brought to you by CORE

Title:

Factors Underlying Age-related Changes in Discrete Aiming

Author names and affiliations:

Florian Van Halewyck¹, Ann Lavrysen¹, Oron Levin¹, Matthieu P. Boisgontier¹, Digby Elliott², Werner F. Helsen¹

¹ KU Leuven, Department of Kinesiology, Movement Control and Neuroplasticity Research Group,

Tervuursevest 101, 3001 Leuven - Belgium

² Research Institute for Sport and Exercise Sciences, Liverpool John Moores University, Tom Reilly Building, Byrom Street, L3 3AF Liverpool - United Kingdom

Corresponding author:

Prof. Dr. Werner Helsen

E-mail: werner.helsen@faber.kuleuven.be

Telephone: +32-16-32.90.68

Fax: +32-16-32.91.97

Abstract

2 Age has a clear impact on one's ability to make accurate goal-directed aiming movements. Older adults 3 seem to plan slower and shorter-ranged initial pulses towards the target, and rely more on sensory feedback 4 to ensure endpoint accuracy. Despite the fact that these age-related changes in manual aiming have been 5 observed consistently, the underlying mechanism remains speculative to date. In an attempt to isolate four 6 commonly suggested underlying factors, young and older adults were instructed to make discrete aiming 7 movements under varying speed and accuracy constraints. Results showed that older adults were physically 8 able to produce fast primary submovements, and that they demonstrated similar movement-planning 9 capacities as young adults. On the other hand, considerable evidence was found supporting a decreased 10 sensory feedback-processing efficiency and the implementation of a play-it-safe strategy in old age. In 11 conclusion, a combination of the latter two factors seems to underlie the age-related changes in manual 12 aiming behavior. 13 14 Keywords: Manual aiming, Motor Control, Aging, Kinematics

Factors Underlying Age-related Changes in Discrete Aiming

2 According to the *multiple-process model of limb control* (Elliott et al. 2010), manual aiming 3 movements such as pressing a light button or picking up a glass of wine consist of two consecutive phases: 4 a primary submovement and a homing-in phase. The primary submovement corresponds to the initial pulse 5 towards the vicinity of the target. Although this pre-programmed movement phase is traditionally 6 associated with open-loop control (Woodworth 1899), recent work has shown that subtle movement 7 trajectory corrections can occur during the primary submovement (Khan et al. 2006; Saunders and Knill 8 2003). Still, the main body of closed-loop control occurs during the homing-in phase. Here, proprioceptive 9 and visual feedback is used to reduce any spatial discrepancy between hand and target positions (i.e., *limb*-10 *target control*). Previous research has shown that the primary submovement generally undershoots the 11 target to allow corrections to occur in the same direction as the initial pulse (Engelbrecht et al. 2003; 12 Helsen et al. 1998). This type of correction entails lower energy-costs than correcting for target overshoots, 13 as reversals involve overcoming the inertia of a zero-velocity situation and the limb traveling a greater total 14 distance (Elliott et al. 2004; Elliott et al. 2010; Welsh et al. 2007). 15 By slowing down their primary submovement, older adults tend to undershoot the target to a 16 greater extent than young controls. As a consequence, they need more time-consuming adjustments during 17 the homing-in phase to end their aiming movement accurately onto the target. This ultimately results in 18 greater overall movement times (Ketcham et al. 2002; Poston et al. 2009). Although these age-related 19 movement adaptations during manual aiming have been described rather consistently, their underlying 20 mechanism remains speculative. Nevertheless, several factors have already been suggested to cause the 21 abovementioned age-related differences in manual aiming. Though often allocated different names, four

factors can generally be distinguished: (1) an inability to produce fast movements, (2) an impaired

programming of aiming movements, (3) a decline in sensory feedback-processing efficiency, and (4) an
adapted aiming strategy.

Factor 1: Ability to produce fast primary submovements. The gradual age-related decline in muscle strength (i.e., sarcopenia) may limit older adults' ability to produce fast initial pulses towards the target (Walker et al. 1997). Slower primary submovements may compel older adults to undershoot the target to a greater extent, consequently resulting in longer homing-in phases. The traditionally observed movement adaptations in old age may thus be caused by older adults' physical inability to generate the
same amount of force as young controls (Pratt et al. 1994).

3 Factor 2: Programming the aiming movement. Alternatively, several researchers have suggested 4 that a reduced ability to accurately program the movement may underlie the movement adaptations in old 5 age (Pohl and Winstein 1998; Rey-Robert et al. 2012). Specifically, older adults are thought to have 6 augmented levels of motor noise, thereby increasing the random, unintentional error inherent to human 7 force production (Walker et al. 1997). This view is supported by studies reporting increased motor output 8 variability in old age during force production tasks in general (Christou and Carlton 2001; Galganski et al. 9 1993), as well as during manual aiming in particular (Ketcham et al. 2002; Pratt et al. 1994). Taking into 10 account the linear relationship between movement velocity and movement endpoint variability (Schmidt et 11 al. 1979), a simple way to cope with increased levels of variability would be to slow down the initial pulse 12 towards the target. As described for Factor 1, reducing the primary submovement speed could easily result 13 in the set of movement adaptations typically observed in older adults' aiming behavior. These movement 14 adaptations may therefore reflect older adults' reaction to a decreased ability to accurately program the 15 movement.

16 Factor 3: Sensory feedback-processing efficiency. Instead of impaired movement programming 17 capacities, various researchers have proposed that older adults may encounter difficulties during the 18 processing of online sensory feedback (Boisgontier et al. 2012; Boisseau et al. 2002; Chaput and Proteau 19 1996; Coats and Wann 2011). This limitation would explain why the homing-in phase of the movement is 20 longer in older adults. Despite the fact that sensory feedback-processing efficiency is extremely difficult to 21 quantify, basic evidence supporting this hypothesis has recently arisen. In contrast to previous work, Welsh 22 et al. (2007) for instance conducted a study in which young and older adults initially undershot the target to 23 the same extent. Though both age groups exhibited a similar number of corrective submovements during 24 the homing-in phase to accurately hit the target, older adults needed more time to complete these 25 corrections. As there was no evidence for increased processing demands in the older adults, the authors 26 suggested that adjusting the movement trajectory based on sensory feedback takes longer in old age (Welsh 27 et al. 2007). In addition to this kinematic evidence, Temprado et al. (2013) recently confirmed this outcome using *efficiency functions* and *Brinley plots*. In sum, a reduced efficiency in sensory feedback processing
 may well underlie the movement alterations observed in older adults' manual aiming behavior.

Factor 4: Aiming strategy. As older adults tend to be more cautious when performing motor tasks
(Boisseau et al. 2002), the hypothesis of older adults adopting a different aiming strategy has also gained
recent interest. To avoid the high energy costs associated with overshooting the target, older adults are
thought to deliberately undershoot the target to a great extent (Elliott et al. 2010; Welsh et al. 2007).
Afterwards, they may rely completely on limb-target control to ensure endpoint accuracy. This prudent
approach is known as the *play-it-safe* strategy believed to be adopted by older adults.

9 Finally, it should be noted that older adults may also change their aiming strategy to cope with
10 physical limitations such as an impaired programming of the aiming movement or a less efficient
11 perceptual feedback processing. The age-related differences in manual aiming may thus also be caused by a
12 combination of factors (Rey-Robert et al. 2012).

The aim of this study was to investigate which of these four commonly identified factors underlie(s) the age-related movement adaptations during manual aiming. Young and older adults therefore performed manual aiming movements under different conditions. These different aiming conditions allowed us to isolate all four factors, and compare them between age groups. In line with the literature, it was expected that Factors 2, 3 and 4 would cause the movement alterations observed during manual aiming in old age.

19

Methods

20 Participants

21 Twenty-two young (age range: 19 - 26 years old) and 24 older (60 - 72 years old) volunteers 22 participated in the study. Young adults were recruited on the university campus, whereas older adults were 23 recruited via a local senior club. All participants were right-handed according to the Edinburgh Handedness 24 Inventory (Oldfield 1971) and had normal or corrected-to-normal vision. Fine motor skills were considered 25 intact, as all participants met the age- and gender-dependent criteria for the Nine Hole Pegboard Test 26 (Mathiowetz et al. 1985; Oxford Grice et al. 2003). To control for mild dementia or other anomalies in 27 cognitive functioning, older adults were exposed to a *Mini-Mental State Examination* (Folstein et al. 1975). 28 The minimum score for inclusion was set at 28 out of 30, which all achieved. Both young and older adults

1 were subdivided based on their physical activity levels as measured by a Baecke questionnaire. As a 2 previous study revealed the traditional age-related movement adaptations are best observed when 3 comparing active older adults to active young controls (Van Halewyck et al. 2014a), the current analysis 4 only focuses on the physically active subsamples. The study was approved by the Medical Ethics 5 Committee of the KU Leuven and was conducted in accordance with the 1964 Declaration of Helsinki. 6 Prior to the experiment, written informed consent was obtained from all participants.

7 **Apparatus**

8 The apparatus was identical to the one used in previous work (Van Halewyck et al. 2014a; Van 9 Halewyck et al. 2014b). Participants sat in a comfortable chair with their preferred, right forearm in an 10 orthosis. The axis of the orthosis was aligned with the anatomical axis of the wrist joint and positioned in a 11 way that participants could only flex and extend their wrist in the horizontal plane. A high-precision shaft 12 encoder with an accuracy of 0.006° and sampling frequency of 250 Hz was attached onto the orthosis. In all 13 conditions, wrist angular position was presented as a 1.5 cm diameter circular cursor on a 60 cm computer 14 monitor, which was located at a standardized distance of 125 cm in front of the participant at eye level. 15 Apart from this cursor, two fixed targets also appeared on the monitor. These square targets had a width of 16 1 cm and stood 18 cm apart. In short, the task consisted of moving the cursor from the right target to the 17 left, corresponding to a wrist flexion movement. In conditions in which the left target had to be entirely 18 surrounded by the cursor, the aiming movement had an index of difficulty (ID) of 6.2 bits (ID: 19 log2[2*18/(1.5-1)]). The exact instructions per condition are further explained in the Task and Protocol 20 section. 21

Concurrent to the hand movement, eye closure was recorded using an Applied Science

22 Laboratories (ASL) 6000 pan-tilt eye-tracker system (Bedford, MA) with a sampling frequency of 240 Hz.

23 As both effectors were registered at different sampling frequencies, custom-written software was used to

24 ensure the high-precision shaft encoder and ASL started sampling simultaneously (i.e., at the same

25 millisecond). This allowed us to temporally link both effectors after data were collected.

26 **Task and Protocol**

27 Participants performed blocks of 10 aiming movements in three different conditions (CONTROL, 28 ACCURACY and SPEED). In all conditions, participants were asked to start the block by positioning the

1 cursor around the right target and to wait for the first GO-stimulus. As soon as the right target turned red 2 (GO-stimulus), they were instructed to aim towards the left, corresponding to a wrist flexion movement. 3 After movement completion, participants were asked to return to the right starting target to prepare for the 4 next GO-stimulus. The interval between two consecutive GO-stimuli varied randomly between 6000, 6500, 5 7000, 7500 and 8000 ms to avoid movement anticipation. The experiment started with an extensive 6 familiarization phase in which three CONTROL aiming blocks were practiced. Then, a first experimental 7 session consisting of five CONTROL aiming blocks was performed. After a 30-minute break, a second 8 experimental session started in which the order of the ACCURACY and SPEED blocks was 9 counterbalanced.

10 **CONTROL condition.** Participants were instructed to surround the left target as fast and 11 accurately as possible after the GO-stimulus (ID: 6.2 bits). Once the left target was entirely surrounded by 12 the cursor, participants were asked to briefly close their eyes to indicate their movement had ended. All 13 participants performed five blocks of 10 aiming movements, resulting in 50 aiming movements per 14 participant.

15 ACCURACY condition. Similar to the CONTROL condition, participants were instructed to 16 surround the left target as fast and accurate as possible with the cursor after the GO-stimulus (ID: 6.2 bits). 17 Participants were told that the time between the GO-stimulus and the end of the aiming movement would 18 be accumulated over all ACCURACY condition movements. Both the young and older participant who 19 needed the least amount of total time, would receive a €25 gift voucher. However, participants were also 20 told that primary submovements overshooting the target, as well as endpoint inaccuracy, would be 21 penalized with an additional 2000 ms. Thus although participants were motivated to move quickly, the 22 emphasis was shifted towards endpoint accuracy with a particular concentration on the avoidance of target 23 overshoots. Again, participants performed five blocks of 10 aiming movements, resulting in 50 aiming 24 movements in this condition.

SPEED condition. In contrast to the CONTROL and ACCURACY conditions, the task's accuracy demands were eliminated in the SPEED condition: Participants now reacted to the GO-stimulus by making identical, ballistic aiming movements *beyond* the left target. To prevent fatigue, only three SPEED condition blocks were performed resulting in 30 aiming movements per participant.

- 1 Factor isolation
- 2

To address which factor may be the underlying mechanism for the age-related movement adaptations in manual aiming, an attempt was made to isolate the four abovementioned factors.

Factor 1: Ability to produce fast primary submovements. Potential age-related declines in the ability to produce fast primary submovements were examined via peak velocity values in the SPEED condition (Walker et al. 1997). For this variable, we disregarded conditions that required accuracy constraints as age-related slowing could be caused here by specific aiming strategies rather than a physical limitation. If older adults would be unable to produce the same level of primary submovement speed as young controls, an age-related decline in muscle strength (i.e., sarcopenia) could be a mechanism underlying the movement adaptations traditionally observed in old age.

11 Factor 2: Programming the aiming movement. In line with the study of Welsh et al. (2007), 12 potential age-related difficulties to program consistent actions were examined by comparing the temporal 13 and spatial variability at four kinematic markers. This was done by first calculating the absolute time it took 14 participants to reach peak acceleration, peak velocity, peak deceleration, and the end of the movement in all 15 SPEED condition aiming movements. Then, the standard deviation of these kinematic marker timings was 16 calculated per block and used as an indicator of temporal variability. A similar procedure involving the 17 absolute positions in the primary direction of the movement at the kinematic markers was used to 18 determine the spatial variability per block. Again, we limited our analysis to the SPEED condition to rule 19 out potential strategy differences between young and older adults. Also, as participants were instructed to 20 make *identical* ballistic movements, all participants strived towards the lowest possible temporal and 21 spatial movement variability in this condition. Thus, if older adults were to show greater temporal and/or 22 spatial variability of kinematic markers than younger adults, this would indicate age-related difficulties 23 associated with accurately programming the aiming movement.

Factor 3: Sensory feedback-processing efficiency. Sensory feedback processing ability is
extremely difficult to disentangle from movement execution abilities in behavioral experiments.
Nevertheless, Walker et al. (1997) attempted to isolate the sensory component by asking participants to
release a pressed button in order to indicate their aiming movement had ended. They considered the time
between the end of the aiming movement and the release of the button a basic indicator for the processing

1 speed of visual feedback. Though not perfect, this approach may provide the best behavioral method for 2 comparing the processing speed of sensory feedback between groups. Instead of focusing on a distal motor 3 component such as the finger muscles, it may nevertheless be more appropriate to involve a more proximal 4 motor component to minimize conduction time (Boisgontier et al. 2014; Kimura 2001). As described in the 5 Task and Protocol section, participants were therefore asked to briefly close their eyes in the CONTROL 6 condition to indicate the cursor accurately surrounded the target and the aiming movement had ended. 7 Based on the original study of Walker et al. (1997), the time between the end of the hand movement and 8 the closure of the eves was considered the *verification time* of the movement. Though this verification time 9 still contains a minimal motor component associated with the eyelids, its duration is clearly dominated by 10 visual feedback processing. If older adults demonstrate longer verification times, this was considered to 11 reflect an age-related slowing in sensory feedback processing. 12 Factor 4: Aiming strategy. To investigate age-related differences in aiming strategy, an 13 ACCURACY condition was added to the experiment. As described in the Task & Protocol section, 14 inaccurate movement endpoints and primary submovements overshooting the target were penalized in this 15 condition. Age-related differences in aiming strategy would be supported by two specific outcomes. On the 16 one hand, if older adults adopt a play-it-safe strategy to ensure endpoint accuracy and prevent target 17 overshoots in the CONTROL condition, the ACCURACY condition instructions should have a minimal 18 effect on their aiming kinematics. On the other hand, if the ACCURACY condition results in young adults 19 demonstrating aiming characteristics traditionally described in older adults, these movement adaptations 20 might be viewed as a more universal strategy used to ensure endpoint accuracy and prevent target 21 overshoots. Besides endpoint accuracy, we therefore compared the five variables that are traditionally 22 altered in older adults' aiming movements (i.e., peak velocity, relative distance of the primary 23 submovement, relative duration of the homing-in phase, number of corrective submovements, and overall 24 movement time) between the CONTROL and ACCURACY conditions. If young adults change their 25 aiming kinematics significantly in the direction of older adults, and if older adults in turn keep these 26 variables unchanged between conditions, our findings would be consistent with a play-it-safe strategy in 27 older adults.

28 Data Analysis

1	Prior to the calculation of the dependent variables, a first order low-pass Butterworth filter with a
2	cut-off frequency of 20 Hz was applied on the hand movement data. The filtered data were differentiated
3	twice to obtain instantaneous hand velocity and acceleration profiles. The criteria to define all dependent
4	variables are described in detail in a previous study (Van Halewyck et al. 2014a). First, the mean score and
5	standard deviation were calculated per block for all variables. Then, Factors 1 to 3 were compared between
6	the two age groups using independent t-tests. Finally, our specific expectations regarding aiming strategy
7	allowed us to calculate a priori comparisons for Factor 4. Specifically, we determined whether young and
8	older adults changed their aiming kinematics going from the CONTROL to the ACCURACY condition.
9	The significance level in all tests was set at $p < .05$. Results are displayed as group mean score \pm standard
10	error of the mean (SEM).
11	Results
12	To highlight the validity of our test set-up, we start our Results section with some notable group
13	differences in the CONTROL condition. As expected, all five movement adaptations traditionally described
14	in old age were observed in older participants: lower peak velocities, shorter-ranged primary
15	submovements, relatively greater homing-in phase durations, more corrective submovements, and greater
16	overall movement times (all $p < .01$; see Table 1).
17	Factor 1: Ability to produce fast primary submovements
18	In contrast to the CONTROL condition, older adults $(311.6 \pm 26.2 \text{ cm/s})$ did not move significantly
19	slower than young adults $(321.9 \pm 27.0 \text{ cm/s})$ in the SPEED condition ($p = .93$; see Figure 1).
20	Factor 2: Programming the aiming movement
21	As displayed in Figure 2A, temporal variability in the SPEED condition was comparable between
22	groups at all kinematic markers (all $p > .18$). Similarly, no significant differences were observed for spatial
23	variability (all $p > .05$; see Figure 2B).
24	Factor 3: Sensory feedback-processing efficiency
25	In the CONTROL condition, significantly greater verification times were detected in older (498 \pm
26	81 ms) compared to young adults (297 \pm 45 ms ; $p < .01$; see Figure 3).
27	Factor 4: Aiming strategy

1	Endpoint accuracy: Before focusing on the five specific variables of interest, we should highlight
2	that only young adults increased their percentage of aiming movements resulting in target hits in the
3	ACCURACY condition (94.4 \pm 2.7 %) as compared to the CONTROL condition (91.1 \pm 3.5 %; <i>p</i> < .05). In
4	contrast, older adults did not change endpoint accuracy between conditions (going from 85.4 ± 3.7 in the
5	CONTROL condition to 86.4 \pm 4.5 in the ACCURACY condition; $p = .71$; see Figure 4A).
6	Peak velocity: Compared to the CONTROL condition (83.9 ± 8.6 cm/s), young adults tended to
7	speed up their initial pulse towards the target in the ACCURACY condition (92.4 \pm 8.9 cm/s; $p = .06$).
8	Older adults, on the other hand, demonstrated similar peak velocity values (65.9 ± 7.8 cm/s in the
9	CONTROL condition and 70.9 ± 6.1 cm/s in the ACCURACY condition; $p = .37$; see Figure 4B).
10	Relative distance of primary submovement: Young adults also tended to undershoot the target to
11	a slightly greater extent in the ACCURACY condition (67.7 \pm 3.8 % of target distance) compared to the
12	CONTROL condition (71.3 \pm 4.1 % of target distance; $p = .08$). Older adults, on the other hand, did not
13	shorten their primary submovement in the ACCURACY condition (61.0 \pm 4.4 % of target distance in the
14	CONTROL condition and 60.8 ± 4.5 % of target distance in the ACCURACY condition; $p = .95$; see
15	Figure 4C).
16	Relative duration of the homing-in phase: Young adults spent proportionally more time on the
17	homing-in phase during ACCURACY condition aiming movements (69.4 \pm 3.0 % of the movement time)
18	compared to CONTROL condition aiming movements (63.9 \pm 3.5 % of the movement time; <i>p</i> < .01).
19	Again, older adults did not adapt their aiming movements in this respect (68.0 ± 3.1 of the movement time
20	in the CONTROL condition and 69.5 ± 3.0 of the movement time in the ACCURACY condition; $p = .63$;
21	see Figure 4D).
22	Number of corrective submovements: Compared to the CONTROL condition (2.3 ± 0.3), young
23	adults significantly increased their number of corrective submovements during the ACCURACY condition
24	$(2.7 \pm 0.3; p < .05)$. In contrast, the older adults did not change their number of corrections in the hand
25	movement trajectory (2.8 \pm 0.3 in the CONTROL condition and 3.0 \pm 0.3 in the ACCURACY condition; <i>p</i>
26	= .22; see Figure 4E).
77	Overall movement times. Young adults significantly increased their movement times going from

Overall movement time: Young adults significantly increased their movement times going from28the CONTROL condition (906 \pm 64 ms) to the ACCURACY condition (969 \pm 66 ms; *p* <.05). Again, the</td>

1	difference in older adults' movement times did not reach the level of significance $(1081 \pm 65 \text{ ms in the})$
2	CONTROL condition and 1116 ± 71 ms in the ACCURACY condition; $p = .41$; see Figure 4F).
3	Discussion
4	The aim of this study was to determine the mechanism(s) underlying the movement adaptations
5	traditionally observed in older adults' aiming behavior. Four commonly suggested factors were isolated in
6	different aiming conditions, and compared between age groups. After discussing the observations for each
7	factor separately, a general conclusion is provided.
8	Factor 1: Ability to produce fast primary submovements
9	Older adults generally make slower and shorter-ranged primary submovements compared to young
10	adults, suggesting they may encounter difficulties generating fast initial pulses towards the target (Pratt et
11	al. 1994). Results from the SPEED condition nevertheless indicate that an age-related degradation in force
12	generation capacity (i.e., sarcopenia) is not the limiting factor during goal-directed aiming movements.
13	Without accuracy constraints, older adults demonstrated similar primary submovement speeds as young
14	controls (see Figure 1). The age-related differences in movement speed that were observed in the
15	CONTROL condition must therefore be caused by factors other than an age-related physical limitation to
16	produce fast primary submovements. Instead, Figure 1 suggests older adults may intentionally slow down
17	the primary submovement to a greater extent during CONTROL condition movements in order to deal with
18	the imposed accuracy constraints. Age-related strategy differences to cope with the speed-accuracy trade-
19	off are discussed in greater detail when interpreting the results associated with Factor 4.
20	Factor 2: Programming the aiming movement
21	We also investigated whether movement programming capacities are degraded in old age by

looking into the movement trajectory's consistency during SPEED condition movements. As is evident in
 Figures 2A and 2B, similar levels of temporal and spatial variability were observed at all kinematic
 markers. This outcome suggests that movement-planning capacities do not deteriorate with age¹.

At first glance, this result seems to be contradicted by several studies reporting greater levels of movement variability in older adults (Ketcham et al. 2002; Pratt et al. 1994), and is therefore not in line with our original predictions. There are, however, several possible explanations for this dissimilarity in results. For instance, in contrast to previous studies, we specifically instructed participants to make

1 *identical*, ballistic aiming movements. As such, all participants strived towards minimal movement 2 trajectory variability, which may not have been the case in previous research. Also, instead of focusing on 3 the entire movement trajectory, other variability analyses (e.g., Ketcham et al. 2002; Pratt et al. 1994) were 4 limited to two kinematic markers late in the movement (i.e., end of the primary submovement and end of 5 the movement) in aiming conditions with high accuracy constraints. For this reason, greater variability 6 levels in older adults may well represent other factors than an age-related deterioration in movement-7 planning capacities. To our knowledge, the only other aging study to perform a more comprehensive 8 variability analysis was the previously mentioned investigation of Welsh and colleagues (2007). In line 9 with our current results, they too found equal variability levels at the same kinematic markers among young 10 and older adults. Based on both analyses, we may therefore conclude that movement-planning capacities 11 remain intact in old age.

12 Factor 3: Sensory feedback-processing efficiency

13 In the CONTROL condition, participants were asked to indicate their movement had ended by 14 briefly closing their eyes when the cursor surrounded the end target. As explained in the Factor Isolation 15 section, the time span between the end of the hand movement and the closure of the eyes (i.e., verification 16 time) can be seen as an indicator for visual feedback processing speed. Since older adults demonstrated 17 significantly greater verification times (see Figure 3), our results provide clear evidence for slower visual 18 feedback processing in old age. This finding is supported by several studies reporting older adults generally 19 need more time than young controls to process the same amount of information (Coats and Wann 2011; 20 Temprado et al. 2013; Welsh et al. 2007). Also, when the amount of sensory information to be processed is 21 increased by, for instance, presenting additional information (Boisgontier et al. 2012; Boisseau et al. 2002) 22 or increasing the number of choices in a multiple-choice task (Falkenstein et al. 2006; Yordanova et al. 23 2004), older adults have been shown to prolong their reaction and movement times relative to young adults. 24 Thus these studies are consistent with our conclusion that an age-related decrease in sensory feedback-25 processing efficiency may underlie the movement alterations traditionally observed in older adults.

26 Factor 4: Aiming strategy

Finally, we examined whether age-related changes in aiming strategy could also provide an explanation for movement alterations in old age. In short, older adults are thought to adopt a *play-it-safe* strategy by deliberately undershooting the target to a greater extent, and relying more on limb-target control during the homing-in phase (Elliott et al. 2010; Welsh et al. 2007). This cautious approach is believed to prevent the high energy costs associated with target overshoots, and may help ensure high levels of endpoint accuracy. To reveal potential strategy differences between both age groups, an ACCURACY condition was added to the experiment. Here, participants were financially rewarded for ending all aiming movements accurately onto the target without overshooting it initially. Our expectations regarding the ACCURACY condition were largely confirmed.

8 Firstly, on the variables of interest, older adults did not exhibit any difference in performance 9 between the CONTROL and ACCURACY conditions. This result seems to suggest they already 10 emphasized endpoint accuracy and the prevention of target overshoots under normal aiming circumstances 11 (i.e., CONTROL condition). Alternatively, it could also reflect the fact that older adults are less able to 12 adapt their aiming movements to specific instructions or contexts (see Pratt et al. 1994; Seidler-Dobrin and 13 Stelmach 1998). However, this potential limitation does not seem applicable to our task, as older adults 14 were clearly able to change their aiming characteristics in response to our SPEED condition instructions 15 (see Figure 1).

16 Secondly, when comparing the CONTROL to the ACCURACY condition data in young adults, 17 three of the five variables changed significantly towards the pattern typically seen in older adults (i.e., 18 relative duration of the homing-in phase, number of corrective submovements, and overall movement time; 19 all p < .05; see Figure 4D, 4E and 4F). Moreover, a fourth variable only just failed to reach the level of 20 significance (relative distance of the primary submovement; p = .08; see Figure 4C). Making these 21 movement adjustments resulted in an increased percentage of target hits (see Figure 4A). Thus these 22 modification to the movement trajectory seem to reflect an effective approach to ensure endpoint accuracy. 23 The only variable not to meet the expected outcome was peak velocity (see Figure 4B). The finding that 24 only young adults were able to increase the maximum speed of their initial pulse and yet demonstrate 25 higher levels of endpoint accuracy suggests that in the ACCURACY condition they adopted a strategy of 26 moving to the target area quickly so that they had more real and proportional time to use sensory feedback 27 during the homing phase of their movement. This explanation is consistent with other work involving 28 young adults (e.g., Hansen et al. 2006).

All in all, since most variables met the expected outcome, the overall picture provides evidence for
 older adults adopting a play-it-safe strategy under natural circumstances².

3 General Conclusion

4 In sum, results of the SPEED condition showed that older adults were physically able to move as 5 fast as young controls. The movement slowing typically observed in older adults thus appears to be caused 6 by factors other than the physical inability to produce fast primary submovements (Factor 1). Also in the 7 SPEED condition, the absence of age-related differences in temporal and spatial variability suggest that 8 older adults' movement programming capacities remain intact as well (Factor 2). Instead, the traditional 9 aiming movement adaptations in old age appeared to be caused by two other key mechanisms. On the one 10 hand, older adults showed greater verification times. This outcome suggests less efficient sensory feedback 11 processing in old age (Factor 3), and is strongly supported by the recent literature (Boisgontier et al. 2012; 12 Boisseau et al. 2002; Falkenstein et al. 2006; Temprado et al. 2013; Welsh et al. 2007; Yordanova et al. 13 2004). On the other hand, evidence was found for older adults adopting a *play-it-safe strategy* during 14 manual aiming (Factor 4; Elliott et al. 2010; Welsh et al. 2007). Compared to the CONTROL condition, 15 older participants' aiming characteristics stayed relatively unchanged in the ACCURACY condition, 16 whereas the movements of young adults shifted to resemble those of older adults. The former suggests that 17 older adults already emphasized endpoint accuracy and the prevention of target overshoots in the 18 CONTROL condition; the latter seems to imply that this approach is indeed an effective strategy to end 19 aiming movements accurately. In summary, the movement adaptations traditionally observed in old age 20 thus appear to reflect less efficient sensory feedback processing in combination with a play-it-safe strategy. 21 Acknowledgements 22 Werner F. Helsen and Florian Van Halewyck would like to acknowledge the KU Leuven Research 23 Council for financially supporting this research project. The authors also wish to thank Ig. Marc Beirinckx 24 and Ig. Paul Meugens for providing invaluable guidance in designing the research equipment.

1	References
2	Boisgontier MP, Olivier I, Chenu O, Nougier V (2012) Presbypropria: the effects of physiological ageing
3	on proprioceptive control. Age 34: 1179-1194. doi: 10.1007/s11357-011-9300-y
4	Boisgontier MP, Wittenberg GF, Fujiyama H, Levin O, Swinnen SP (2014) Complexity of central
5	processing in simple and choice multilimb reaction-time tasks. PLoS One. doi:
6	10.1371/journal.pone.0090457
7	Boisseau E, Scherzer P, Cohen H (2002) Eye-hand coordination in aging and in Parkinson's disease.
8	Aging Neuropsychol C 9: 266-275. doi: 10.1076/Anec.9.4.266.8769
9	Chaput S, Proteau L (1996) Aging and motor control. J Gerontol B-Psychol 51: 346-355.
10	Christou EA, Carlton LG (2001) Old adults exhibit greater motor output variability than young adults
11	only during rapid discrete isometric contractions. J Gerontol A-Biol 56: 524-532.
12	Coats RO, Wann JP (2011) The reliance on visual feedback control by older adults is highlighted in tasks
13	requiring precise endpoint placement and precision grip. Exp Brain Res 214: 139-150. doi:
14	10.1007/s00221-011-2813-x
15	Elliott D, Hansen S, Grierson LE, Lyons J, Bennett SJ, Hayes SJ (2010) Goal-directed aiming: two
16	components but multiple processes. Psychol Bull 136: 1023-1044. doi: 10.1037/a0020958
17	Elliott D, Hansen S, Mendoza J, Tremblay L (2004) Learning to optimize speed, accuracy, and energy
18	expenditure: a framework for understanding speed-accuracy relations in goal-directed aiming.
19	J Motor Behav 36: 339-351. doi: 10.3200/JMBR.36.3.339-351
20	Engelbrecht SE, Berthier NE, O'Sullivan LP (2003) The undershoot bias: learning to act optimally under
21	uncertainty. Psychol Sci 14: 257-261.
22	Falkenstein M, Yordanova J, Kolev V (2006) Effects of aging on slowing of motor-response generation.
23	Int J Psychophysiol 59: 22-29. doi: 10.1016/j.ijpsycho.2005.08.004
24	Folstein, MF, Folstein SE, McHugh PR (1975). "Mini-mental state". A practical method for grading the
25	cognitive state of patients for the clinician. J Psychiatr Res 12: 189-198.
26	Galganski ME, Fuglevand AJ, Enoka RM (1993) Reduced control of motor output in a human hand
27	muscle of elderly subjects during submaximal contractions. J Neurophysiol 69: 2108-2115.

1	Hansen S, Glazebrook CM, Anson JG, Weeks DJ, Elliott D (2006) The influence of advance information
2	about target location and visual feedback on movement planning and execution. Can J Exp
3	Psychol 60: 200-208. doi: 10.1037/cjep2006019
4	Heath M (2005) Role of limb and target vision in the online control of memory-guided reaches. Motor
5	Control 9: 281-311.
6	Helsen WF, Elliott D, Starkes JL, Ricker KL (1998) Temporal and spatial coupling of point of gaze and
7	hand movements in aiming. J Motor Behav 30: 249-259. doi: 10.1080/00222899809601340
8	Ketcham CJ, Seidler RD, Van Gemmert AW, Stelmach GE (2002) Age-related kinematic differences as
9	influenced by task difficulty, target size, and movement amplitude. J Gerontol B-Psychol 57: 54-
10	64.
11	Kimura J (2001) Electrodiagnosis in diseases of nerve and muscle: principles and practice. Oxford
12	University Press, New York
13	Khan MA, et al. (2006). Inferring online and offline processing of visual feedback in target-directed
14	movements from kinematic data. Neurosci Biobehav R 30: 1106-1121. doi:
15	10.1016/j.neubiorev.2006.05.002
16	Mathiowetz V, Volland G, Kashman N, Weber K (1985) Adult norms for the Box and Block Test of
17	manual dexterity. Am J Occup Ther 39: 386-391.
18	Messier J, Kalaska JF (1999) Comparison of variability of initial kinematics and endpoints of reaching
19	movements. Exp Brain Res 125: 139-152.
20	Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory.
21	Neuropsychologia 9: 97-113.
22	Oxford Grice K, Vogel KA, Le V, Mitchell A, Muniz S, Vollmer MA (2003) Adult norms for a
23	commercially available Nine Hole Peg Test for finger dexterity. Am J Occup Ther 57: 570-573.
24	Pohl PS, Winstein CJ (1998) Age-related effects on temporal strategies to speed motor performance. J
25	Aging Phys Activ 6: 45-61.
26	Poston B, Van Gemmert AW, Barduson B, Stelmach GE (2009) Movement structure in young and
27	elderly adults during goal-directed movements of the left and right arm. Brain Cognition 69: 30-
28	38. doi: 10.1016/j.bandc.2008.05.002

1	Pratt J, Chasteen AL, Abrams RA (1994) Rapid aimed limb movements: age differences and practice
2	effects in component submovements. Psychol Aging 9: 325-334.
3	Rey-Robert B, Temprado JJ, Lemaire P, Berton E (2012) Combining movement kinematics, efficiency
4	functions, and Brinley plots to study age-related slowing of sensorimotor processes: insights from
5	Fitts' task. Gerontology 58: 171-180. doi: 10.1159/000329347
6	Saunders JA, Knill DC (2003) Humans use continuous visual feedback from the hand to control fast
7	reaching movements. Exp Brain Res 152: 341-352. doi: 10.1007/s00221-003-1525-2
8	Schmidt RA, Zelaznik H, Hawkins B, Frank JS, Quinn JT (1979). Motor-output variability: a theory for
9	the accuracy of rapid motor acts. Psychol Rev 47: 415-451.
10	Seidler-Dobrin RD, Stelmach GE (1998) Persistence in visual feedback control by the elderly. Exp Brain
11	Res 119: 467-474. doi: 10.1007/S002210050362
12	Temprado JJ, Sleimen-Malkoun R, Lemaire P, Rey-Robert B, Retornaz F, Berton E (2013) Aging of
13	sensorimotor processes: a systematic study in Fitts' task. Exp Brain Res 228: 105-116.
14	doi: 10.1007/s00221-013-3542-0
15	Van Halewyck F, Lavrysen A, Levin O, Boisgontier MP, Elliott D, Helsen WF (2014a) Both age and
16	physical activity level impact on eye-hand coordination. Hum Movement Sci. doi:
17	Van Halewyck F, Lavrysen A, Levin O, Elliott D, Helsen WF (2014b) The impact of age and physical
18	activity level on manual aiming performance. J Aging Phys Activ. doi:
19	http://dx.doi.org/10.1123/japa.2013-0104
20	Walker N, Philbin DA, Fisk AD (1997) Age-related differences in movement control: adjusting
21	submovement structure to optimize performance. J Gerontol B-Psychol 52: 40-52.
22	Welsh TN, Higgins L, Elliott D (2007) Are there age-related differences in learning to optimize speed,
23	accuracy, and energy expenditure? Hum Movement Sci 26: 892-912. doi:
24	10.1016/j.humov.2007.04.004
25	Woodworth RS (1899) The accuracy of voluntary movement. Psychol Rev 3: 1-119.
26	Yordanova J, Kolev V, Hohnsbein J, Falkenstein M (2004) Sensorimotor slowing with ageing is mediated
27	by a functional dysregulation of motor-generation processes: evidence from high-resolution
28	event-related potentials. Brain 127: 351-362. doi: 10.1093/brain/awh042

Footnotes

19

2 ¹To demonstrate that SPEED condition movements were indeed based primarily on planning processes, an 3 additional *coefficient of determination* (\mathbb{R}^2) analysis was performed (Heath 2005; Khan et al. 2006; Messier 4 and Kalaska 1999). In short, such analysis examines the proportion of movement endpoint variability that 5 can be explained by the limb position at different kinematic markers. The rationale behind this regression 6 technique is the following: In case of aiming movements purely based on planning processes, one should 7 be able to predict the movement endpoint based on (early) kinematic marker positions, as no corrections 8 occur late in the movement. Accurate predictions are reflected by high R^2 values. On the other hand, if 9 aiming movements are strongly modified based on online feedback during the homing-in phase, movement 10 endpoints are more difficult to predict from (early) kinematic marker positions. These types of movements 11 are typically associated with low R^2 values. Results of this additional R^2 analysis showed that the 12 percentage of explained endpoint variance in the SPEED condition exceeded 94.0 % in both groups when 13 movement endpoints were estimated based on the peak velocity position, whereas this value exceeded 99.0 14 % when the estimation was based on peak deceleration position. This analysis thus confirms that SPEED 15 condition aiming movements were primarily based on movement-planning capacities, as originally 16 intended. 17

18 ²Again, an additional analysis was performed to control these outcomes. To further investigate the aspect 19 of deliberate slowing in older adults, we calculated the mean peak velocity values of all CONTROL 20 condition aiming blocks relative to the participant's highest peak velocity value in the SPEED condition. 21 The rationale was that if older adults deliberately slow down their aiming movements to a greater extent 22 than young adults, they should systematically demonstrate lower *relative* peak velocity values. In contrast 23 to absolute peak velocity values, such analysis takes into account personal capacities as well. Results 24 showed that under natural circumstances, older adults $(14.1 \pm 2.2\%)$ indeed aimed at a lower percentage of 25 their maximal movement speed compared to young adults $(21.4 \pm 3.0\%; p < .01)$, thereby further 26 supporting the play-it-safe strategy in old age.

1	Table Captions
2	Table 1: Traditional age-related differences in aiming kinematics in the CONTROL condition. Note:
3	Results are presented as <i>mean</i> ± SEM. All five expected differences between age groups were observed in
4	the CONTROL condition. Adapted from "Both age and physical activity level impact on eye-hand
5	coordination" by Van Halewyck et al. 2014a, Hum Movement Sci. Copyright 2014 by Elsevier.
6	

1	Figure Captions
2	Figure 1: Factor 1: Ability to produce fast primary submovements. Comparison of mean peak
3	velocities in the SPEED condition. CONTROL condition data are also displayed for the sake of
4	completeness. Group scores are presented as mean \pm SEM. Significant group differences are highlighted by
5	*** (if $p < .01$), nonsignificant group differences by <i>ns</i> (if $p > .05$).
6	
7	Figure 2: Factor 2: Programming the aiming movement. Comparison of (A) temporal and (B) spatial
8	variability at four kinematic markers in the SPEED condition. <i>Abbreviations</i> : PA = Peak acceleration; PV =
9	Peak velocity; PD = Peak deceleration; END = End of aiming movement. Nonsignificant group differences
10	are highlighted by <i>ns</i> (if $p > .05$).
11	
12	Figure 3: Factor 3: Sensory feedback-processing efficiency. Comparison of the mean verification time
13	in the CONTROL condition. Group scores are presented as mean \pm SEM. Significant group differences are
14	highlighted by *** (if $p < .01$),
15	
16	Figure 4: Factor 4: Aiming strategy. Comparison of (A) endpoint accuracy, (B) peak velocity, (C)
17	relative distance of the primary submovement, (D) relative duration of the homing-in phase, (E) number of
18	corrective submovements, and (F) overall movement time between conditions to investigate the play-it-safe
19	strategy. Significant group differences are highlighted by *** (if $p < .01$) or * (if $p < .05$), nonsignificant
20	group differences by ns (if $p > .05$).

Table 1

Parameter	Unit	Young	Older	<i>p</i> -value
Peak velocity	cm/s	83.9 ± 8.6	65.9 ± 7.8	< .01
Relative distance primary submovement	% target distance	72.5 ± 4.1	61.0 ± 4.4	<.01
Relative duration homing-in phase	% movement time	63.0 ± 3.6	68.0 ± 3.1	<.01
Number of corrective submovements	/	2.3 ± 0.3	2.8 ± 0.3	<.01
Overall movement time	ms	892 ± 62	1074 ± 65	<.01









