., Shimony, J.S., Williams, L.E., Akbudak, E., Conturo, T.E., McAvoy, M., Morris, J.C., Snyder, A.Z., 2004. Differential vulnerability of anterior white matter in nondemented aging with minimal acceleration in dementia of the Alzheimer type: evidence from diffusion tensor imaging. *Cereb. Cortex* 14 (4), 410–423.
- Hutchinson, S., Kobayashi, M., Horkan, C.M., Pascual-Leone, A., Alexander, M.P., Schlaug, G., 2002. Age-related differences in movement representation. *NeuroImage* 17 (4), 1720– 1728.
- Jonides J, Marshuetz C, Smith EE, Reuter-Lorenz PA, Koeppe RA, and Hartley A. Age differences in behavior and PET activation reveal differences in interference resolution in verbal working memory. *J Cogn Neurosci* 12: 188-196, 2000.
- Kaiser, L.G., Schuff, N., Cashdollar, N., Weiner, M.W., 2005. Age-related glutamate and glutamine concentration changes in normal human brain: 1 H MR spectroscopy study at 4 T. *Neurobiol. Aging* 26, 665– 672.
- Ketcham, C. J., R. D. Seidler, et al. (2002). "Age-related kinematic differences as influenced by task difficulty, target size, and movement amplitude." *J Gerontol B Psychol Sci Soc Sci* 57(1): P54-64
- Larsson L, Grimby G, Karlsson J. Muscle strength and speed of movement in relation to age and muscle morphology. *J Appl Physiol.* 1979; 46(3): 451-6.
- Liu, R.S., Lemieux, L., Bell, G.S., Sisodiya, S.M., Shorvon, S.D., Sander, J.W., et al., 2003. A longitudinal study of brain morphometrics using quantitative magnetic resonance imaging and difference image analysis. *NeuroImage* 20,

22–33.

- Mattay, V.S., Fera, F., Tessitore, A., Hariri, A.R., Das, S., Callicott, J.H., Weinberger, D.R., 2002. Neurophysiological correlates of age-related changes in human motor function. *Neurology* 58 (4), 630– 635.
- Morrison, J.H., Hof, P.R., 1997. Life and death of neurons in the aging brain. *Science* 278 (5337), 412–419.
- Nyberg L, Forkstam C, Petersson KM, Cabeza R, and Ingvar M. Brain imaging of human memory systems: between-systems similarities and within-system differences. *Cognitive Brain Research* 13: 281-292, 2002.
- Oldfield RC. (1971) The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia* 9: 97-113.
- Pohl PS, Winstein CJ, and Fisher BE. The locus of age-related movement slowing: sensory processing in continuous goal-directed aiming. *Journals of Gerontology Series B, Psychological Sciences & Social Sciences* 51: 94-102, 1996.
- Raz, N., Gunning, F.M., Head, D., Dupuis, J.H., McQuain, J., Briggs, S.D., Loken, W.J., Thornton, A.E., Acker, J.D., 1997. Selective aging of the human cerebral cortex observed in vivo: differential vulnerability of the prefrontal gray matter. *Cereb. Cortex* 7 (3), 268–282.
- Reuter-Lorenz PA, Jonides J, Smith EE, Hartley A, Miller A, Marshuetz C, and Koeppel RA. Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *J Cogn Neurosci* 12: 174-187, 2000.
- Sainburg RL, Ghez C and Kalakanis D. Intersegmental dynamics are controlled by sequential anticipatory, error correction, and postural mechanisms. *Journal of Neurophysiology* 81: 1040 - 1056, 1999
- Sainburg RL, Kalakanis D. Differences in control of limb dynamics during dominant and nondominant arm reaching. *Journal of Neurophysiology* 83: 2661-75, 2000.
- Sainburg RL. Evidence for a Dynamic-Dominance Hypothesis of Handedness. *Experimental Brain Research* 142: 241-58, 2002.
- Scahill, R.I., Frost, C., Jenkins, R., Whitwell, J.L., Rossor, M.N., Fox, N.C., 2003. A longitudinal study of brain volume changes in normal aging using serial registered magnetic resonance imaging. *Arch. Neurol.* 60 (7), 989– 994.
- Schultz AB. Mobility impairment in the elderly: challenges for biomechanics research. *J Biomech.* 1992 May; 25(5): 519-28. Review.
- Schwiegerling, J., 2004, “Ocular Function: Visual Acuity”, Field Guide to Visual and Ophthalmic Optics, SPIE Press, Bellingham, WA. Vol: FG04. 124 p.
- Seidler, R. D., J. L. Alberts, et al. (2002). "Changes in multi-joint performance with age." *Motor Control* 6(1): 19-31.
- Shimoyama, I., Ninchoji, T., Uemura, K., 1990. The finger-tapping test. A quantitative analysis. *Arch. Neurol.* 47, 681–684.
- Smith, C.D., Umberger, G.H., Manning, E.L., Slevin, J.T., Wekstein, D.R., Schmitt, F.A., et al., 1999. Critical decline in fine motor hand movements in human aging. *Neurology* 53, 1458– 1461.
- Spiriduso W, Eakin R, and Francis K. Manual force control and tremor in older adults and patients with Parkinson's disease. *Gerontologist* 44: 10-10, 2004.
- Tulving E, Kapur S, Craik FIM, Moscovitch M, and Houle S. Hemispheric Encoding/Retrieval Asymmetry in Episodic Memory - Positron Emission Tomography Findings. *Proc Natl Acad Sci USA* 91: 2016-2020, 1994.
- Ward, N.S., Frackowiak, R.S., 2003. Age-related changes in the neural correlates of motor performance. *Brain* 126 (Pt4), 873– 888.

7. RESPONSIBILITY NOTICE

The authors of this study are only those responsible for the printed material included in this paper.