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The Impact of Age and Physical Activity Level on Manual Aiming Performance

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Abstract

Older adults traditionally adapt their discrete aiming movements, thereby travelling a larger proportion of the movement under closed-loop control. As the beneficial impact of a physically active lifestyle in old age has been described for several aspects of motor control, we compared the aiming performance of young controls to active and sedentary older adults. To additionally determine the contribution of visual feedback, aiming movements were executed with and without saccades. Results showed only sedentary older adults adopted the typical movement changes, highlighting the impact of a physically active lifestyle on manual aiming in old age. In an attempt to reveal the mechanism underlying the movement changes, evidence for an age-related decline in force control was found, which in turn resulted in an adapted aiming strategy. Finally, prohibiting saccades did not affect older adults' performance to a greater extent, suggesting they do not rely more on visual feedback than young controls.

Keywords: aging, physical activity, manual aiming, eye movements

The Impact of Age and Physical Activity Level on Manual Aiming Performance

Ever since Woodworth’s classic work on manual aiming (1899) motor control researchers have shown that goal-directed upper limb movements traditionally consist of two phases: a primary submovement and a homing-in phase. The former can be defined as the initial impulse towards the vicinity of the target (mainly open-loop control), whereas the latter phase is associated with feedback-based corrections as the limb approaches the target (primarily closed-loop control; e.g., Elliott, Helsen, & Chua, 2001). The relative contribution of open- versus closed-loop processes to the control of goal-directed movements changes across the lifespan: Young adults generally end their primary submovement just before the target to only make a small adjustment in the same direction as the initial pulse, whereas older adults undershoot the target to a greater extent. By making shorter-ranged and slower primary submovements, older adults need a greater number of time-consuming adjustments during the homing-in phase, resulting in longer overall movement times (Ketcham, Seidler, Van Gemmert, & Stelmach, 2002; Poston, Van Gemmert, Barduson, & Stelmach, 2009; Pratt, Chasteen, & Abrams, 1994;Walker, Philbin, & Fisk, 1997).

Though these age-related changes in aiming behavior have been described consistently, a study by Lyons and colleagues (1996) reported no differences between young and older adults’ movement times, accuracy levels, and primary submovement trajectories. To explain these unexpected results, Lyons and colleagues (1996) argued that older adults may make a better use of kinesthetic feedback for the control of goal-directed movement. As an alternative explanation, the possible influence of a physically active lifestyle in old age was raised. Indeed, recent evidence suggests that maintaining a physically active lifestyle during aging allows older adults to slow declines in their sensorimotor functions. For instance, better maintenance of interlimb coordination skills

(Capranica, Tessitore, Olivieri, Minganti, & Pesce, 2004; Cortis et al., 2009) and more accurate proprioceptive perception (Adamo, Alexander, & Brown, 2009; Proske & Gandevia, 2012) were observed in active older adults compared to sedentary controls. Therefore, the first aim of the current study was to explore whether a physically active lifestyle also attenuates the typical age-related changes in manual aiming. To address this question, aiming performances in active and sedentary older adults were compared with those observed in young controls.

To understand how physical activity may help to reduce these traditional age-related changes, one should nonetheless know what mechanism underlies the movement adaptations in old age. We shortly present two possibilities: A first hypothesis is that older adults generally engage in more closed-loop control to cope with a deteriorated ability to reliably tune muscular forces (Christou & Carlton, 2001; Galganski, Fuglevand, & Enoka, 1993). This theory assumes that when an older adult produces a force, the noise associated with the resulting movement is greater than when a younger adult produces that same force (Walker et al., 1997). An increased noise-to-force ratio might compel older adults to make less forceful and thus shorter primary submovements in order to reduce their endpoint variability. As a result, the homing-in phase of the movement becomes longer but also more predictable. However, the theory has recently been challenged by Welsh and colleagues (2007) showing older adults' primary submovements are not more variable in time and space than those of young adults. They proposed the alternative that older adults adopt a play-it-safe strategy to avoid the higher energy costs associated with target overshoots: When correcting for an overshoot, one does not only have to overcome the inertia of a zero-velocity situation, but also reverse the roles of the agonist and antagonist muscle groups (Elliott et al., 2001; Engelbrecht, Berthier, & O'Sullivan, 2003). Undershooting the target to a greater extent and making more use of sensory feedback to safely guide the hand to the target may be considered a secure strategy to prevent overshoots and save energy. Here, we attempted to investigate which of these two proposals is consistent with the traditional movement adaptations in old age. Similar to the study of Welsh and colleagues, we examined movement variability to compare the noise-to-force ratios between groups. On the other hand, the hypothesis that the typical movement adaptations represent a play-it-safe strategy to prevent target overshoots was tested by adding an aiming condition in which there was no time for the movement adaptations (cyclical aiming). If this cyclical aiming condition results in an increased amount of target overshoots, particularly for sedentary older adults, it would provide support for the play-it-safe hypothesis.

Irrespective of which abovementioned hypothesis is correct, the greater proportion of the movement occurring under closed-loop control suggests that sensory feedback processing becomes increasingly important in old age. As online feedback consists of proprioceptive and visual information, it is appropriate to look at the impact of aging on both sources of feedback. On the one hand, a clear age-related decline in proprioception has been described consistently in upper limb-matching tasks (e.g., Adamo et al., 2009; Adamo, Martin, & Brown, 2007; Wright, Adamo, & Brown, 2011). On the other hand, the motor system of the eye seems to be only mildly affected or perhaps even spared by the aging process (Kadota & Gomi, 2010; Pratt, Dodd, & Welsh, 2006). Many have therefore suggested that older adults increase their reliance on visual feedback during the execution of manual aiming movements (Rand & Stelmach, 2011a, 2011b; Seidler-Dobrin & Stelmach, 1998), possibly as a means to compensate for declines in proprioceptive acuity. In this theoretical context, the experimental data are rather controversial (Chaput and Proteau 1996; Coats and Wann, 2011; Lyons, Elliott, Swanson, & Chua, 1996; Pratt et al., 1994), and there is no general agreement about this sensory reweighting in older adults. To determine whether visual feedback is indeed of increased importance, particularly in sedentary older adults, the aiming task in the current experiment was executed with and without saccades. Eye movements were recorded throughout the experiment to control for the extent by which the aiming movements were executed with visual guidance when saccades were allowed. This additional measurement finally allowed us to look into the differential use of eye movements among groups.

In summary, the present study was designed to identify differences between young controls and active and sedentary older adults during visually-guided aiming tasks. These three participant groups were asked to aim as fast and accurate as possible towards fixed targets. To determine the exact contribution of visual information, the aiming movements were performed with or without saccades. The task was executed in a discrete or cyclical way, putting less or more time constraint upon the movements. This experiment enabled us to test the following three hypotheses: First, older adults were expected to adopt the traditional movement adaptations when they were allowed sufficient time in the discrete aiming task. However, if an active lifestyle could indeed counteract the age-related changes in manual aiming behavior, these movement characteristics should only emerge in the sedentary older adults. Specifically, we expected the discrete aiming movements of sedentary older adults to be characterized by slower and shorter-ranged primary submovements, and relatively more time spent in the homing-in phase compared to the young and active older adults. Together this would result in longer overall movement times. Second, by looking into the temporal and spatial variability of the movements, we aimed to verify whether an increased noise-to-force ratio may be responsible for these movement adaptations in sedentary older adults. Conversely, the play-it-safe hypothesis would be supported by sedentary older adults showing an increased amount of target overshoots during cyclical aiming. Third, it was hypothesized that sedentary older adults depend more on visual feedback during manual aiming. This would be reflected in a larger drop in accuracy levels when eye movements were prohibited.

Method

Participants

Fifteen young and 28 older adults participated in the study on a voluntary basis. Young participants were recruited via flyers distributed over the university campus, whereas active and sedentary older adults were recruited at local running and senior clubs, respectively. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). They self-claimed to be in good health and to have normal or corrected-to-normal vision. The latter was controlled by asking them to read the task instructions on the screen prior to the experiment. Here, visual acuity demands were considerably higher compared to those required in the experimental task. Since all participants were able to read the instructions aloud, we assumed visual acuity was sufficient for the experimental task. Participants performed a Nine Hole Pegboard Test (NHPT; Mathiowetz, Volland, Kashman, & Weber, 1985) to check for intact fine motor skills and were excluded if their score did not meet the age- and gender-dependent inclusion criteria described by Oxford Grice and colleagues (2003). Two older participants were excluded from the study for this reason. To exclude participants with dementia or other severe anomalies in cognitive functioning, a Mini-Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975) was administered to the older participants. The minimum score for inclusion was set at 27 out of 30, which all achieved. Physical activity levels as measured by the Baecke questionnaire (Baecke, Burema, & Frijters, 1982; Voorrips, Ravelli, Dongelmans, Deurenberg, & Van Staveren, 1991) were used to divide the older participants in two groups: participants with Baecke scores over the median score of 7.3 were attributed to the physically active subgroup, whereas participants scoring under the median were attributed to the sedentary subgroup. This resulted in three groups: young controls (n=15), physically active older participants (n=13) and sedentary older participants (n=13). The general characteristics of these groups are summarized in Table 1. The study was approved by the Medical Ethics Committee of the KU Leuven and was conducted in accordance with the 1964 Declaration of Helsinki. Prior to the experiment, written informed consent was obtained from all participants.

Task and Apparatus

The task and apparatus were similar to those used in several previous studies (e.g., Lavrysen, Elliott, Buekers, Feys, & Helsen, 2007; Lavrysen et al., 2008; Lavrysen et al., 2012). Participants sat in a comfortable chair and wore an orthosis on the preferred, right forearm. The axis of this orthosis was aligned with the anatomical axis of the wrist joint and positioned in a way that the hand could only move in the horizontal plane. A high-precision shaft encoder with an accuracy of 0.0055° and sampling frequency of 250 Hz was attached onto the orthosis. Wrist angular position was presented as a 1.5 cm diameter circular cursor on a 60 cm computer monitor, located at a standardized distance of 100 cm in front of the participant at eye level. Apart from this cursor, two fixed targets also appeared on the monitor. The size of these targets, each marked by two vertical lines, depended upon aiming conditions that are further explained in the Protocol section. The task consisted of moving the cursor from target to target by making flexion/extension wrist movements after an auditory cue. Participants were asked to make the movements as fast and accurate as possible, and to wait for the next auditory cue with the cursor between the target boundaries. Point of gaze (PG) was recorded using an Applied Science Laboratories (ASL) 6000 pan-tilt eye-tracker system (Bedford, MA) with a sampling frequency of 240 Hz and an accuracy of 0.5°. A comfortable neck rest was installed onto the participant's chair to prevent head movements and the loss of PG signal. Prior to the experiment, a nine-point calibration was performed for every participant.

Protocol

As illustrated in Figure 1, participants started the experiment with two familiarization blocks in which the different conditions were practiced. These blocks consisted of four 25-second trials in which aiming movements were performed at a self-selected pace. In the first trial, participants made horizontal aiming movements over a distance of 27.5 cm on the screen (corresponding to a wrist angle of 52°) towards targets of 5.2 cm (wrist angle of 10°), resulting in an index of difficulty (ID) of 3.4 bits (Fitts, 1954). In the second trial, the ID was increased to 4.4 bits by decreasing the target sizes to 2.6 cm (wrist angle of 5°). As these trials were conducted with eye movements, this visual condition was called free vision. Afterwards, the two trials were repeated in a fixation condition. Here, participants were asked to fixate the eyes on an additional vertical line in the middle of the screen, thus prohibiting eye movements. Even though peripheral vision was still available, this manipulation made accurate aiming more difficult by depriving the effective use of central vision (Binsted & Elliott, 1999).

After the familiarization, participants proceeded with the main experiment. Blocks again consisted of four consecutive trials in which the conditions and sequence remained identical to the familiarization blocks. The only difference was that instead of moving at a self-selected pace, participants were instructed to start their aiming movement at the onset of a 50-ms auditory cue and to move as fast and accurate as possible towards the target. Every trial consisted of 25 auditory cues, and thus 25 aiming movements. First, participants did two blocks of the discrete aiming task in which the auditory cue was presented every 1500 ms. After a 20-minute break, the experiment continued with two blocks in which the interval between auditory cues was shortened to 500 ms, resulting in cyclical aiming movements. In total 400 aiming movements were recorded for each participant.

Dependent Variables

Prior to the calculation of all dependent variables, a first order low-pass Butterworth filter with a cut-off frequency of 20 Hz was applied on both the hand and eye movement data. The filtered hand position data were differentiated to obtain instantaneous velocity, and then differentiated again to obtain instantaneous acceleration. The first and final two movements of a trial were not considered in the analysis.

Hand movement time. The hand movement time was defined as the time between hand movement initiation (first sample when the standard deviation (SD) of the velocity profile was inferior to 0.75 mm/s for 80 ms from peak velocity backwards) and termination (first sample when the SD of the velocity profile was inferior to 3 mm/s for 120 ms from peak velocity onwards). Both criteria were validated based on a visual inspection in Matlab.

Endpoint accuracy. If the entire cursor fell within the target boundaries at hand movement termination, this was considered a target hit. If the cursor fell short or long of the target, this was considered a target under- or overshoot, respectively. The percentage of target hits was calculated for every trial and regarded as endpoint accuracy. The percentages of target under- and overshoots were assessed accordingly.

Peak velocity. The highest velocity found in the primary submovement was considered peak velocity.

Relative distance and duration of the primary submovement. The end of the primary submovement was defined as the sample of the second zero-line crossing in the acceleration profile. For every aiming movement, we calculated the distance travelled up to this point relative to the distance between the middle of both targets. In addition, the time spent during this primary submovement was also determined relative to the hand movement time.

Temporal and spatial variability. Identical to the calculations for the end of the primary submovement, the relative duration and distance travelled up to the moment of peak acceleration (highest acceleration during the primary submovement) and peak velocity were computed. By then calculating the mean SD of the relative durations and distances of all three kinematic markers, we were able to get a better view on the temporal and spatial variability of the movements across multiple aiming attempts.

Primary saccade amplitude. Primary saccade initiation and termination were determined similarly as in previous studies of our lab (e.g., Helsen, Elliott, Starkes, & Ricker, 1998): Saccade onset was the last point when at least 24 sequential gaze coordinate samples (i.e., 100 ms) had an SD equal to or higher than 1°. The end of a saccade (or fixation onset) was defined as the first of 24 gaze samples with a SD lower than 1°. The primary saccade was considered only if it travelled at least 50% of the total distance between the two targets. Its amplitude was calculated and is expressed relative to the distance between the middle of both targets.

Aiming movements with corrective saccades. This variable was defined as the percentage of aiming movements in which the primary saccade was followed by a fixation and at least one consecutive corrective saccade. The calculation of corrective saccades was done using the same SD criterion as for primary saccades.

Data Analysis

First, because the assumptions for parametric statistics were not met, the general characteristics of all three groups were compared using a Kruskall-Wallis analysis of variance (ANOVA; see Table 1). Then**,** a custom-written Matlab-script computed the means and SDs for all abovementioned variables per trial. As the aim of this study was not to compare the discrete with the cyclical aiming task, but rather participant groups' performance within each task, the data were separated in two sets: one with all data for discrete aiming and one for cyclical aiming. Hand movement variables were analyzed using a 3 GROUP (young, active older, sedentary older) x 2 VISUAL CONDITION (free vision, fixation) x 2 ID (3.4 bits, 4.4 bits) mixed-model ANOVA. Separate analyses were performed on the discrete and cyclical aiming data. Due to the absence of saccades in the fixation condition, variables concerning eye movements were calculated and analyzed only for the free vision condition. Because the task consisted of a one-dimensional horizontal aiming movement, only the horizontal eye movement data were taken into account. Post-hoc tests (Tukey's honestly significant differences) were conducted when appropriate. For all analyses, the significance level was set at $p < .05$. Due to the specific focus of the study, only significant differences including a GROUP effect are presented.

Results

Discrete Aiming

Hand movement time. A main effect of GROUP [$F(2, 298) = 48.92$, $p < .01$] indicated sedentary older adults needed more time to perform the aiming movements (732 ± 98 ms) than young (615 ± 84 ms) and active older (619 ± 107 ms) participants (see Figure 2A).

Endpoint accuracy. No main or interaction effects regarding the percentage of target hits, undershoots or overshoots were observed.

Peak velocity. A significant GROUP effect [$F(2, 298) = 21.56$, $p < .01$] revealed lower peak velocities in sedentary older adults (857 ± 142 mm/s) than in young (1140 ± 163 mm/s) and active older (1121 ± 160 mm/s) adults (see Figure 2B).

Relative distance of the primary submovement. A main effect of GROUP [$F(2, 298) = 26.87$, $p < .01$] indicated that sedentary older participants travelled relatively shorter distances during their primary submovement (80.7 ± 8.2%) compared to young (87.2 ± 7.5%) and active older (88.3 ± 7.7%) adults (see Figure 2C). The primary submovement of sedentary older adults thus undershot the target to a greater extent.

Relative duration of the primary submovement. A significant GROUP effect was also found for the relative duration of the primary submovement [$F(2, 298) = 8.33$, $p < .05$], signaling that sedentary older adults had relatively shorter primary submovements (52.6 ± 9.1%) compared to young (56.5 ± 11.0%) and active older (58.3 ± 10.0%) adults (see Figure 2D). In other words, sedentary older adults spent a greater proportion of the hand movement time during the homing-in phase of the movement.

Temporal and spatial variability. Temporal variability at peak acceleration appeared to be lower in the young compared to the older groups (both $p < .01$; see Figure 3A). Similar results were observed for peak velocity when comparing young controls to active older ($p < .05$) and sedentary older adults ($p < .01$). At the end of the primary submovement, however, the temporal variability was no longer significantly different among groups. With respect to space, lower SDs were noticed for the relative distance travelled up to peak acceleration in the young compared to the older groups (both $p < .01$; see Figure 3B). These group differences became statistically nonsignificant at peak velocity and at the end of the primary submovement.

Primary saccade amplitude. A main effect of GROUP [$F(2, 148) = 9.44$, $p < .01$] revealed that young adults' primary saccade amplitude (89.7 ± 6.4%) was greater than those of active (81.1 ± 7.4%) and sedentary (82.3 ± 7.8%) older adults (see Figure 4A).

Aiming movements with corrective saccades. A main effect of GROUP [F(2, 148) = 10.14, p < .01] indicated young adults performed fewer hand movements with corrective saccades (32.5 ± 15.6%) compared to active (52.5 ± 19.3%) and sedentary (51.2 ± 20.8%) older adults (see Figure 4B).

Cyclical Aiming

Hand movement time. No main or interaction effects regarding hand movement time were observed in the cyclical aiming task. Figure 5A clearly shows all groups were able to make the aiming movements within 500 ms on average, thereby respecting the high pace of the auditory cues.

Endpoint accuracy. This strict time constraint resulted in a main effect of GROUP concerning the percentage of target hits [F(2, 298) = 30.63, p < .01]: Young adults' percentage of target hits (54.5 ± 12.8%) was higher compared to the active (42.7 ± 14.0%) and sedentary (40.1 ± 14.7%) older participants. In accordance with their high endpoint accuracy, young adults had a lower percentage of movements resulting in a target undershoot (22.5 ± 9.5%) compared to sedentary older adults (31.2 ± 10.4%), who in turn made relatively fewer target undershoots than active older adults (37.9 ± 12.8%) [F(2, 298) = 22.85, p < .01]. Sedentary older adults did make more target overshoots (28.7 ± 10.9%) compared to both the young (22.9 ± 9.5%) and active older (19.4 ± 8.6%) adults [F(2, 298) = 8.29, p < .01].

Peak velocity. As in the discrete aiming task, a main effect of GROUP was found [F(2, 298) = 4.37, p < .05] showing sedentary older adults aimed with lower peak velocities (1267 ± 174 mm/s) than young (1344 ± 142 mm/s) and active older (1380 ± 163 mm/s) adults (see Figure 5B).

Relative distance of the primary submovement. Interestingly, a significant GROUP effect was found [$F(2, 298) = 10.57$, $p < .01$], indicating active older adults travelled a relatively greater distance during their primary submovement (99.0 ± 4.7%) compared to young (96.6 ± 4.7%) and sedentary older (96.5 ± 5.4%) adults (see Figure 5C).

Relative duration of the primary submovement. A main effect of GROUP [$F(2, 298) = 3.93$, $p < .05$] showed that young adults used relatively less time to perform their primary submovement (71.9 ± 11.2%) than sedentary older adults (75.9 ± 10.9%). Post-hoc analysis revealed that active older adults (72.9 ± 9.1%) did not significantly differ from young or sedentary older adults (See Figure 5D).

Temporal and spatial variability. Young adults had a lower temporal variability at peak acceleration compared to active older adults ($p < .01$), who in turn had lower SDs than sedentary older adults (also $p < .01$; see Figure 6A). Comparable results were found at peak velocity: Young controls were more consistent than active older adults ($p < .01$), who in turn had lower SDs than their sedentary counterparts ($p < .05$). As in the discrete aiming task, all temporal differences became statistically nonsignificant at the end of the primary submovement. Analysis of the spatial variability revealed that the young had lower SDs compared to active and sedentary older adults at peak acceleration (both $p < .01$) and at peak velocity ($p < .05$ and $p < .01$, respectively; see Figure 6B). Again, these differences became statistically nonsignificant at the end of the primary submovement.

Primary saccade amplitude. A main effect of GROUP [$F(2, 148) = 7.68$, $p < .01$] indicated the young adults' primary saccade travelled on average further (91.6 ± 6.2%) compared to those of active (85.5 ± 4.1%) and sedentary (84.7 ± 6.9%) older adults (see Figure 7A).

Aiming movements with corrective saccades. Contrary to the discrete aiming task, no main effect of GROUP was observed concerning the use of corrective saccades.

Discussion

In this study, we examined differences in manual aiming behavior between young controls and active and sedentary older adults. In an attempt to reveal the mechanism responsible for these changes, two aiming conditions (discrete aiming vs. cyclical aiming) were used. Furthermore, two visual conditions (free vision vs. fixation) were included to determine the contribution of visual feedback during the task. In short, this experiment enabled us to investigate the following three hypotheses: First, only sedentary older adults were expected to adopt the traditional age-related movement adaptations in the discrete aiming task. Second, by looking into the movement variability, we examined whether an increased noise-to-force ratio could underlie these movement adaptations. On the other hand, the recent hypothesis of the play-it-safe strategy would be supported by sedentary older adults adapting their aiming movements to a greater extent when confronted with higher accuracy constraints, and an increased amount of target overshoots in the cyclical aiming task. Third, sedentary older adults were expected to rely more on visual feedback during the aiming movements. This hypothesis would be supported by a greater drop in the accuracy levels of sedentary older adults when eye movements were prohibited.

Only sedentary older adults adapt their discrete aiming movements.

Compared to both other groups, sedentary older adults needed more time (see Figure 2A) to perform accurate goal-directed movements in the discrete aiming task. Their movements were characterized by slower (2B) and shorter-ranged (2C) primary submovements, resulting in a relatively larger proportion of time spent in the homing-in phase (2D). As hypothesized, these typical age-related movement adaptations (Ketcham et al., 2002; Poston et al., 2009; Pratt et al., 1994; Walker et al., 1997) were thus only found in the sedentary older adults, but not in the physically active older adults. Moreover, for the majority of variables the differences between active and sedentary older adults were more pronounced than between active older adults and young controls. In one case active older adults even performed better than young controls (i.e., relative distance of the primary submovement in the cyclical aiming condition; see Figure 5C), underlining the impact of a physically active lifestyle on older adults' aiming performance. This observation should not come as a surprise, as the beneficial influence of a physically active lifestyle in old age has already been described comprehensively in motor control literature. For instance, the age-related degradation in interlimb coordination has shown to be attenuated in older adults with a history in gymnastics (Capranica et al., 2004) and soccer (Cortis et al., 2009). Also, upper-limb proprioception has been demonstrated to be only mildly affected in physically active older adults compared to sedentary controls (Adamo et al., 2009). Besides a general effect of physical activity level, Adamo and colleagues (2009) reported an even greater impact in older adults specifically involved in upper-limb activities (e.g., needlework, drawing, playing tennis, etc.). Taking into account the substantial role of proprioception in accurate aiming, the latter study has two major consequences for the interpretation of our data. First, the general effect of physical activity implies that a better conservation of proprioception among active older adults could mediate the observed differences in manual aiming performance between active and sedentary older adults. Second, the specific impact of upper-limb training on proprioception suggests even greater differences in aiming behavior could have emerged if our active subsample was limited to older adults specifically involved in upper-limb activities. Future research may therefore investigate whether this distinct impact of upper-limb training also applies to manual aiming. To clarify how physical activity in general and upper-limb training in particular may impact the age-related changes in manual aiming, we first shed some light on the mechanism underlying the movement adaptations typically observed in older adults.

Evidence for both the increased noise-to-force ratio and the play-it-safe strategy hypotheses.

Two possible mechanisms underlying the typical age-related changes in aiming behavior were investigated. On the one hand, the theory of an increased noise-to-force ratio (Walker et al., 1997) was explored by looking at the variability of the movements. Although differences did not always reach the level of significance, sedentary older adults generally exhibited the greatest temporal and spatial variability, whereas the lowest variabilty was nearly always detected in young controls (see Figure 3 and 6). These data not only demonstrate a general age-related increase in noise-to-force ratio, they also suggest that maintaining a physically active lifestyle in old age may counteract this increase. Interestingly, differences in movement variability between active and sedentary older adults emerged particularly in the cyclical aiming task when sedentary older adults could not apply the traditional movement adaptations to cope with their increased noise-to-force ratios. Despite our relatively small sample sizes, distinct group differences were observed particularly in early kinematic markers, as one would expect in the case of a deteriorated ability to plan and tune muscular forces in the sedentary older adults.

On the other hand, Welsh and colleagues (2007) have proposed an alternative hypothesis in which the age-related changes in aiming behavior are explained by a play-it-safe strategy that is generally adopted by older adults to prevent costly target overshoots. In line with this hypothesis, conditions in which the strategy cannot be adopted due to a strict time constraint (e.g., cyclical aiming task) should result in an increased number of target overshoots. If we look at the cyclical aiming data, we indeed notice more target overshoots among sedentary older adults compared to the other groups. This finding supports previous results in a proprioceptive aiming task at the lower limbs (Boisgontier & Nougier, 2013) and suggests the observed movement adaptations were indeed a successful way to prevent target overshoots. Interestingly, evidence for this being a well-chosen strategy can also be derived from the cyclical aiming movement data: The strict time constraint in this condition forced all participants to move the hand very rapidly. Here, sedentary older adults proved to be physically able to move at the speeds reached by young and active older adults in the discrete aiming condition. Based on these results we can thus conclude that in the discrete aiming condition sedentary older adults were physically able to move at similar speeds as young and active older adults, but intentionally choose not to do so. In contrast, active older adults may not slow down the initial pulse because their force control is not degraded to the same extent as their sedentary counterparts.

Taken together, our data suggest that instead of one distinct mechanism, the movement adaptations observed in sedentary older adults may be caused by a combination of both increased noise-to-force ratios and the play-it-safe strategy. If moving at the same speed as young controls, sedentary older adults' primary submovements have a greater temporal and spatial variability due to increased noise-to-force ratios (Christou & Carlton, 2001; Galganski et al., 1993). This high variability results in a greater amount of target overshoots (Elliott et al., 2001; Engelbrecht et al., 2003). When sufficient time is available, the movements are slowed down to prevent the high energy cost associated with target overshoots. This finally results in slower and shorter-ranged primary submovements with limited spatial variability. However, as can be derived from the temporal and spatial variability of the movement (see Figures 3 and

6), maintaining high levels of physical activity may counteract the increase in noise-to-force ratio among older adults, thereby decreasing the need to adopt a play-it-safe strategy.

Sedentary older adults do not rely more on visual feedback.

Finally, it was also hypothesized that sedentary older adults depend more on visual information for the control of their aiming movements. This sensory reweighting would be supported by a steeper decline in endpoint accuracy among sedentary older adults when eye movements were prohibited. As can be derived from the lack of a significant GROUP x VISUAL CONDITION interaction on endpoint accuracy, the fixation condition did not affect sedentary older adults' aiming performance to a greater extent than any other group. This seems to imply sedentary older adults do not rely more on visual feedback during manual aiming compared to young or active older adults. However, the lack in significant interaction could also be due to the visual conditions used in the experiment: In the fixation condition, peripheral vision was still available possibly guiding the hand onto the target. To exclude the use of peripheral vision, future experiments may add visual conditions that take away visual information of the cursor position instead of only prohibiting eye movements.

To control the eyes effectively fixated the midline during the fixation condition, eye movements were registered throughout the experiment. Though not specifically the focus of our study, we noticed both active and sedentary older adults demonstrated hypometric primary saccades in the free vision condition (see Figures 4 and 7), and a higher occurrence of corrective saccades (see Figure 4). The latter was observed only in the discrete aiming task, perhaps because the strict time constraint of the cyclical task allowed less time for corrective saccades. These results are consistent with a recent study of Rand and Stelmach (2011a) in which similar results of hypometric primary saccades and greater amounts of corrective saccades were described among elderly participants during two-segment manual aiming. One could therefore argue that the play-it-safe approach may not be limited to the hand but also occurs in saccadic behavior, even in active older adults. Future studies focusing on the coupling between eye and hand movements may further clarify how this altered eye movement strategy contributes to accurate manual aiming in old age.

Conclusions

The current study underlines the beneficial effect of a physically active lifestyle on manual aiming performance in old age. In the discrete aiming task, active older adults performed similar to young controls without modifying their aiming behavior, whereas sedentary older adults adopted the traditional age-related movement adaptations. Evidence for these movement adaptations being a well-chosen strategy was derived from the cyclical aiming task data. However, slightly different from the traditional interpretation, the idea was raised sedentary older adults adopted a play-it-safe strategy to prevent costly target overshoots in the face of an increased noise-to-force ratio. Although no causal inferences should be drawn here, it seems as if there is a strong link between physical activity level and the preservation of an efficient manual control during discrete aiming movements in older adults that deserves further attention.

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Table Captions:

Characteristic	Young	Old	
		Active	Sedentary
n	15	13	13
Male/female	6/9	8/5	6/7
Age (in years)	**23.5 ± 0.8 *****	63.9 ± 2.5	65.1 ± 3.6
Baecke score	7.8 ± 1.0	8.3 ± 1.2	**6.1 ± 0.9 *****
Oldfield score	82.1 ± 12.2	89.9 ± 12.7	90.9 ± 11.6
NHPT (in seconds)	**16.9 ± 2.1 *****	19.0 ± 1.8	19.5 ± 2.4
MMSE score	/	29.5 ± 0.7	29.4 ± 0.8

Table 1: Participant Characteristics. Note: Results are presented as median (interquartile range) when appropriate. A Kruskal-Wallis one-way analysis of variance was used to compare the group scores. Significant group differences are highlighted by * and *** (in case p < .05 and p < .01, respectively). Abbreviations: NHPT = Nine Hole Peg Test; MMSE = Mini Mental State Examination. High Baecke scores indicate a physically active lifestyle, low Baecke scores a rather sedentary lifestyle; Oldfield scores indicate handedness (-100: extremely left-handed, +100: extremely right-handed).

Figure captions:

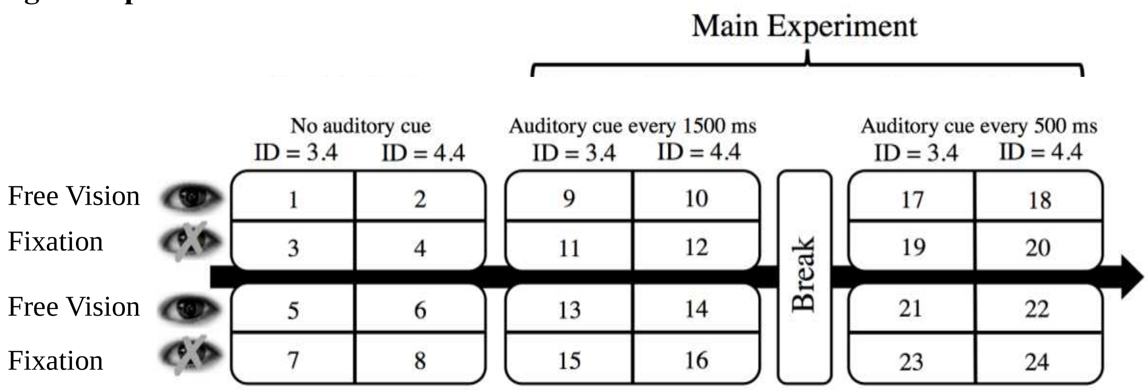

Figure 1: Schematic overview of the experimental design. The sequence of trials is clarified by the increasing numbers and remained identical for all participants. Left: familiarization, middle and right: main experiment, divided into discrete and cyclical aiming (auditory cue every 1500 and 500 ms, respectively). Each trial of the main experiment consisted of 25 aiming movements.

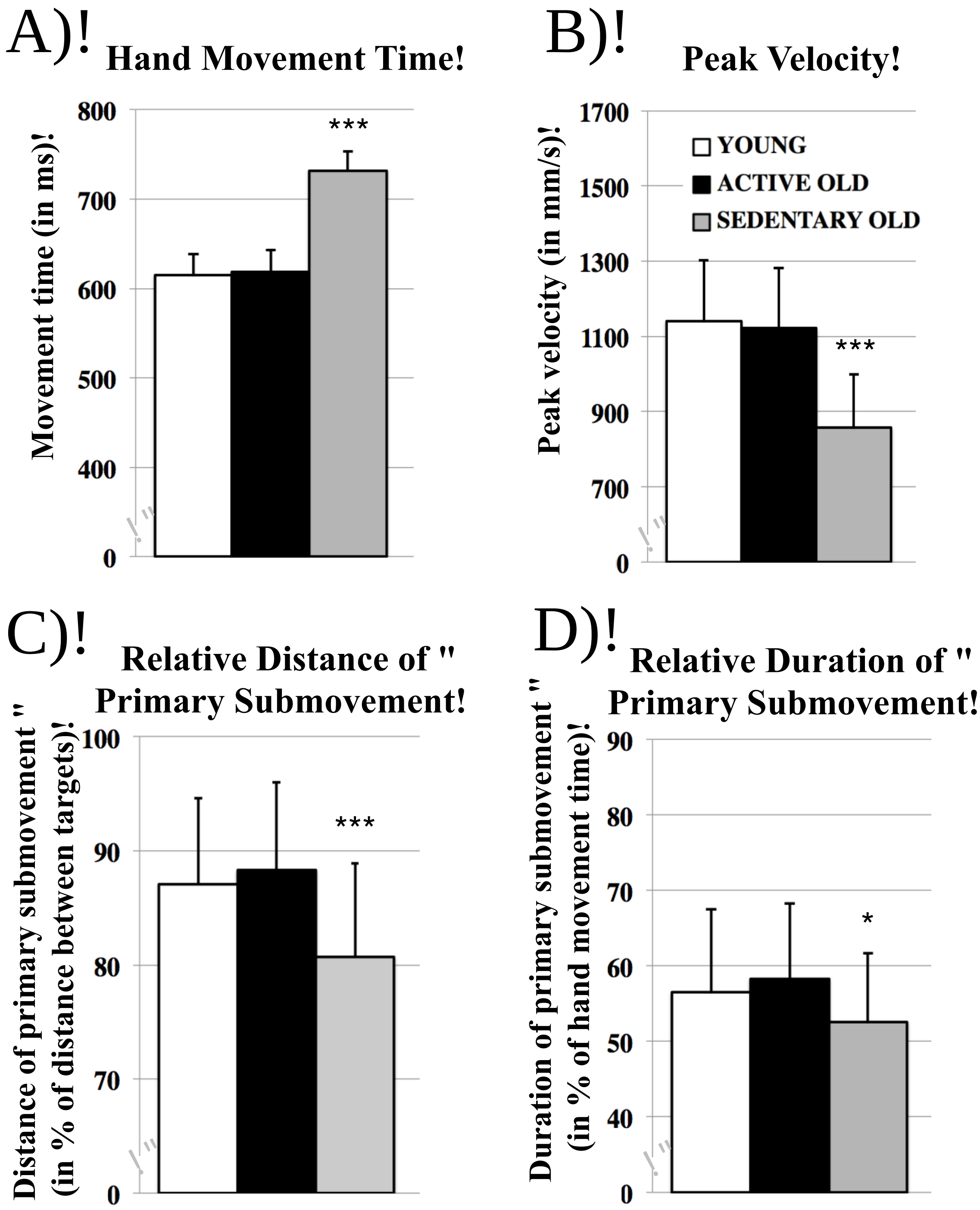

Figure 2: Hand movement results in the discrete aiming task. Comparison of mean group scores. Error bars represent standard deviations. (A) Hand movement time; (B) Peak velocity of the hand; (C) Relative distance travelled during the primary submovement; (D) Relative duration of the primary submovement. * $p < .05$. *** $p < .01$.

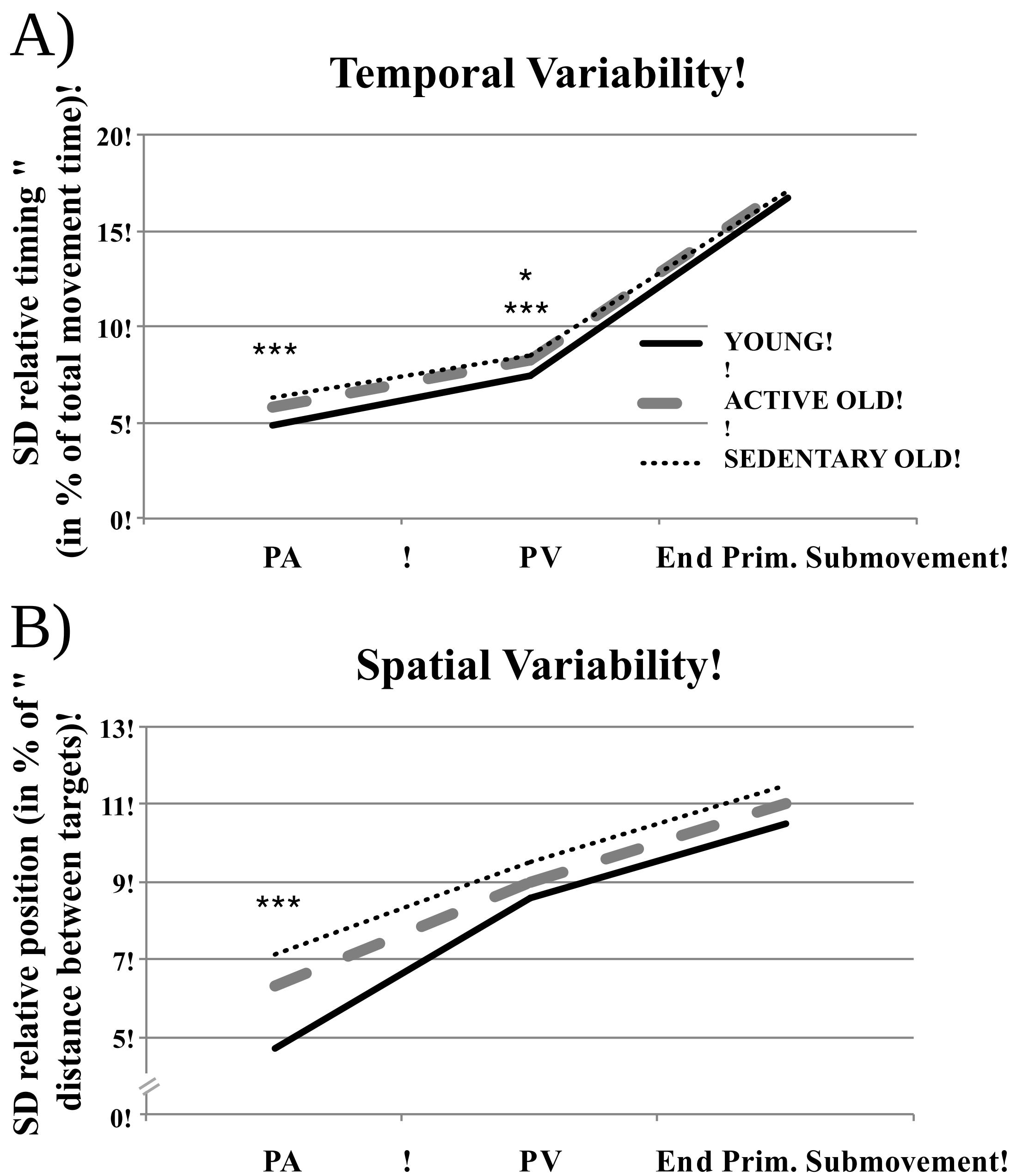

Figure 3: Spatial (A) and temporal (B) variability of three kinematic markers in the discrete aiming task. *Abbreviations:* SD = standard deviation; PA = moment of peak acceleration; PV = moment of peak velocity; End Prim. Submovement = end of the primary submovement. * $p < .05$. *** $p < .01$.

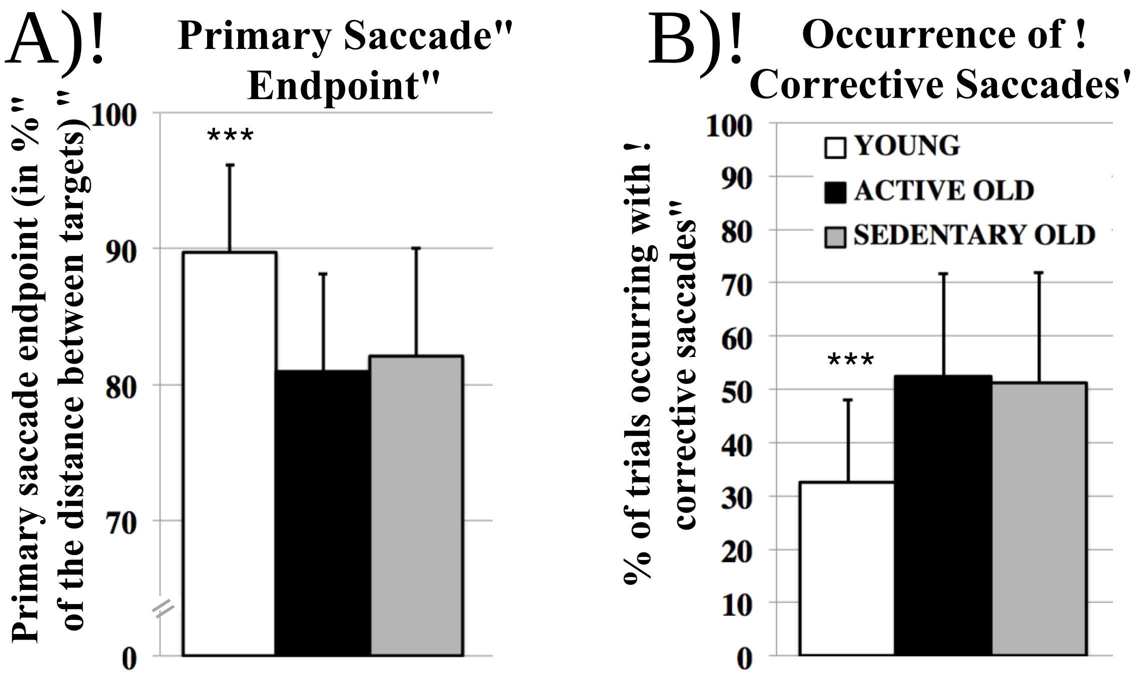

Figure 4: Eye movement results in the discrete aiming task. Comparison of mean group scores. Error bars represent standard deviations. (A) Primary saccade amplitude; (B) Proportion of aiming movements occurring with corrective saccades. * $p < .05$. *** $p < .01$.

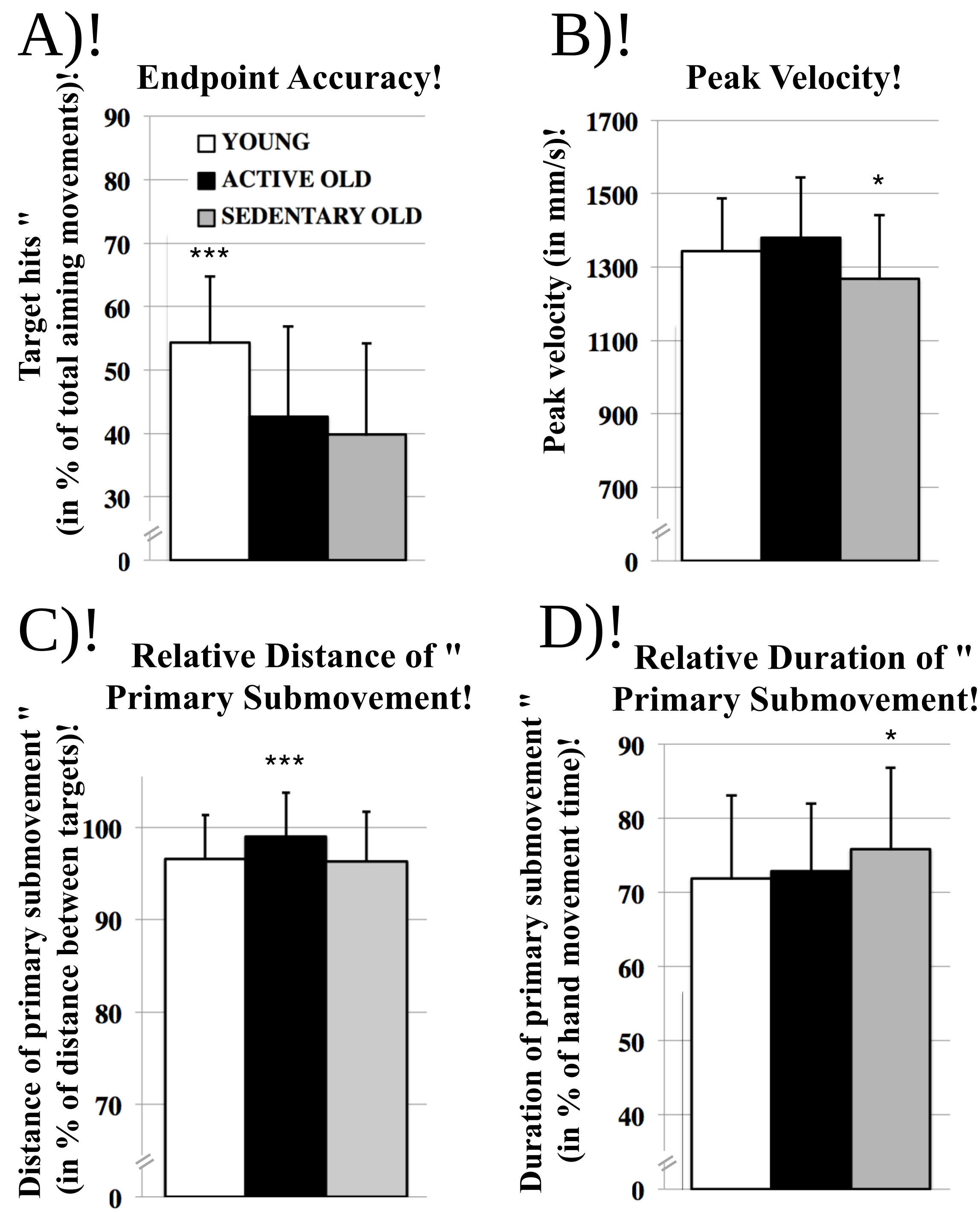

Figure 5: Hand movement results in the cyclical aiming task. Comparison of mean group scores. Error bars represent standard deviations. (A) Hand movement time; (B) Peak velocity of the hand; (C) Relative distance travelled during the primary submovement; (D) Relative duration of the primary submovement. * $p < .05$. *** $p < .01$.

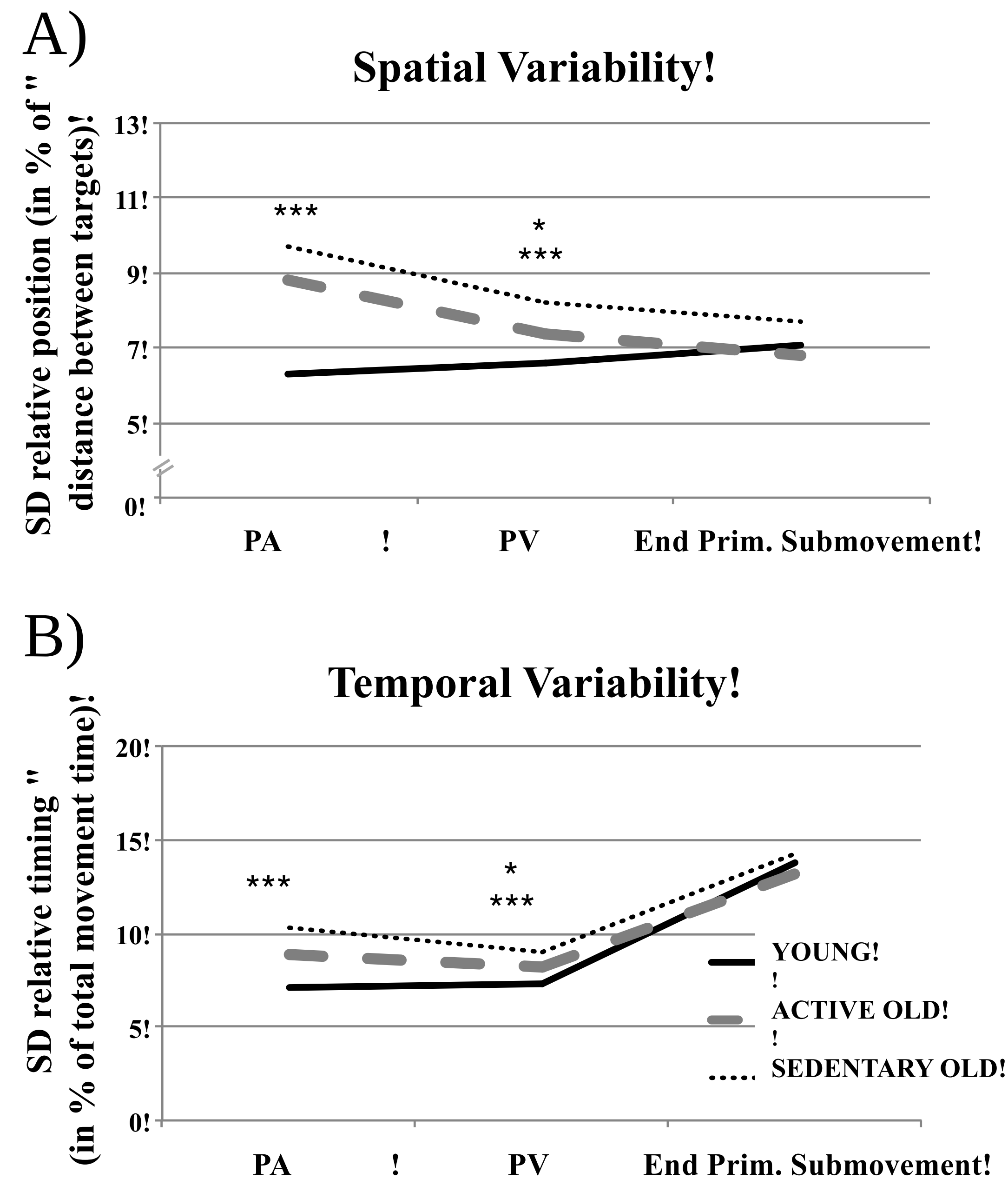

Figure 6: Spatial (A) and temporal (B) variability of three kinematic markers in the cyclical aiming task. *Abbreviations:* SD = standard deviation; PA = moment of peak acceleration; PV = moment of peak velocity; End Prim. Submovement = end of the primary submovement. * $p < .05$. *** $p < .01$.

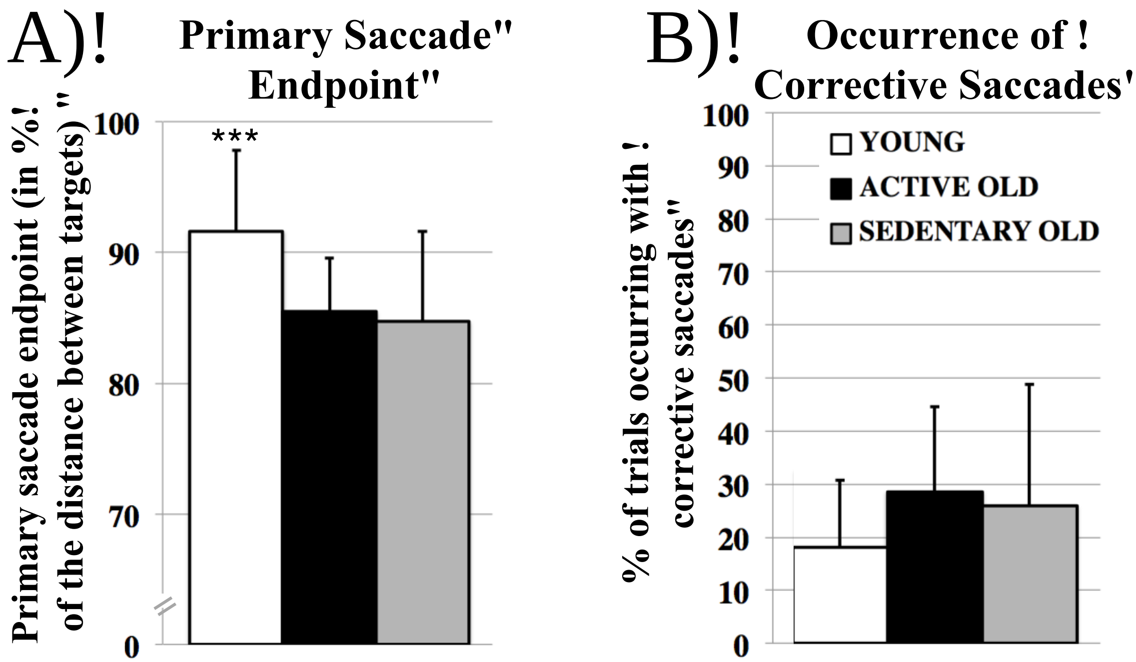

Figure 7: Eye movement results in the cyclical aiming task. Comparison of mean group scores. Error bars represent standard deviations. (A) Primary saccade amplitude; (B) Proportion of aiming movements occurring with corrective saccades. * $p < .05$. *** $p < .01$.