

1 Does somatosensory acuity influence the extent of internal model
2 recalibration in young and older adults?

3 Koenraad Vandevoorde^{a,b}, Jean-Jacques Orban de Xivry^{a,b}

4 ^a *Movement Control and Neuroplasticity Research Group, Department of Movement Sciences, KU Leuven, 3001 Leuven,*
5 *Belgium, ^b Leuven Brain Institute (LBI), KU Leuven, 3000 Leuven, Belgium*

6 **Corresponding author:** Jean-Jacques Orban de Xivry; Movement Control and Neuroplasticity Research Group, Department
7 of Movement Sciences, KU Leuven, Tervuursevest 101 bus 1501, B-3001 Leuven, Belgium; Tel: +32 16376603; E-mail
8 address: jj.orban@kuleuven.be

9 **Conflict of interest:** The authors declare no competing financial interests.

10

11 Abstract

12 The ability to adjust movements to changes in the environment declines with aging. This age-related
13 decline is caused by the decline of explicit adjustments. However, automatic adjustment of movement,
14 or internal model recalibration, remains intact and might even be increased with aging. Since
15 somatosensory information appears to be required for internal model recalibration, it might well be
16 that an age-related decline in somatosensory acuity is linked to the increase of internal model
17 recalibration. One possible explanation for an increased internal model recalibration is that age-
18 related somatosensory deficits could lead to altered sensory integration with an increased weighting
19 of the visual sensory-prediction error. Another possibility is that reduced somatosensory acuity results
20 in an increased reliance on predicted sensory feedback. Both these explanations led to our
21 preregistered hypothesis: we expect a relation between the decline of somatosensation and the
22 increased internal model recalibration with aging. However, we failed to support this hypothesis. Our
23 results question the existence of reliability-based integration of visual and somatosensory signals
24 during motor adaptation.

25 New & Noteworthy

26 Is somatosensory acuity linked to implicit motor adaptation? The latter is larger in old compared to
27 younger people? In light of reliability-based sensory integration, we hypothesized that this larger
28 implicit adaptation was linked to an age-related lower reliability of somatosensation. Over two
29 experiments and 130 participants, we failed to find any evidence for this. We discuss alternative
30 explanations for the increase in implicit adaptation with age and the validity of our somatosensory
31 assessment.

32 Introduction

33 As we grow older, our movements become less fluent, slower and more variable (Krampe, 2002; Yan
34 et al., 1998). Besides altered movement parameters, aging also has an effect on the ability to adjust
35 our movement to changes in the environment. The ability to adapt movement remains possible until
36 old age. However, older adults are slower with respect to younger adults to adjust their movement
37 and they do not always adjust their movement to the same extent as younger adults (Fernández-Ruiz
38 et al., 2000; Seidler, 2007, 2006; Vandevorode and Orban de Xivry, 2019). This age-related decline of
39 motor adaptation is caused by the decline of the cognitive component of motor adaptation (Hegele
40 and Heuer, 2010; Heuer and Hegele, 2014, 2008; Huang et al., 2017; Vandevorode and Orban de Xivry,
41 2020, 2019). This is in contrast with the implicit component of adaptation, which appears to remain
42 intact with aging (Heuer and Hegele, 2008; Vandevorode and Orban de Xivry, 2019). The implicit
43 component of motor adaptation, or internal model recalibration, is the adaptation of movement in
44 response to sensory prediction errors (Morehead et al., 2017; Shadmehr et al., 2010; Taylor and Ivry,
45 2011). Sensory prediction errors occur when the actual sensory feedback is not matching with the
46 predicted sensory feedback (Miall and Wolpert, 1996). For instance, in a typical visuomotor rotation
47 experiment a rotation of the cursor is introduced with respect to the unseen hand movement:
48 Participants expect visual feedback at the position of the hand, but it occurs at a different rotation
49 angle. A sensory-prediction error causes a drift of the hand movement in the opposite direction of this
50 error and this happens without conscious control (Morehead et al., 2017). Learning from sensory
51 prediction errors appears to depend on the cerebellum since it is reduced in cerebellar patients
52 (Morehead et al., 2017; Tseng et al., 2007). In a series of three different experiments, we recently
53 demonstrated that implicit motor adaptation does not deteriorate with aging and sometimes even
54 increased (Vandevorode and Orban de Xivry, 2019). However, this observation of increased function
55 is surprising since cerebellar brain structure shrinks with aging (Raz et al., 2005; Walhovd et al., 2011).
56 In this paper, we want to test the hypothesis that age-related sensory deficits are linked to the
57 increased reaction to sensory prediction errors. Indeed, the acuity of somatosensation (Goble et al.,
58 2009; Shaffer and Harrison, 2007) declines with aging. For instance, human and animal studies have
59 shown that the number and properties of cutaneous and joint mechanoreceptors are altered with age
60 (Aydoğ et al., 2006; Johnson, 2001; Miwa et al., 1995; Shaffer and Harrison, 2007; Swash and Fox, 1972;
61 Verrillo et al., 2002). Furthermore, these age-related changes in the peripheral nervous system are
62 accompanied by changes in the central nervous system that contribute to the decline in somatosensory
63 function with aging (Goble et al., 2009).

64 One explanation for the increased internal model recalibration with aging is that age-related sensory
65 deficits could lead to altered sensory integration, which might be based on the reliability of sensory
66 inputs (van Beers et al., 2002). For instance, if we assume that age-related changes in visual acuity are

67 smaller than those in somatosensory acuity, the weight of somatosensory input could decrease in
68 elderly people compared to young people during optimal combination of visual and somatosensory
69 inputs (Ernst and Banks, 2002). This up weighting of visual feedback could result in a larger estimated
70 error, which would yield in turn an increased learning (learning rate is equal but estimated error is
71 larger).

72 Another possibility is that age-related sensory deficits could lead to an increased reliance on the
73 predictive pathway (Deravet et al., 2018; Kording and Wolpert, 2004; Orban de Xivry et al., 2013). Such
74 a shift in the balance between somatosensory and predictive pathways might account for an increase
75 in sensory attenuation with age (Parthasarathy et al., 2020; Wolpe et al., 2016). Sensory attenuation
76 is the reduced perceived intensity of sensation from self-generated sensory feedback compared with
77 external actions. Wolpe et al. (2016) observed a link between this increased sensory attenuation and
78 altered somatosensory acuity with aging.

79 Following both of these explanations, our research hypothesis is that age-related somatosensory
80 deficits are linked to the increased reaction to sensory-prediction errors (enhanced internal model
81 recalibration).

82 Note that this hypothesis departs from other lines of research in which impairment in somatosensory
83 function or disruption of the somatosensory cortex have been linked to an impairment in internal
84 model recalibration. Some studies have suggested an impaired internal model for deafferented
85 patients (Ghez et al., 1990, Vercher et al. 2003), while others suggested that deafferented patients can
86 still trigger the internal model using alternative cues (Hermsdöfer et al., 2008). Recent work has shown
87 that motor adaptation remains possible after proprioceptive loss (Miall et al., 2018) and that an
88 increased weighting of vision vs proprioception was associated with force-field adaptation (Sexton et
89 al., 2019). Furthermore, it has been shown that disruption of the somatosensory cortex impairs
90 internal model recalibration (Mathis et al., 2017).

91 In order to verify our research hypothesis, we designed two paradigms that quantified internal model
92 recalibration and upper limb somatosensory acuity, and investigated the relation between these two
93 properties. In a first paradigm, we used a cued adaptation task that allowed us to assess explicit and
94 implicit components of motor adaptation (Morehead et al., 2015). In a second (preregistered)
95 paradigm, we assessed implicit adaptation by applying a task-irrelevant clamped feedback task in
96 which participants' reaching movement adapted implicitly to the visual error of constant size
97 (Morehead et al., 2017). In both paradigms, we assessed somatosensory acuity in two ways: position
98 sense, the ability to identify the static location of a body part, and kinesthetic sense, ability to identify
99 body motion ((Goble et al., 2009; Herter et al., 2014)). We measured position sense with the arm
100 position-matching task, which required participants to mirror-match positions of the right dominant
101 arm with the left arm as accurate as possible without visual feedback (Dukelow et al., 2010). In a large

102 cohort of 209 individuals, it is shown that this ability declines with aging (Herter et al., 2014). We
103 measured kinesthetic sense with a custom-developed task that resembled a previously described
104 perceptual boundary tasks (Darainy et al., 2013; Kitchen and Miall, 2020; Ostry et al., 2010). Our
105 research hypothesis predicted a negative relationship between internal model recalibration and
106 somatosensory acuity. That is, the more somatosensory acuity is degraded in an individual, the larger
107 the recalibration of the internal model is.

108 Methods

109 Participants

110 In total 133 healthy adults were recruited and participated after providing written informed consent.
111 Sixty-two participated in paradigm 1 and 71 participated in paradigm 2.

112 Sixty-two participants were included in the final analyses for paradigm 1 (Table 1). These 62
113 participants consisted of 30 young adults (between 20 and 32 years old, age: 22.9 ± 2.7 years, mean \pm
114 SD; 15 females) and 32 older adults (between 61 and 75 years old, age: 67.6 ± 4.5 years; 13 females).
115 The somatosensation data from these participants has not been presented before, while the
116 adaptation result were already presented in (Vandevoorde and Orban de Xivry, 2020) (as dual-task
117 design E2).

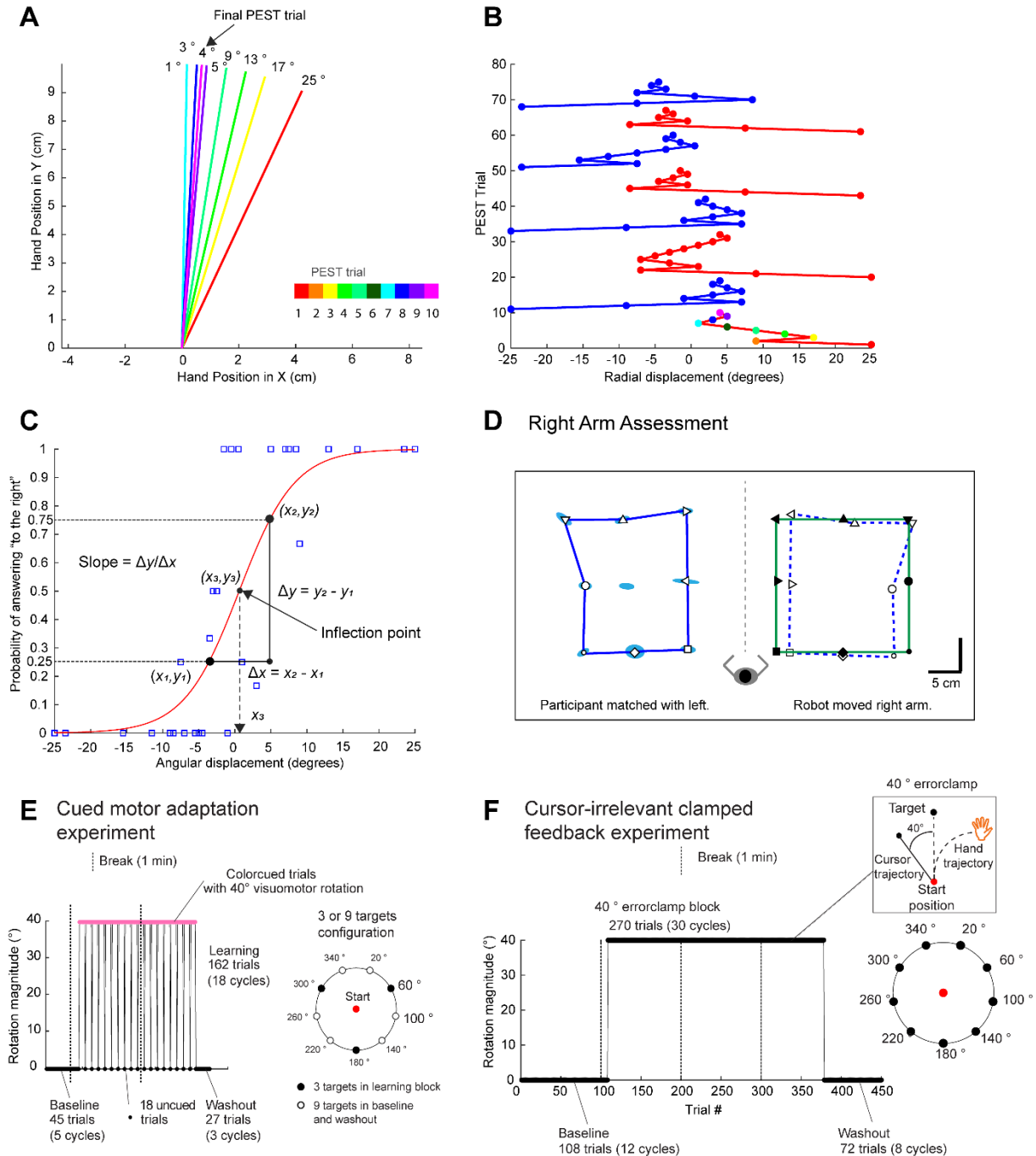
118 Seventy participants were included in the final analyses for paradigm 2 (Table 1). Data from one older
119 adult were excluded because she didn't move with the right speed to the targets and often started
120 reaching movements before the targets appeared. The 70 participants consisted of 40 young adults
121 (between 19 and 30 years old, age: 22.0 ± 2.5 years, mean \pm SD; 16 females) and 30 older adults
122 (between 61 and 75 years old, age: 67.3 ± 4.1 years, mean \pm SD; 10 females).

123 The Edinburgh handedness questionnaire (Oldfield, 1971) revealed that all participants were right-
124 handed. All participants were screened with a general health and consumption habits questionnaire.
125 None of them reported a history of neurological disease or was taking psychoactive medication. In
126 older adults general cognitive functions was assessed using the Mini-Mental State Examination
127 (MMSE) (Folstein et al., 1975). All elderly scored within normal limits (MMSE-score ≥ 26). The protocol
128 was approved by the local ethical committee of KU Leuven, Belgium (project number: S58084).
129 Participants were financially compensated for participation (10 €/h).

130 Experimental setup

131 For somatosensory acuity testing (Figure 1A-C), we used the KINARM End-Point Lab robot (BKIN
132 Technologies Ltd., Kingston, Canada). Participants were seated in a chair and controlled the handle of
133 the right robot with their right dominant hand. During the two somatosensory tasks, visual feedback
134 of their own hand was blocked. Visual feedback was displayed on the virtual reality display component

135 of the End-Point Lab on a semi-transparent mirror, horizontally mounted in front of the participant.
 136 This feedback was provided as a white cursor dot, which was properly aligned with the real position of
 137 their hand. The End-Point Lab allowed real-time control and data acquisition at 1 KHz.
 138



139 **Figure 1: Experimental paradigm for assessing somatosensory acuity and internal model recalibration.** **A)** Perceptual
 140 boundary test. Experiment is designed to test how well participants can discriminate angular deviations. An example of first
 141 PEST run for with an initial deviation of 25°. **B)** An example of a sequence of eight PEST runs for one (imaginary) participant.
 142 The first run is the same as the one shown in Fig 1A. The angular direction is shown on the horizontal axis and the PEST trial
 143 number shown on the vertical axis. The colored sequence is the same as the sequence indicated in fig1A. **C)** Psychometric
 144 accuracy curve with indication of inflection point and slope. Y-axis shows the probability of answering "deviation to the right"
 145 for a specific amount of angular displacement. Psychometric curve is constructed with data from Fig1B. **D)** Right arm
 146 assessment of position matching task for one (imaginary) participant. Robot moved the right arm and participant matched
 147 with the left arm. **E)** Cued motor adaptation experiment. **F)** Cursor-irrelevant clamped feedback experiment. The experiment
 148

149 *background for the visuomotor rotation experiment was black and targets were white, the opposite as visualized here in Figure*
150 *1E-F.*

151 For visuomotor rotation experiments (Figure 1E-F), participants were seated in front of a table. With
152 their right hand, participants performed a reaching task on a digitizing tablet (Intuos pro 4; Wacom Co.
153 Ltd., Kazo, Japan) with a digitizing pen. A wooden cover above the tablet prevented visual feedback
154 from their moving arm. Movement trajectories were recorded at 144 Hz. Visual feedback was
155 displayed on a 27 inch, 2560 x 1440 optimal pixel resolution LCD monitor with 144 Hz refresh rate
156 (S2716DG, Dell), vertically mounted in front of the participant.

157 [Experimental protocols](#)

158 [Organization of experiments](#)

159 Two different paradigms were used (Table 1). Paradigm 1 consisted of an assessment of
160 somatosensation before the cued motor adaptation experiment. Paradigm 2 consisted of an
161 assessment of position matching and perceptual boundary before the task-irrelevant feedback task,
162 which was followed by a second assessment of perceptual boundary only.

163 *Table 1: Description of the two paradigms for assessing somatosensory acuity and internal model recalibration.*

	Number of participants	Somatosensation (Before motor adaptation)	Motor adaptation experiment	Somatosensation (After motor adaptation)
Paradigm 1 (P1)	30 young 32 old	Position matching Perceptual boundary	Cued motor adaptation	/ /
Paradigm 2 (P2) (preregistered)	40 young 30 old	Position matching Perceptual boundary Pre	Task-irrelevant feedback task	Perceptual boundary Post

164

165 [Preregistration](#)

166 Design and analysis procedure of Paradigm 2 were preregistered online:
167 <https://osf.io/qg3t2/registrations>. This preregistration included the main hypotheses, the key
168 dependent variables, the amount of participants, the main analyses and some of the secondary
169 analyses investigated. In the preregistration, we mentioned that we would include 30 participants per
170 group. However, for this study, we included 10 additional subjects in the young adults group but these
171 additional participants did not change the outcome of our study. Including these 10 additional subjects
172 or not, did not yield different results for the task-irrelevant feedback experiment (Figure 5), for the
173 arm position matching task and perceptual boundary test (Figure 6) or for the relationship between
174 adaptation and somatosensation (Figure 7). To be concise, we reported only the results with all
175 participants included.

176 [Perceptual boundary test](#)

177 The perceptual boundary test (Figure 1A-B) was an adapted version of the test described in (Ostry et
178 al., 2010). In our task, participants made right arm reaching movement while their movement was
179 constrained to a certain angular deviation relative to a straight line to the target. No visual feedback

180 was provided during reaching; only at the end of the return to the center, a short instance of visual
181 feedback was applied to simplify the return to the start position. Returning to start was simplified by
182 using a viscosity gradient. Participants were instructed to verbally indicate whether they were deviated
183 to the left or to the right of a reference position (straight ahead). By gradually decreasing the angular
184 deviation, it became possible to estimate how accurately participants could discriminate angular
185 deviations. In order to obtain an efficient estimation of the perceptual boundary for each individual, a
186 parameter estimation by sequential testing (PEST) procedure was applied (Taylor and Creelman, 1967).
187 This algorithm starts with a large deviation and depending on the individual's response, it decreases
188 the size of the deviation progressively until the deviation falls below a minimum threshold. Every time
189 an individual uses the same response for the current trial compared to the previous trial (i.e. "right"
190 stays "right", or "left" stays "left"), the size and direction of the angular deviation in the next trial
191 remain the same as for the current trial. Every time an individual uses a different response for the
192 current trial compared to the previous trial (i.e. "right" becomes "left", or "left" becomes "right"), the
193 step size of the angular deviation will halve and the deviation will switch direction in the next trial
194 compared to the current trial. In our task, eight PEST runs were applied. The first four started with an
195 initial angular deviation of 25 °, the last four started with an initial angular deviation of 23.5 °. The
196 first initial deviation was always 25 ° to the right of the target (Figure 1A). Every following PEST run had
197 a first initial deviation with an opposite direction from the previous PEST run initial deviation. For
198 example, the first PEST run was 25° to the right and the second PEST run was 25° to the left. In total
199 four PEST runs started from the right and four started from the left. Our minimum threshold was 1.5
200 °: As soon as a step size fell below this minimum threshold, the current PEST would stop and the next
201 PEST run would be initiated.

202 In the original task of (Ostry et al., 2010), lateral deviations were used instead of angular deviations.
203 We induced angular deviations in order to make the boundary test more similar to the deviations
204 experienced during visuomotor rotation. Also other parameters of the task were resembling our
205 visuomotor rotation experiment: the reaching distance from start to target was 10 cm and reach timing
206 was between 125 ms and 375 ms. However, only one target was presented in front of the participant,
207 instead of nine targets as in the visuomotor rotation experiments.

208 First, participants could get familiar with the required reaching speed. They received the following
209 instructions: "First, you can practice the speed of the movement and afterwards I will explain the real
210 task. You have to move a white dot to the red square in the center by moving your right arm. As you
211 enter the red square, a white circle of 10 cm radius will appear and the white dot will disappear. A
212 small gap exists at the top of the circle, you will have to move your hand through this gap with the
213 right speed. If you move too slow, the circle will become blue. If you move too fast, the circle will turn

214 orange. If you move with the correct speed, the circle becomes green.” Participants could practice the
215 speed of their movement until they moved a couple of times with the correct speed. After this, we
216 started perceptual boundary test and instructed participants: “Now, we start the real task. In this task,
217 you will make reaching movements with the same speed as before. However, now the robot will
218 constrain your movement to a certain direction, either to the left of the gap or to the right of the gap.
219 Your task is to say to me whether you think it was to the left or to the right. In every trial a deviation
220 exists, so you always have to say either left or right, you can also guess if you are not sure.”

221 [Arm Position Matching task](#)

222 The Arm Position Matching task was available as a Standard Test on the Dexterit-E Software provided
223 with the KINARM End-Point Lab. The test allowed assessing position sense of the hands in horizontal
224 workspace (Dexterit-E 3.7 User Guide). In this test, the robot passively moved one hand to a particular
225 position and participants were required to mirror-match this position with their other hand (Figure
226 1D). This requires passive position sense for one arm and active movement and position sense of the
227 other arm (Dukelow et al., 2010).

228 In this task, the robot passively displaced the right hand and then stopped at a particular location. The
229 participants had to match the position of the right hand with their left hand in a mirror fashion. There
230 were nine possible targets organized in a 3x3 matrix. Participants could take as much time as they
231 wanted and had to indicate verbally when they had matched the position. After the verbal response,
232 the examiner started the following trial. Each of the nine target locations was randomly presented in
233 one block. In total, six blocks or 54 trials were assessed for each participant.

234 [Cued motor adaptation](#)

235 This visuomotor rotation experiment was described before as experiment E2 in (Vandevorde and
236 Orban de Xivry, 2020), here it is part of our first paradigm (Table 1). The cued motor adaptation
237 experiment allowed to assess implicit and explicit adaptation by the introduction of a color cued cursor
238 that indicated the presence or absence of a 40° visuomotor rotation (Figure 1E). A short reaching
239 baseline of 45 trials (5 cycles) was implemented. A learning block of 162 trials (18 cycles) and a short
240 washout of 27 trials (3 cycles) followed the baseline. A single start point location (filled red circle) was
241 used. Nine targets (open and filled white circles on black background) were presented during reaching
242 trials of the dual-task baseline and during baseline and washout trials. Three targets (filled white circles
243 on black background) were used during the learning block. Nine targets were presented pseudo-
244 randomly in cycles during baseline and washout with each of the nine targets presented once per cycle.
245 In the learning block, 9-trial-cycles consisted of three 3-trial-subcycles because only three targets were
246 used. In each subcycle, each of the three targets was presented once. The learning block consisted of
247 18 cycles (or 54 subcycles or 162 trials).

248 The cursor dot remained white the entire baseline and washout blocks. However, during the two
249 adaptation blocks, the cursor became a pink square (i.e. cued trial) instead of a white cursor dot. This
250 cue indicated the presence of a 40° rotation. In each adaptation block, the cursor became again a white
251 cursor dot (i.e. uncued trials) for a few trials, indicating the absence of the perturbation. The
252 instructions were: “First, the cursor will be a white dot, but at some point the cursor will change to a
253 pink square. At that moment, something special will happen but you still have to try to do the same
254 thing, reach to the target with the cursor. The cursor will sometimes change back to a white dot. These
255 trials with a white dot are normal reaching trials like in baseline.” The change in behavior induced by
256 the cue was thus a measure of the explicit component of adaptation as participants could use the cue
257 to switch off any conscious strategies they were applying to counteract the perturbation (Morehead
258 et al., 2015). We reinforced the awareness of cue switches (signaling a cued trial among uncued ones
259 or an uncued trial among cued ones) with a warning sound played before each cue switch and with a
260 text that indicated the cue switch, displayed for 5 s: 'Attention! The color of the cursor has changed.'
261 Eighteen uncued trial were presented in the adaptation block. These uncued trials were equally
262 distributed over the whole adaptation block and among the three targets (six uncued trials per target).

263 One trial of the cued adaptation experiment took exactly 4.5 seconds. First, participants performed a
264 target reach. Immediately after the reaching, extra fixation time was added in order to obtain exactly
265 4.5 seconds per trial. After 4.5 seconds, the next trial started automatically. If participants exceeded 3
266 seconds for the reaching movement, a warning sign was shown and a high pitch was played in order
267 to instruct participants to speed up. The correct reaching time was between 175 ms and 375 ms, which
268 was indicated with a target color change. If reaching time was above 375 ms, the target became purple.
269 If reaching time was below 175 ms, the target became red. Two breaks of 1 min were given to
270 participants, one before the 4th cycle (trial 36) of the baseline and one before the 9th cycle (trial 81) of
271 the learning block.

272 [Task-irrelevant clamped feedback](#)

273 The task-irrelevant clamped feedback experiment assessed internal model recalibration and is adapted
274 from Morehead et al. (2017). This experiment was part of our preregistered second paradigm (Table
275 1). In this visuomotor rotation task, the cursor direction of motion was made completely irrelevant by
276 dissociating it from the hand direction of motion (Figure 1F). That is, in these task-irrelevant clamped
277 feedback trials, participants were instructed to ignore the cursor that is always rotated 40 ° with
278 respect to the target direction and to try to move their hand accurately towards the target in the
279 absence of relevant visual feedback of hand position. Targets were presented in cycles of nine trials
280 with each cycle consisting of the nine targets presented randomly (Figure 1F). In total, the experiment
281 consisted of 450 trials or 50 cycles: Baseline consisted of 12 cycles (or 108 trials), task-irrelevant

282 clamped feedback trials were presented for 30 cycles (or 270 trials) and washout consisted of eight
283 cycles (or 72 trials). One-minute breaks were given to the participants before trial 99, 200 and 300. In
284 baseline, participants could win points for accuracy. However, during the adaptation block,
285 participants were clearly informed that it was not possible to win extra points, because the cursor
286 could never reach the target during these trials. To keep participants motivated during the adaptation
287 block, the amount of remaining trials was visualized on the monitor. Every trial had a fixed duration of
288 2.5 s/trial. If the reach and return to the start location were performed in less than 2.5 s, an extra
289 amount of time was added to obtain exactly 2.5 s for the current trial before starting the next trial.
290 During this extra amount of time, we only showed the cursor dot and the start position. If taking longer
291 than 2.5 s for the reaching or for the reaching & returning, the next trial was automatically initiated.
292 The trial duration was rather long, because we wanted to make sure that young and older adults
293 behaved similarly during target reaching. Older adults, in general, took longer to return back to the
294 start position. The reaching time to the target was constrained to a minimum of 125 ms and a
295 maximum of 375 ms. If reaching time was below 125 ms the target become red and low-beep sound
296 played, if above 375 ms the target become purple and a high-beep sound played. During cursor-
297 irrelevant feedback trials, only the sound feedback indicated incorrect reaching time. Participants
298 could get familiar with the experiment by practicing 10 baseline trials, 10 cursor-irrelevant feedback
299 trials (of different rotation directions) and 10 washout trials.

300 [Additional details for the two visuomotor rotation experiments](#)

301 Each visuomotor rotation experiment consisted of a series of reaching movements to a single white
302 circular target located 10 cm away from the central starting position. For each trial, the participant had
303 to rapidly move his or her right hand to move a white cursor through the target.

304 The feedback cursor, which represented hand position (when there was no perturbation) was visible
305 until movement amplitude exceeded 10 cm. At this point, a white square marked the position where
306 movement amplitude reached 10 cm, providing visual feedback about the end point accuracy of the
307 reach. The white square had sides of 5 mm. The cursor position froze at the end of each reaching
308 movement and was visible for 1 s. The two visuomotor rotation experiments first started with baseline
309 trials (no perturbation) with normal cursor feedback (i.e. the cursor represents the actual hand
310 position) and continued with perturbation trials where the feedback was either rotated or irrelevant.
311 Before baseline, each participant performed some familiarization trials to make sure that they
312 understood the instructions and that they performed the task correctly.

313 The diameters of the starting point and the target were both 10 mm and the cursor dot had a diameter
314 of 5 mm. Targets were presented in pseudo random order in cycles of nine trials per cycle. Target
315 position are shown in Figure 1E-F.

316

317 While returning to the central starting position, the cursor disappeared and only a half white arc of
318 180° (i.e. return arc) was visible. The radius of the return arc depended on the position of the pen on
319 the tablet, i.e. the radius of the arc was equal to the angular distance between the position of the hand
320 and the starting point. The center of the return arc was the central starting position. To reduce the
321 time for returning to the starting point, the cursor became visible as soon as the hand was within a
322 region near the central starting position (20 mm x 20 mm). The reach area was divided in three
323 different zones of 120°. The return arc was centered in the same 120° zone as where the participant's
324 (invisible) hand was. Participants had to move their hand in the opposite direction of the arc in order
325 to return to the starting location. The arc allowed participants to return to the starting position and at
326 the same time prevented the participants from using the visual feedback during the return movement
327 to learn about the perturbation. If taking longer than 1.5 s to return, the cursor became visible again
328 as such returning to start became very easy.

329

330 Participants were instructed to score as many points as possible by hitting the target with the cursor.
331 When hitting the target, the participant received 50 points. When hitting targets correctly on
332 consecutive trials, 10 bonus points were received for every additional trial with a correct hit (e.g. 60
333 points were received the second trial after hitting targets correctly on two consecutive trials, 70 points
334 were received the third trial after hitting targets correctly on three consecutive trials). When reaching
335 in close proximity of the target, the participant received 25 points. In P2, the zone for receiving 25
336 points was an additional 6 mm at both sides of the target. In P2, the zone for receiving 25 points was
337 an additional 5 mm at both sides of the target. The reward for near misses is implemented for keeping
338 participants motivated even when they are not achieving very high accuracies. This was clearly
339 instructed on beforehand. To receive points, participants were required to reach the target between
340 175 and 375ms after movement onset. The cumulative score of all previous trials was displayed
341 throughout the experiment, except during the cursor-irrelevant feedback block. During cursor-
342 irrelevant feedback trials, no score could be obtained since the cursor could never hit the target.

343 The experimenter (KV) was present during the entire experiment to motivate the participants to
344 achieve the highest possible score and to make sure that the participant performed the task correctly.
345 The experimenter regularly reported that the participant was performing well, even when the score
346 was below average.

347

348 [Data analysis](#)

349 [Data availability](#)

350 Data and scripts will be available on Open Science Framework (OSF)

351 (https://osf.io/qg3t2/?view_only=30b338a6792c45c2b229838a7f2a216e).

352 [Preprocessing](#)

353 In task-irrelevant feedback experiment (P2), the first trial after each of the two breaks of the
354 adaptation block was removed since only one older participant could respond quick enough. The other
355 older adults were not yet ready to make a reaching movement within the 2.5 s trial time after the 1
356 min break. Removing this one trial did not affect our comparison between young and older adults.

357 [General](#)

358 The statistically significant threshold was set at $p < 0.05$ for the ANOVA's, t-tests and robust linear
359 regression. We reported effect sizes (eta squared η^2 for ANOVA and Cohen's d for two-sample t-test)
360 as well as F or t and p-values. For robust linear regression, we reported standardized beta coefficients
361 β and p-values of these coefficients. Multiple comparisons are corrected by applying Bonferroni
362 corrections. Confidence intervals (CI) are reported for eta squared η^2 , Cohen's d and standardized
363 beta coefficients β .

364 For eta squared η^2 , we calculated CI 95 % by 10.000 bootstraps of the two age groups and calculating
365 the corresponding statistics. For Cohen's d, CI 95 % was calculated with the formula:

$$[d - 1.96 \sigma(d), d + 1.96 \sigma(d)] \quad (1)$$

366 With $\sigma(d)$:

$$\sigma(d) = \sqrt{\frac{N_1 + N_2}{N_1 N_2} + \frac{d^2}{2(N_1 + N_2)}} \quad (2)$$

367

368 as specified in Hedge and Olkin (2014). For standardized beta coefficients β , we used the following
369 formula:

$$[\beta - 1.96 SE(\beta), \beta + 1.96 SE(\beta)] \quad (3)$$

370 With $SE(\beta)$, the standard error of the standardized beta coefficients β .

371 [Analysis 1: Implicit adaptation level](#)

372 In paradigm 1, implicit adaptation was assessed with cued motor adaptation. We applied the same
373 analysis as described in (Vandevorde and Orban de Xivry, 2020). The adaptation block of cued

374 adaptation was corrected for baseline errors by subtracting the average error of the last two baseline
375 cycles. We analyzed the data in all the uncued trials of the learning block (18 uncued trials). The amount
376 of implicit adaptation was calculated as the average of the uncued trials (Morehead et al., 2015). One
377 2-way ANOVA was used, with the between-subject factors, age and rotation direction, and with the
378 implicit adaptation as dependent variable.

379 In task-irrelevant clamped feedback task (preregistered paradigm 2), the hand angle of the last ten
380 cycles (90 trials) of the clamped visual feedback block were averaged to obtain the implicit adaptation
381 level. Baseline accuracy measurement of unperturbed reaching allows to control for age-differences
382 in unperturbed conditions. All adaptation trials are corrected for baseline accuracy by subtracting the
383 average error of the last two baseline cycles (18 trials). One 2-way ANOVA was used, with the between-
384 subject factors, age and rotation direction, and with the implicit adaptation as dependent variable.

385 Analysis 2: Position matching task

386 This analysis was **preregistered** for paradigm 2. Somatosensory acuity was defined as the absolute
387 error XY and as the variability XY (Dukelow et al., 2010; Herter et al., 2014). For calculating variability,
388 first the standard deviation was calculated for each of the six target locations for x and y direction
389 separately. Next, the mean of these standard deviations of all six target locations resulted in the
390 variability for the x and y direction (Var_x, Var_y). Variability XY was calculated with the following
391 formula:

$$Var_{xy} = \sqrt{Var_x^2 + Var_y^2} \quad (4)$$

392

393 For calculating absolute error (systematic shift) between the active and passive hand the same
394 procedure was followed. First, absolute error was calculated for each of the six target locations for x
395 and y direction separately. Next, the mean of these absolute errors of all six target locations resulted
396 in the absolute error for the x and y direction ($AbsError_x, AbsError_y$). Absolute errors XY was finally
397 calculated as follows:

$$AbsError_{xy} = \sqrt{AbsError_x^2 + AbsError_y^2} \quad (5)$$

398 A separate unpaired two-tailed t-test was used to compare each variable (Var_{xy} and $AbsError_{xy}$)
399 between the two age groups.

400 Analysis 3: Slope and inflection point from perceptual boundary test

401 This analysis was **preregistered** for paradigm 2. Each trial of the perceptual boundary test resulted in
402 a binary response, either left or right. The probability of a “rightward direction” answer could be

403 calculated from the responses that participants gave for all deviations that they experienced. This
404 allowed us to create a sigmoidal probability response curve (Figure 1C) as a function of experienced
405 angular deviations. Function, *glmfit*, was used in Matlab to fit the probability of a “rightward direction”
406 answer to the tested angular deviations with a logistic regression function, with p , the probability, b ,
407 the coefficient estimate, X , the tested angular deviations:

$$\log\left(\frac{p}{1-p}\right) = b * X \quad (6)$$

408 The output of this function was the coefficient estimate b . Afterwards, we provided the coefficient
409 estimate, b , to the *glmval* function, which computed predicted values for all angular deviations that
410 were not tested between -25° and $+25^\circ$. The final output was the psychometric curve for each
411 participant that showed the probability of answering “right” for every angular deviation between -25°
412 and $+25^\circ$.

413 The psychometric curve allowed us to calculate the following two preregistered variables: The first
414 variable was the slope of the psychometric accuracy curve, measured as the slope of the straight line
415 between the 25 % and the 75% chance points. The second variable was the inflection point of the
416 psychometric curve, more specifically the point that crossed the x-axis (x_3 in Figure 1C). The slope
417 describes how sensitive someone can discriminate angular displacements during reaching movements.
418 The inflection point describes which direction someone feels as the zero angular displacement, i.e.
419 straight ahead of the body of the participant.

420 The perceptual boundary test was performed before the cued adaptation experiment (P1), which
421 resulted in two output variables: slope and inflection point. An unpaired two-tailed t-test was used to
422 compare each variable between the two age groups. In P2, the perceptual boundary test was also
423 performed before and after the task-irrelevant feedback experiment, which resulted in four output
424 variables: slope-pre, slope-post, inflection point-pre and inflection point-post. A repeated-measures
425 ANOVA was used, with the within-subject factor, test time, with the between-subject factors, age and
426 rotation direction, and with slope as dependent variable. A second repeated-measures ANOVA was
427 performed, with the same within- and between-subject factors, but with inflection point as dependent
428 variable.

429 [Analysis 4: Relationship between implicit adaptation level and somatosensation \(Paradigm 1\)](#)

430 Robust linear regression (*robustfit* in Matlab) (Holland and Welsch, 1977) was performed between the
431 measure of implicit adaptation and somatosensory acuity in order to verify that correlations between
432 these two variables were not influenced by between group differences in the variables. Implicit
433 adaptation (Y) was estimated using a linear combination of somatosensation variable (X), a binary age

434 vector (G) and the interaction of X and G in the regression equation with intercept A and regression
435 coefficients (B,C,D):

$$Y = A + B \cdot X + C \cdot G + D \cdot X \cdot G \quad (7)$$

436 Standardized beta coefficients (β) will be obtained instead of regression coefficients (B,C,D) when first
437 converting variables X and Y to z-scores and afterwards applying linear regression.

438 We applied robust linear regression (Equation (7)) four times with data from paradigm 1 and corrected
439 for multiple testing with Bonferonni ($\alpha = 0.0125$). For every regression, the implicit adaptation level as
440 described in Analysis 1 was used as the Y-variable. The X-variable could be any of the two measures of
441 somatosensation as described in Analysis 2 (Var XY and AbsError XY), or any of the two measures of
442 somatosensation as described in Analysis 3 (slope, inflection point).

443 [Analysis 5: Preregistered relationship between implicit adaptation level and somatosensation](#)
444 [\(Paradigm 2\)](#)

445 In addition, for paradigm 2, robust linear regression (Equation (7)) was a preregistered analysis to
446 investigate the hypothesis that increased internal model recalibration was related to somatosensation
447 decline. In total, robust linear regression (Equation (7)) was performed four times for paradigm 2. We
448 corrected for multiple testing with Bonferonni ($\alpha = 0.0125$). For every regression, task-irrelevant
449 implicit adaptation level as described in Analysis 1 was used as the Y-variable. The X-variable could be
450 any of the two measures of somatosensation as described in Analysis 2 (Var XY and AbsError XY), or
451 any of the two measures of somatosensation as described in Analysis 3 (slope-pre, inflection point
452 pre).

453 [Analysis 6: Relationship between implicit adaptation and change in somatosensation](#)
454 [\(Paradigm 2\)](#)

455 We calculated the change in inflection point between post and pre condition. This difference was
456 multiplied with -1 for participants that experienced a clockwise rotation in paradigm 2 in order to take
457 into account the influence of perturbation direction. This difference was compared to zero with a one-
458 sample t-test.

459 Robust linear regression was used to verify whether a relationship existed between difference of
460 inflection point (Analysis 4) and level of internal model recalibration (Analysis 1). Additionally, we
461 verified whether the aftereffect at the end of the washout period of task-irrelevant feedback
462 experiment (P2) was correlated with the difference of inflection point.

463 [Analysis 7: Comparison between somatosensory acuity from position matching task and](#)
464 [perceptual boundary test](#)

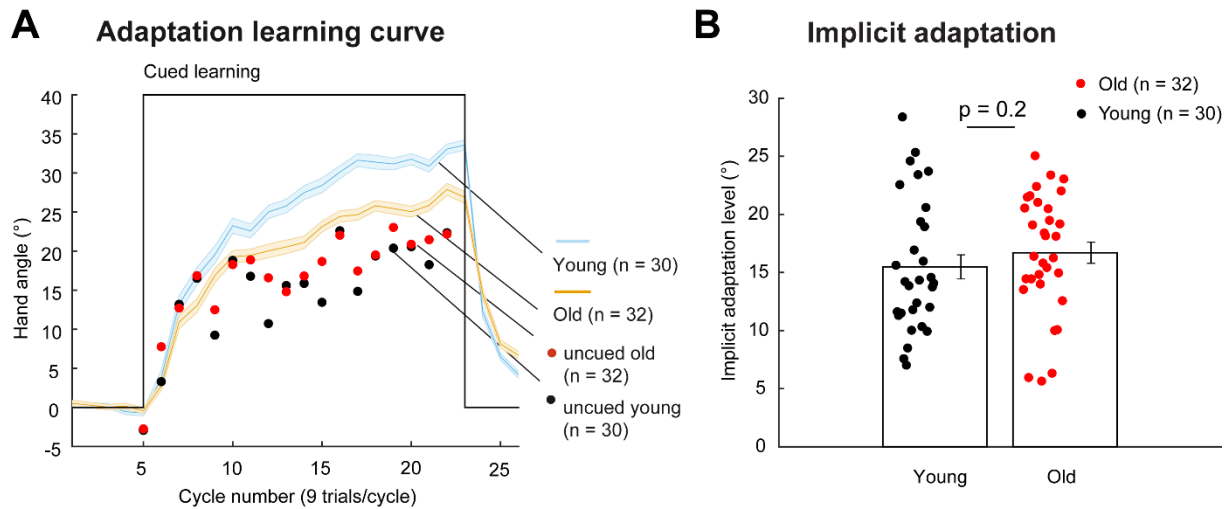
465 Data were obtained for both tests in both paradigms (P1 & P2), which allowed us to combine data of
466 all 133 participants for this comparison. Four variables were described for the position matching task
467 (Analysis 2: Var XY and AbsError XY) and two variables were described in the perceptual boundary test
468 (Analysis 3: slope, inflection point). We didn't include the measurement of slope and inflection point
469 from the post-condition since this was only available for paradigm 2. Robust linear regression as
470 described in Analysis 4 was used to compare the variables from both somatosensory acuity tests. Since
471 the two variables of position matching should be compared with the two variables of perceptual
472 boundary test, we had to perform the robust linear regression four times. We corrected for multiple
473 testing with Bonferonni ($\alpha = 0.0125$).

474 [Results](#)

475 We investigated whether an age-related change in internal model recalibration was related to a decline
476 in somatosensation with aging. According to our **preregistered hypothesis**, somatosensory acuity
477 would decline with aging and this age-related decline in somatosensory acuity would be related to the
478 age-related increase of internal model recalibration. To this end, we assessed internal model
479 recalibration with a visuomotor rotation experiment and tested the relationship between the level of
480 internal model recalibration and somatosensory acuity. We quantified somatosensation of the upper
481 limb via a position matching task and a perceptual boundary test that provided us with a measure of,
482 respectively, position and kinesthetic sense.

483 [No evidence that somatosensory acuity is related to implicit adaptation](#)

484 First, we quantified internal model recalibration via implicit adaptation during a cued motor adaptation
485 experiment (Paradigm 1 (P1) Table 1; Figure 1E, (Morehead et al., 2015)) for 30 young (age range: 20-
486 32 years old) and 32 older (age range: 61-75 years old) participants. During the cued motor adaptation
487 experiment, color cues allowed participants to switch their explicit aiming on or off (Figure 1E). The
488 level of implicit adaptation was similar between young and old (Analysis 1) (Figure 2A-B; $F(1,58) = 1.6$,
489 $p = 0.2$, $\eta^2 = 0.02$, $CI_{95-\eta^2} = [0.0000; 0.1179]$). Cued adaptation results were described before in
490 (Vandevorde and Orban de Xivry, 2020), we show these results again for completeness. We observed
491 no decline of implicit adaptation with age as measured with cued motor adaptation (Figure 2).

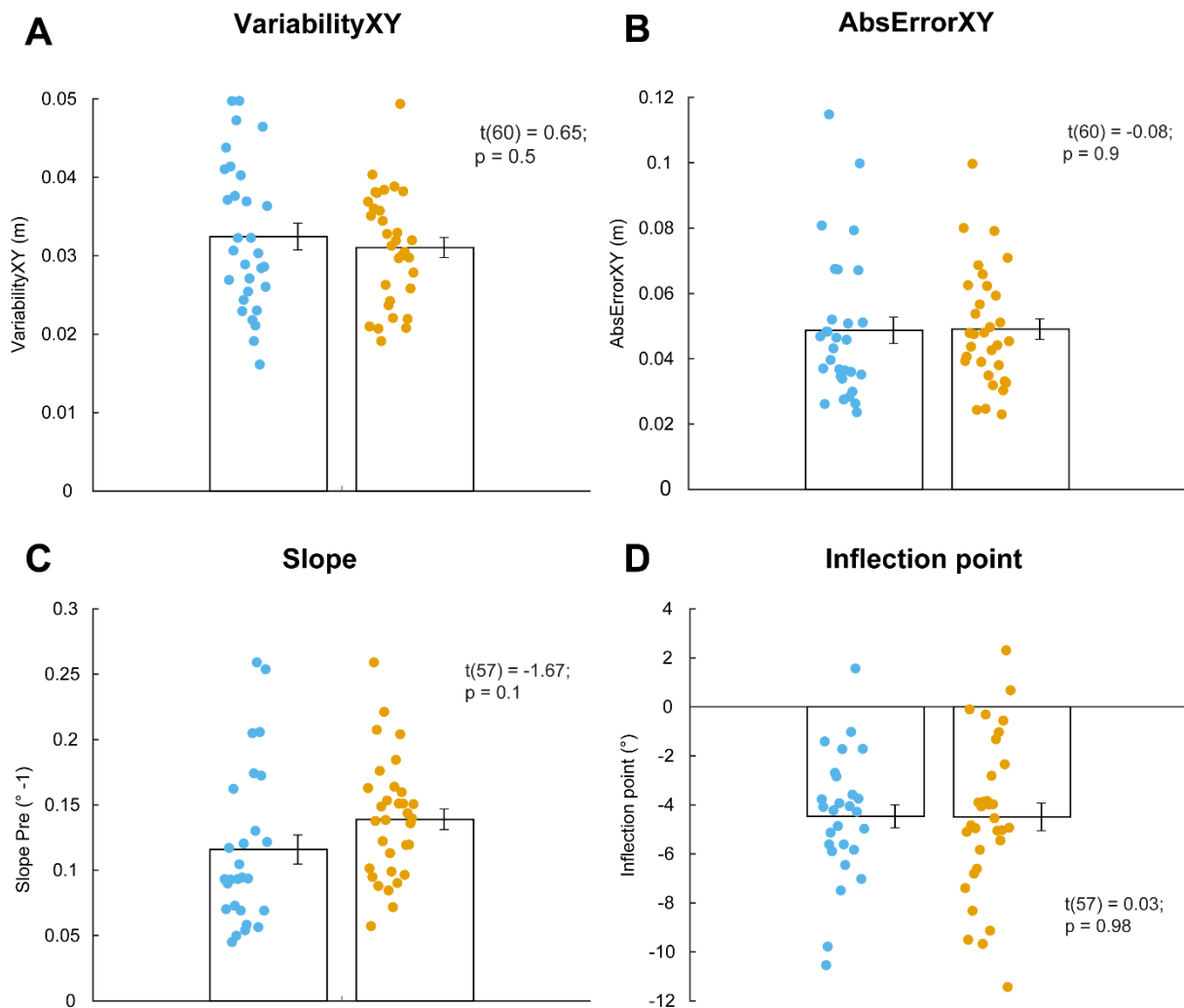


492

493 *Figure 2: Results of cued motor adaptation. A) Evolution of the hand angle over the course of the experiment during cued*
494 *(blue solid lines for young participants and orange ones for old participants) and uncued trials (red dots for older adults and*
495 *black dots for younger adults). Each dot shows the hand angle during one uncued trial as the average of the whole group*
496 *(young or old). The area around the solid lines represents the standard error of the mean. B) Same data as in Figure 2A,*
497 *but shown as individual levels of implicit adaptation measured during uncued trials. Each dot represents the data of one*
498 *participant, which is the average of the hand angles during all 18 uncued trials (dots in panel A). The height of the bars*
499 *represents the inter-individual means and the error bars represent the standard error of the mean.*

500 We measured somatosensory acuity for right dominant arm position and arm movement with two
501 different methods. The first method was the position matching task, in which a robot passively moved
502 the right hand to a position and participants were required to mirror-match this position with their left
503 hand (Dukelow et al., 2010). This provided a measurement of position sense. The second method was
504 the perceptual boundary test to assess kinesthetic sense (Figure 1A-C). In the position-matching task,
505 we focused on two variables, absolute error XY and variability XY (Equations (4) (5) ; Analysis 2). We
506 did not find any evidence that performance for position-matching was reduced with aging in paradigm
507 1 (Figure 3A-B; Analysis 2: VarXY: $t(60) = 0.65$, $p = 0.5$, $d = 0.17$, $CI_{95-d} = [- 0.33, 0.66]$); AbsErXY: $t(60)$
508 $= -0.08$, $p = 0.9$, $d = - 0.02$, $CI_{95-d} = [- 0.52, 0.48]$). In addition, in the perceptual boundary test, we
509 defined two additional variables, the slope and the inflection point of the psychometric accuracy curve
510 (Analysis 3). The perceptual boundary test did not provide any evidence that the slope and the
511 inflection point of the psychometric accuracy curve were different for young and old (Figure 3C-D;
512 Analysis 3: slope: $t(57) = -1.67$, $p = 0.1$, $d = - 0.43$, $CI_{95-d} = [- 0.94, 0.07]$; inflection point: $t(57) = 0.03$,
513 $p = 0.98$, $d = 0.007$, $CI_{95-d} = [- 0.49, 0.51]$).

514

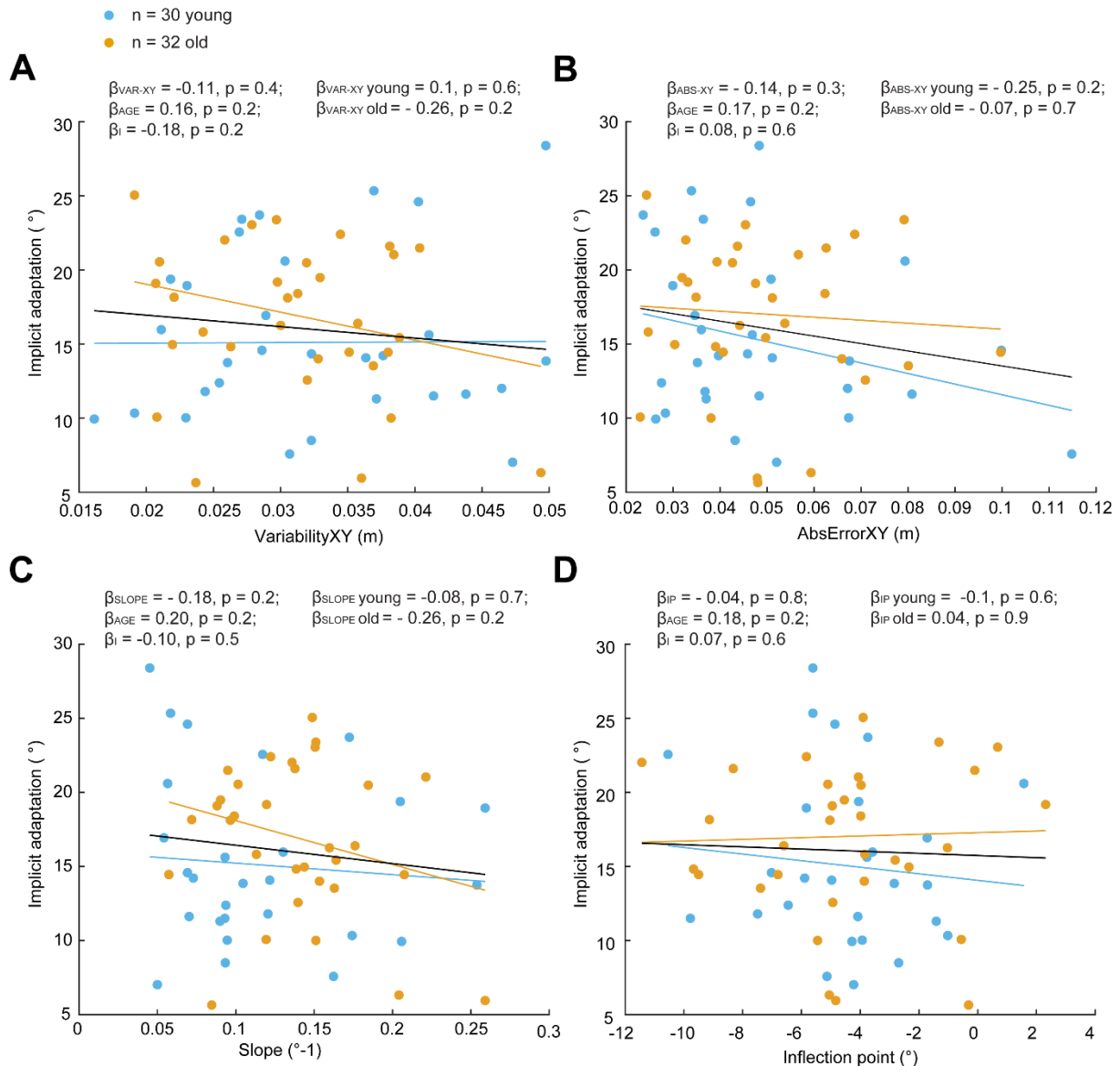


515

516 *Figure 3: Outcomes of the somatosensory tasks, visualized with data from participants of paradigm 1. A-B: Outcomes of the*
 517 *position matching task measured before adaptation: variability of hand position, VariabilityXY, and the absolute error,*
 518 *AbsErrXY. Lower values are associated with better somatosensory acuity. C-D: Outcomes of the perceptual boundary*
 519 *estimation task measured before adaptation. For panel C, higher values are associated with better somatosensory acuity. No*
 520 *such interpretation exists for the inflection point. Each dot represents the data from one participant. The height of the bars*
 521 *represents the inter-individual means and the error bars represent the standard error of the mean. Three of the 30 young*
 522 *participants did not execute the perceptual boundary test.*

523 After verifying how aging affects the level of implicit adaptation and somatosensory acuity, we
 524 explored the relation between these two properties. A decline in somatosensation was expected to be
 525 related to an increased internal model recalibration (negative relationship). However, we failed to find
 526 evidence that the position matching variables was related to the level of implicit adaptation (Equation
 527 (7); Figure 4A-B; Analysis 4; Table 2; $\beta_{\text{VAR-XY}} = 0.11$; $p = 0.4$, $R = -0.04$; $\beta_{\text{ABS-XY}} = -0.14$; $p = 0.3$, $R = -0.16$).
 528 Furthermore, we could not find evidence in favor of a relationship between the perceptual boundary
 529 variables and implicit adaptation level (Figure 4C-D; Analysis 5; Table 2; $\beta_{\text{SLOPE}} = -0.18$; $p = 0.2$, $R = -$
 530 0.13 ; $\beta_{\text{IP}} = -0.04$; $p = 0.8$, $R = -0.05$). Since paradigm 1 did not provide evidence for the hypothesis, we
 531 wanted to confirm the absence of relationship in a second cohort of participants (Table 1). In this
 532 second paradigm, we assessed internal model recalibration with the task-irrelevant feedback

533 experiment (Figure 1), which allows assessing internal model recalibration independently of the
 534 presence of explicit strategy. In addition, the task-irrelevant feedback experiment resulted in an
 535 increased level of internal model recalibration in our previous work (Vandevoorde and Orban de Xivry,
 536 2019).



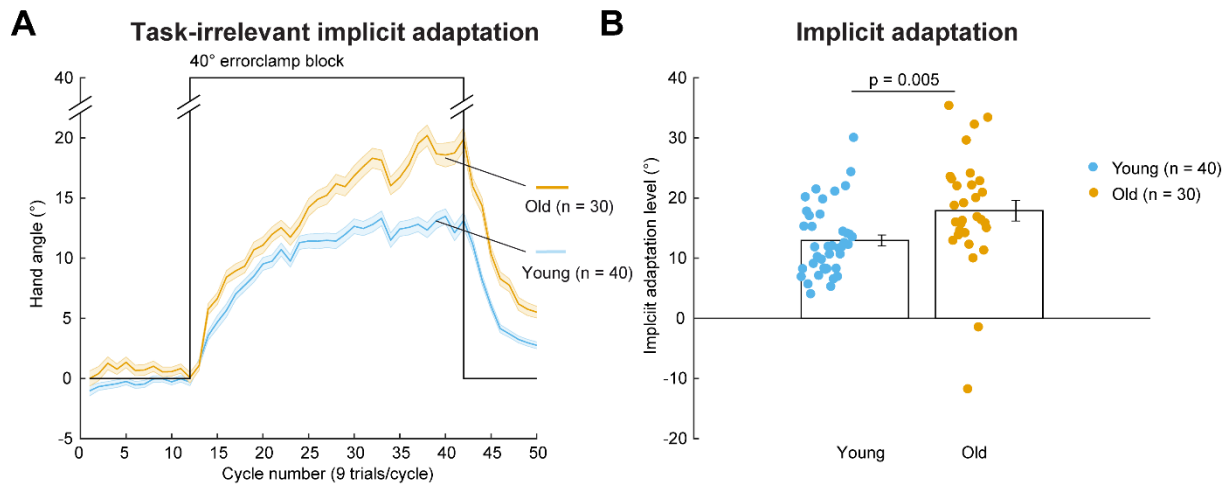
537

538 **Figure 4: Relationship between implicit adaptation and somatosensory acuity. Data from paradigm 1. A-B:** Scatterplot of
 539 the outcomes of the position matching task (data from fig.3A and B) and the extent of implicit motor adaptation from the
 540 cued motor adaptation task (data from Fig.2B). A positive relationship is expected given that better somatosensory acuity is
 541 associated with lower values. **C-D:** Scatterplot of the outcomes of the perceptual boundary task (data from fig.3C and D) and
 542 the extent of implicit motor adaptation from the cued motor adaptation task (data from Fig.2B). A negative relationship is
 543 expected for panel C given that better somatosensory acuity is associated with higher slope values. In all panels, each dot
 544 represent the data of a single participant. Solid lines represent the regression line from the robust regression analysis for both
 545 populations together (black line), for young participants only (blue lines) and for old participants only (orange lines).

546 Evidence for an age-related decline in somatosensory acuity but no evidence that this
 547 is related to the age-related increase in internal model recalibration

548 In the second **preregistered** paradigm (Table 1), we assessed internal model recalibration by applying
 549 task-irrelevant clamped feedback in 40 young (age range: 19-30 years) and 30 older (age range: 61-75

550 years) participants. The motion of the cursor away from the target elicited drift in hand position (Figure
551 1E,(Morehead et al., 2017)). The change in movement direction was larger for older adults compared
552 to younger adults (Analysis 1)(Figure 5A-B; $F(1,66) = 8.5$; $p = 0.005$; $\eta^2 = 0.09$; $CI95-\eta^2 = [0.0065$;
553 $0.2834]$). Two older participants did not follow instructions well as indicated by negative hand angles
554 (Figure 5B), if we would remove these participants as outliers, the effect would be even stronger ($CI95-$
555 $\eta^2 = [0.0726; 0.3617]$).



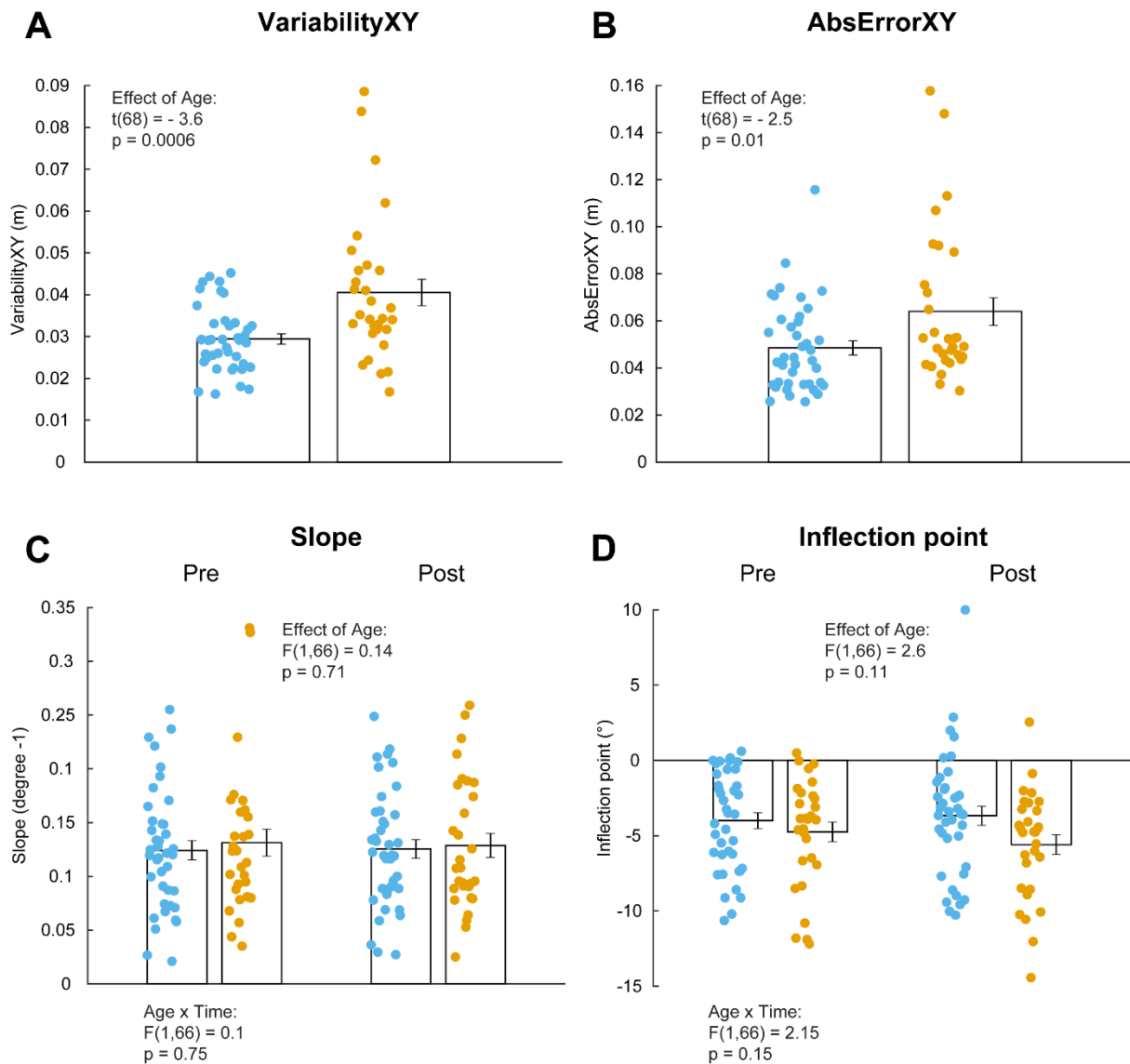
556

557 *Figure 5: Results of task-irrelevant clamped feedback experiment for young and old: A) Evolution of the hand angle over*
558 *the course of the experiment (blue solid lines for young participants and orange ones for old participants). The area around*
559 *the solid lines represents the standard error of the mean. B) Same data as in panel A, but shown as individual levels of implicit*
560 *adaptation measured during the last 10 cycles of the 40 ° errorclamp block. Each dot represents the data of one participant.*
561 *The height of the bars represents the inter-individual means and the error bars represent the standard error of the mean.*

562 We observed an age-related increase of internal model recalibration as measured with task-irrelevant
563 feedback, which replicates our previous work (Vandevoorde and Orban de Xivry, 2019). In contrast to
564 paradigm 1, performance for the position-matching task was reduced with aging for the two
565 preregistered variables in paradigm 2 (Analysis 2; Figure 6A-B: $VarXY: t(68) = -3.6$, $p = 0.0006$, $d = -$
566 0.87 , $CI95-d = [-1.37, -0.38]$; $AbsErXY: t(68) = -2.5$, $p = 0.01$, $d = -0.60$, $CI95-d = [-1.09, -0.12]$).
567 However, there was no evidence that the slope or the inflection point differed across age groups
568 (Analysis 3; slope: Figure 6C: Age: $F(1,66) = 0.14$, $p = 0.71$; $\eta^2 = 0.022$; inflection point: Figure 6D: Age:
569 $F(1,66) = 2.60$, $p = 0.11$; $\eta^2 = 0.037$). Similar results were obtained for the interaction between age and
570 the time point of the perceptual boundary test. No interaction effect between age and time point was
571 observed for the slope of the psychometric curve (Analysis 3; Figure 6C: Age x Time: $F(1,66) = 0.1$, $p =$
572 0.75 ; $\eta^2 = 0.0059$), and the inflection point (Analysis 3; Figure 6D: Age x Time: $F(1,66) = 2.15$, $p = 0.15$;
573 $\eta^2 = 0.15$).

574 Taking the direction of the perturbation into account, we did not find evidence for a difference in slope
575 between pre and post (Analysis 3, $F(1,68) = 0.00042$, $p = 0.98$) or in inflection point (Analysis 3; $F(1,68)$
576 $= 0.39$, $p = 0.54$). In addition, we failed to find evidence for a relationship between our level of internal

577 model recalibration and change in inflection point between pre and post condition (Analysis 6; implicit
578 adaptation: $\beta = 0.005$; $p = 0.5$; Figure 8). Since we performed the perceptual boundary test after a
579 short washout instead of before washout as in (Ostry et al., 2010), we verified whether the last cycles
580 of the aftereffect were linked with the change in inflection point. However, no relationship existed
581 between the aftereffect and change in inflection point between pre and post condition (Analysis 6;
582 aftereffect: $\beta = 0.18$; $p = 0.1$; Figure 8).



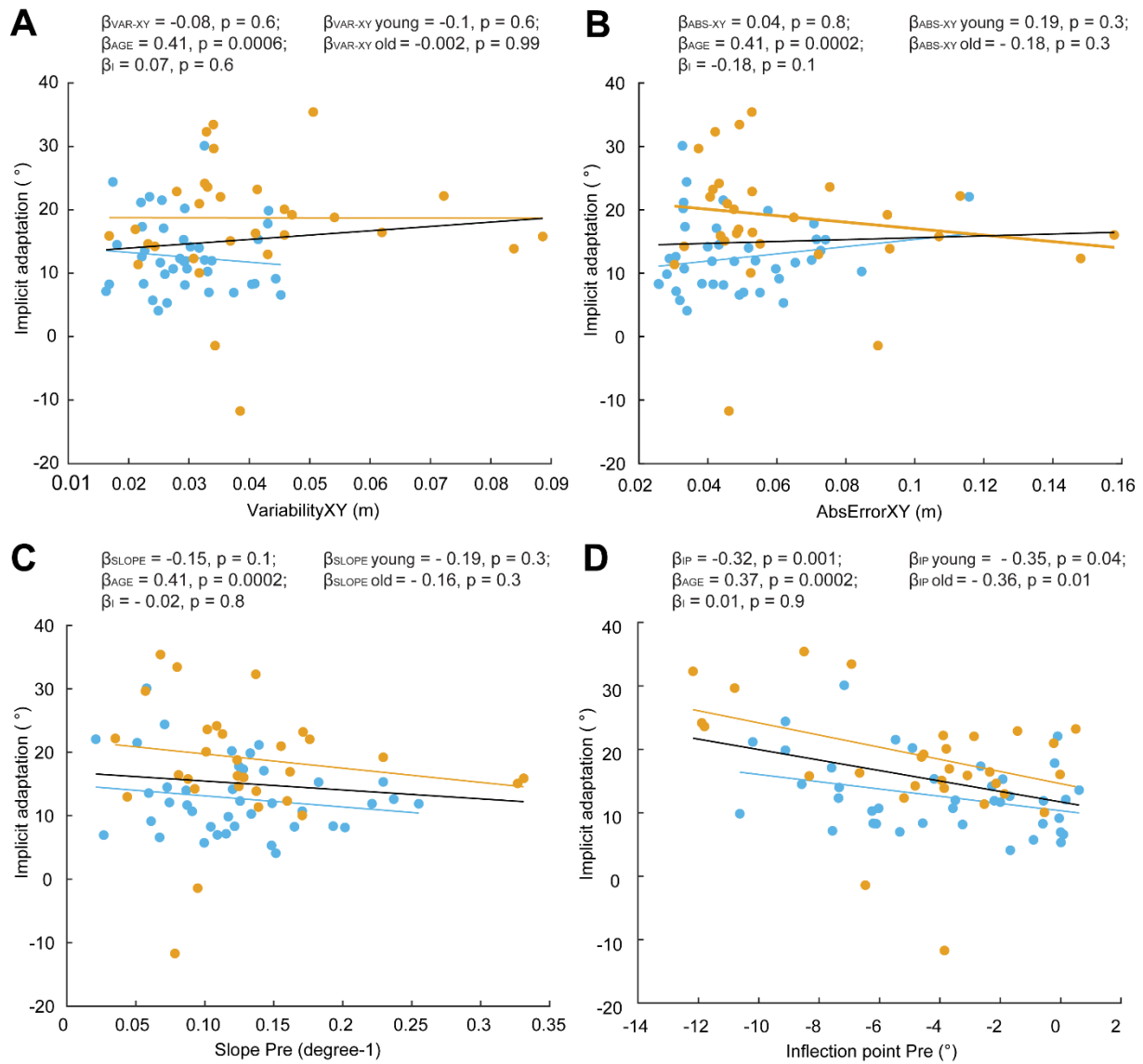
583

584 **Figure 6: Age-related decline of somatosensation, visualized with data from participants of paradigm 2.** A-B: Outcomes of
585 the position matching task measured before adaptation: variability of hand position, VariabilityXY, and the absolute error,
586 AbsErrXY. Lower values are associated with better somatosensory acuity. C-D: Outcomes of the perceptual boundary
587 estimation task measured before (Pre) and after adaptation (post). For panel C, higher values are associated with better
588 somatosensory acuity. No such interpretation exists for the inflection point. Each dot represents the data from one participant.
589 The height of the bars represents the inter-individual means and the error bars represent the standard error of the mean.

590 Next, the **preregistered** relationship between the position matching variables and implicit adaptation
591 level from the task-irrelevant clamped feedback experiment was determined (Analysis 5). However,
592 we did not find evidence that the position matching variables were related to the level of implicit

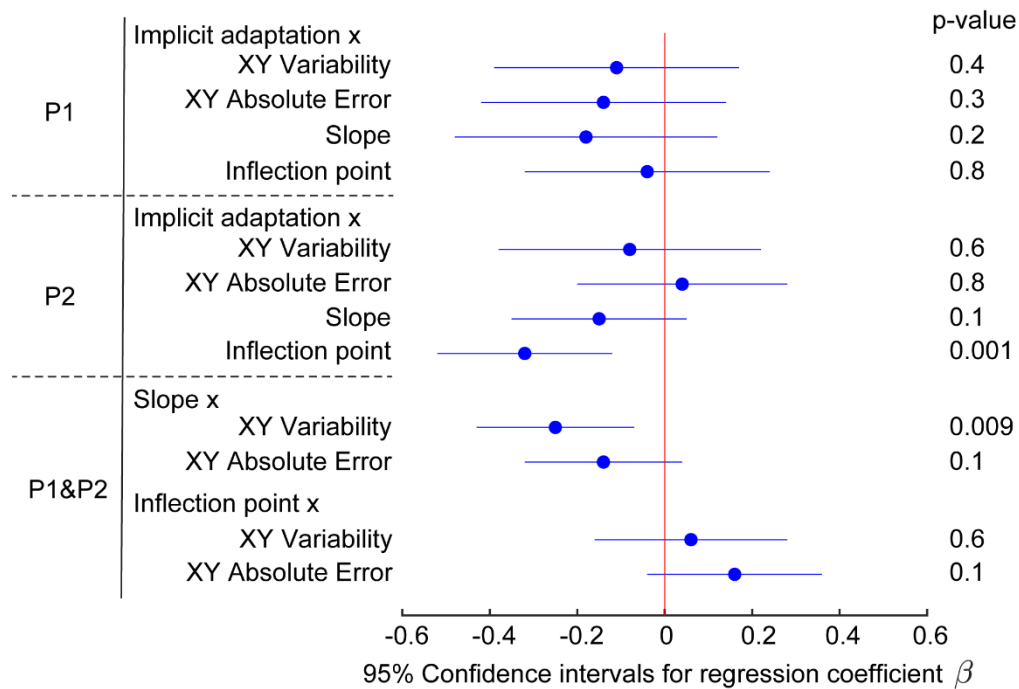
593 adaptation (Figure 7A-B; Table 2; $\beta_{\text{VAR-XY}} = -0.08$; $p = 0.6$, $R = 0.12$; $\beta_{\text{ABS-XY}} = 0.04$; $p = 0.8$, $R = 0.02$) or
594 that perceptual boundary variables were related to the internal model recalibration. There was no
595 evidence for a relationship between slope and implicit adaptation level (Figure 7C; $\beta_{\text{SLOPE}} = -0.15$; $p =$
596 0.1 , $R = -0.11$). Yet, there was evidence for a negative link between inflection point and implicit
597 adaptation (Figure 7D; pre: $\beta_{\text{IP}} = -0.32$, $p = 0.001$, $R = -0.37$). However, it is difficult for us to relate
598 somatosensory acuity and the inflection point. Furthermore, the inflection point was not different
599 between young and old (Figure 6D), which makes it unclear how this variable could explain the age-
600 related changes in implicit adaptation. Overall, no relation existed between somatosensory acuity
601 (measured by the position matching task or by the slope in the perceptual boundary task) and the level
602 of implicit adaptation in both paradigms. Therefore, the **preregistered** hypothesis was not confirmed.
603 Removing the two outliers in the older adult's group did not change the outcome of our results. For
604 completeness, the confidence intervals for all calculated regression coefficients are given (Figure 8).

605 Besides verifying the preregistered hypothesis, we could compare the different methods that we used
606 to measure somatosensory acuity. The position matching task measures position sense, while the
607 perceptual boundary test was a custom developed task measuring kinesthetic sense. Therefore, it is
608 not known how these tasks would compare to each other. Data were obtained for both tasks in both
609 paradigms, which allowed us to combine data of all 133 participants for this comparison. We compared
610 the two preregistered variables of the position matching task to the two preregistered variables from
611 the perceptual boundary test (Analysis 7; Figure 8). We observed a negative relationship between the
612 slope variable of the perceptual boundary curve and VariabilityXY of the position matching task (Figure
613 8; $\beta = -0.25$; $p = 0.009$).



614

615 **Figure 7: No relationship observed between implicit adaptation and somatosensory acuity. Data from paradigm 2. A-B:**
 616 *Scatterplot of the outcomes of the position matching task (data from fig.6A and B) and the extent of implicit motor adaptation*
 617 *from the task-irrelevant clamped feedback task (data from Fig.5B). A positive relationship is expected given that better*
 618 *somatosensory acuity is associated with lower values. C-D: Scatterplot of the outcomes of the perceptual boundary task (data*
 619 *from fig.6C and D) and the extent of implicit motor adaptation (data from Fig.5B). A negative relationship is expected for panel*
 620 *C given that better somatosensory acuity is associated with higher slope values. In all panels, each dot represent the data of*
 621 *a single participant. Solid lines represent the regression line from the robust regression analysis for both populations together*
 622 *(black line), for young participants only (blue lines) and for old participants only (orange lines).*



623

624 *Figure 8: 95% Confidence intervals for regression coefficient (β) from all analyses. The dots represent the mean and the error*
 625 *bar the confidence interval as assessed by bootstrapping. In the first two rows, the dependent variable is the extent of implicit*
 626 *adaptation and each row corresponds to different independent variables. Each row is associated with a different paradigm.*
 627 *In the third row, data from all participants are pooled together. Outcomes from the perceptual boundary task are used as*
 628 *dependent variables and those from the position-matching task are used as independent variables in the regression. In all*
 629 *regressions, age group is added as an additional independent factor. Numbers on the right correspond to the p-values*
 630 *associated with the different regression coefficients.*

631 Discussion

632 In this paper, we aimed to determine whether older adults' increased recalibration of the internal
 633 model could be caused by a reduction of somatosensory acuity with aging. To that end, we quantified
 634 implicit adaptation with cued motor adaptation in a first paradigm, in which color cues indicated the
 635 presence of the perturbation (Morehead et al., 2015). However, we did not find any evidence that the
 636 level of implicit adaptation was related to somatosensory acuity in that experimental context. In a
 637 second paradigm, we assessed internal model recalibration independently of explicit strategy by
 638 providing cursor-irrelevant feedback (Morehead et al., 2017) and observed an increased internal
 639 model recalibration with aging which confirms our previous work (Vandevoorde and Orban de Xivry,
 640 2019). According to our **preregistered hypothesis**, we expected a negative relationship between
 641 internal model recalibration and somatosensory acuity. However, we failed to support this hypothesis
 642 since there was no evidence for a relation between somatosensory acuity and internal model
 643 recalibration, measured in the two different paradigms.

644 Furthermore, we assessed somatosensory acuity as position and kinesthetic sense. An age-related
 645 decline of position sense could be observed in this second paradigm (Figure 6A-B). This difference was
 646 not detected in the first paradigm (Figure 3A-B), but can simply arise because of natural sampling
 647 variability. A difference in position sense replicates the observations that a decline in position sense

648 accompanies healthy aging (Herter et al., 2014). On the contrary, an age-related decline of kinesthetic
649 sense was not observed (Figure 3C-D, Figure 6C-D).

650 Somatosensation and internal model recalibration

651 Studies of deafferented patients show that proprioception is important to maintain an accurate
652 internal model as these patients exhibit impaired inter-segmental coordination. Such coordination
653 relies presumably on internal model function in healthy participants (Ghez et al., 1990; Sainburg et al.,
654 1995). It is therefore hypothesized that arm proprioception might contribute to the maintenance of
655 an accurate internal model (Scarchilli et al., 1999). While a previous study had reported no influence
656 of somatosensory impairment on adaptation to a visuomotor rotation (Bernier et al., 2006), that paper
657 did not assess pure implicit adaptation and these results could have been confounded by the presence
658 of a compensatory explicit strategy. This is why we believe that, if somatosensation was important to
659 maintain the accuracy of the internal model, age-related somatosensory deficits could account for the
660 paradoxical increase in internal model recalibration observed in our previous study (Vandevorde and
661 Orban de Xivry, 2019).

662 Yet, we failed to observe any consistent evidence in favor of that hypothesis. In paradigm 1, there was
663 a slightly larger implicit adaptation for elderly participants compared to younger ones but we did not
664 find any difference in somatosensory function. In paradigm 2, we found some differences in
665 somatosensation between the two age groups (position sense was reduced in older compared to
666 younger adults), while the difference in implicit adaptation was quite large with the elderly exhibiting
667 much more implicit adaptation than young participants. Finally, we failed to find a relationship
668 between somatosensory function and implicit adaptation as could have been expected from studies
669 on deafferented patients (Ghez et al., 1990; Sainburg et al., 1995), which showed that somatosensory
670 function is important for internal model recalibration.

671 While not significant, the β -coefficient for regression between somatosensory acuity (slope parameter)
672 and the extent of implicit motor adaptation was around - 0.2 in both experiments. There is thus the
673 possibility that a significant relationship could be found with many more participants. Yet, it is difficult
674 to conceive that such a weak relationship between somatosensory function and implicit adaptation
675 could explain the large age-related differences in implicit adaptation found in paradigm 2 and in our
676 previous paper (Vandevorde and Orban de Xivry, 2019).

677 Recalibration of proprioception goes along with recalibration of the internal model. Several papers
678 have demonstrated that visuomotor discrepancies (the difference between the visual feedback
679 provided and the direction of hand motion) yield both changes in hand localization and in internal
680 model recalibration and that these two quantities are linked to each other (Gastrock et al., 2020;

681 Salomonczyk et al., 2013; Tsay et al., 2020). Interestingly, this also holds in older people where
682 proprioceptive recalibration and after-effects are comparable to younger people (Cressman et al.,
683 2010).

684 Yet, one could expect that inter-individual differences in proprioceptive acuity could account for
685 differences in proprioceptive or internal model recalibration. Indeed, if visual and proprioceptive
686 information are combined in an optimal manner (van Beers et al., 2002, 1999), a visuo-proprioceptive
687 discrepancy (a difference between the direction of the hand and the direction of the cursor on the
688 screen) is typically resolved by recalibrating the less reliable source of information, here
689 proprioception. If proprioception is less reliable such as in older people (Goble et al., 2009), one could
690 expect that it would be recalibrated even further for that population. Yet, recalibration of
691 proprioception is comparable in young and old participants (Cressman et al., 2010) despite the fact
692 that uncertainty in hand localization was larger in older people.

693 In visuomotor perturbation, internal model recalibration in older people is also comparable to or larger
694 than that of younger people (Cressman et al., 2010; Hegele and Heuer, 2013; Heuer and Hegele, 2008;
695 Reuter et al., 2020, 2018; Vachon et al., 2020; Vandevorde and Orban de Xivry, 2019). We were
696 expecting that the visuo-proprioceptive discrepancy would be responsible for the amplitude of the
697 adaptative response. Over a single trial, the amplitude of the adaptative response grows linearly with
698 the size of the observed error over a small range and then saturates for larger errors (Hutter and Taylor,
699 2018; Kim et al., 2018; Marko et al., 2012). It was suggested that the saturation of the adaptation
700 response could be due to the discrepancy between visual and proprioceptive estimates (Wei and
701 Kording, 2009) where large discrepancies are considered irrelevant for the motor system. The
702 evaluation of this discrepancy requires reliable visual and proprioceptive signals. Unreliable
703 proprioceptive information (e.g. due to aging) should increase the size of errors deemed as relevant
704 and to which the motor system needs to respond and should also yield to a larger adaptative response.
705 Following this theory, the quality of proprioception should be negatively linked to the size of the
706 discrepancies that are deemed relevant and to which the motor system respond. The present
707 experiments did not provide any evidence for this negative link. A similar result has been recently
708 observed with a force-field perturbation (Kitchen and Miall, 2020) where it was found that dynamic
709 proprioceptive acuity, which was measured similarly as we did, was not related to the extent of force-
710 field after-effect in young and old people. Together, these results and ours cast doubts on the fact that
711 vision and proprioception are combined to drive motor adaptation or other age-related effects on
712 motor function such as larger sensory attenuation (Parthasharathy et al., 2020).

713 This finding can be put into the larger debate about the possible combination of vision and
714 proprioception during reaching or motor adaptation tasks. Optimal combination has been
715 hypothesized on the basis of different amount of adaptation across direction (van Beers et al., 2002).
716 In contrast, several papers demonstrate that the two sensory signals contribute differently to sensory
717 motor adaptation. For instance, Hayashi and colleagues (2020) demonstrated that visual and
718 proprioceptive feedback were linked to separate motor memories. Furthermore, Scheidt et al. (2005)
719 showed that adaptation with and without vision was identical but that adaptation to the force-field
720 perturbation was absent when the visual feedback of the cursor was constrained to a straight line
721 going right to the target. This suggests that, during adaptation, visual feedback (the hand going
722 straight) dominated the proprioceptive information about the perturbation (see also Judkins and
723 Scheidt, 2014). Similarly, disrupting proprioception via muscle vibration does not have any effect on
724 the adaptation to a visuomotor rotation where there is a discrepancy between vision and
725 proprioception because, again, vision dominates the adaptation response (Pipereit et al., 2006). Our
726 results are in line with the fact that, during motor adaptation tasks, vision and proprioception are not
727 optimally combined. Note that such optimal integration remains valid during perceptual tasks (Ernst
728 and Banks, 2002; van Beers et al., 1999).

729 [Alternative explanations for increased internal model recalibration with aging](#)

730 We failed to find evidence that an age-related decline in somatosensation with aging was related to
731 internal model recalibration increase with aging. This suggests that internal model recalibration
732 increases with aging, independent from somatosensory deficits. We initially suggested two
733 explanations for the increased internal model recalibration related to somatosensory acuity changes:
734 1) an altered sensory integration with an up weighting of visual feedback because of reduced
735 somatosensory acuity, and 2) an increased reliance on predicted sensory outcome because of reduced
736 somatosensory acuity. However, these two initial explanations seem unlikely given our results and
737 alternative explanations should be explored.

738 First, it could be that visual acuity is the relevant sensory information source for internal model
739 recalibration of arm reaching, and not somatosensory acuity. For that reason, it remains interesting to
740 investigate the relationship between visual acuity and the level of internal model recalibration for a
741 group of young and older adults. This explanation might be related to studies investigating sensory
742 attenuation. Sensory attenuation is the decreased sensation of a self-produced stimulus (Blakemore
743 et al., 2000; Wolpert et al., 1995). Two studies (Parthasarathy et al., 2020; Wolpe et al., 2016)
744 observed an age-related increase of sensory attenuation for force applied to the finger and the upper-
745 limb. This shift in sensory attenuation with aging resulted in increased overcompensation to match a
746 previously applied force. Wolpe et al. (2016) suggested that this shift in sensory attenuation was

747 related to a reduced somatosensory acuity with aging but this was not confirmed by later experiments
748 studies (Parthasharathy et al., 2020). It is not directly related to our observation of increased internal
749 model recalibration with aging, since we applied visual instead of force perturbations. Nevertheless, it
750 is important to verify whether sensory attenuation is not involved in our observation as well. For
751 instance, if the stronger reaction to visual error with aging is related to a reduced visual acuity.

752 A second explanation might be an increased internal model recalibration because of life-long learning
753 from sensory prediction errors. Throughout life, errors of all kind of sizes are experienced, likely
754 creating a growing memory of sensory prediction errors and appropriate responses to them, which
755 could upregulate error-sensitivity with aging (Albert et al., 2020; Herzfeld et al., 2014). This increased
756 internal model recalibration might have arisen as a compensation mechanism for a reduction of explicit
757 aiming with aging (Heuer and Hegele, 2008; Vandevorode and Orban de Xivry, 2020, 2019); this
758 compensation mechanism has also been observed outside an aging context (Bond and Taylor, 2015;
759 Brudner et al., 2016; Christou et al., 2016; Schween and Hegele, 2017; Taylor and Ivry, 2011). Our
760 experiment specifically investigated angular sensory prediction errors. However, it would be useful to
761 verify whether elderly react more to other types of sensory prediction errors such as errors induced
762 by small random force-field perturbations where no explicit aiming strategies can be applied. Future
763 studies should try to determine whether elderly react more to other sensory prediction errors as well,
764 such as observed in gait, speech or force-field adaptation.

765 A third explanation is that older adults are less able to filter the distracting irrelevant visual feedback.
766 Elderly are exhibiting impaired selective attention, which results in lower abilities to enhance task-
767 relevant information and suppress task-irrelevant information (Awh et al., 2006; Gazzaley and Nobre,
768 2012). Applied to increased internal model recalibration, this might result in lower abilities to suppress
769 the task-irrelevant visual feedback and enhance the relevant somatosensory feedback. According to
770 this explanation, no link is required between increased internal model recalibration and
771 (somato)sensory acuity but instead a link might exist between internal model recalibration and
772 working memory assessment that incorporates the ability to filter irrelevant stimuli (McNab and
773 Klingberg, 2008).

774 A fourth possible explanation is that the reward structure might have a different effect on young and
775 older adults. The absence of reward is known to drive the implicit system, while the presence of reward
776 is reducing it (Kim et al., 2019). In our experiments, the absence of reward could have resulted in a
777 bigger driving force for the implicit system of older adults compared to younger adults.

778 Finally, it is possible that conscious reports of somatosensation are irrelevant for motor adaptation
779 because different proprioceptive signals are used from motor control and for perception. For instance,

780 Rand and Heuer (2020) recently that conscious reports of visual and proprioceptive information was
781 not consistent with sensory integration while unconscious proprioceptive signals reflected in the
782 direction of reaching movements were clearly integrated with visual signals. In this case, conscious
783 reports of hand position that are influenced by experimental manipulations like visuomotor rotation
784 (Cressman and Henriques, 2011), might be completely independent of the proprioceptive signals used
785 by the motor system. Such dissociation between conscious perception and action has been reported
786 before for the size-weight illusion (Flanagan and Beltzner, 2000).

787 [Age-related deficits in somatosensation are limited.](#)

788 The position matching task is a reliable, quantitative tool for multijoint upper limb position sense
789 (Dukelow et al., 2010) with an excellent reliability and interrater variability for multijoint limb position
790 sense. The second somatosensory test consisted of a robotic assessment of kinesthetic sense, which
791 had been used before with horizontal (Kitchen and Miall, 2018; Ostry et al., 2010) and angular
792 displacements (Darainy et al., 2013). This test is sensitive enough to detect changes in proprioception
793 induced by force-field adaptation (Ostry et al., 2010). Our measurements were limited to active limb
794 movement since this mimicked best the motor learning paradigm requirements.

795 One limitation of the kinesthetic somatosensory test was the requirement of an overt response since
796 somatosensation is rather a covert process. However, the possibility to guess in case of doubts
797 revealed that the participants were quite accurate despite being clueless. For instance, the examiner
798 (KV) noticed that, although participants answered correctly to the deviation, they often responded
799 that they had no clue whether their answer was correct. An improvement to the task could be to allow
800 participants to give two more answer choices ('maybe left', 'maybe right') or to report the certainty of
801 their response on a scale. The outcomes of both tests could be influenced by central processing abilities
802 and working memory, which are typically reduced with aging. However, we instructed participants
803 clearly and allowed them to practice long enough until they understood the tasks correctly. Therefore,
804 we think that the influence of cognitive decline is negligible in our assessment.

805 We expected that somatosensory acuity would decline with aging in both sensory tests. This
806 expectation appears partially correct for position sense only, while it was not for kinesthetic sense
807 since the slope of the psychometric accuracy curve was similar for young and older adults. Previous
808 literature about kinesthetic sense and aging is limited and inconclusive. One study (Kitchen et al., 2019)
809 reports an age-dependent increase in proprioceptive bias in active multi-joint upper limb movement
810 but not in uncertainty range. In contrast, another study (Cressman et al., 2010) reports a similar bias
811 between age groups but a slightly increased uncertainty range in elderly. In future experiments, it
812 would be interesting to clarify these differences. One might design a more sensitive kinesthetic
813 paradigm, for instance by applying a fixed time duration for each reaching trial, by controlling grip

814 strength or by increasing the number of trials and angular deviations. Finally, one could replace the
815 PEST algorithm by the likely more sensitive Bayesian adaptive QUEST algorithm (Watson and Pelli,
816 1983). However, if an effect between groups exists, it will be small and it is probably not related to
817 age-related deficits in motor adaptation.

818 Conclusion

819 Based on two different motor adaptation experiments, we were able to confirm that internal model
820 recalibration is not impaired with aging but is increased when isolated from the explicit process.
821 However, we failed to support the hypothesis that a decline in somatosensory acuity could explain this
822 increase in internal model recalibration with age. This questions the fact that vision and
823 somatosensation are dynamically combined during motor adaptation. There is a need to incorporate
824 these age-related effects in the current models of sensorimotor adaptation in order to transition from
825 fundamental insights in motor learning to clinical applications.

826 Acknowledgements

827 This work was supported by an internal grant of the KU Leuven (STG/14/054) and by the FWO
828 (1519916N).

829 Literature

- 830 Albert, S.T., Jang, J., Sheahan, H., Teunissen, L., Vandevoorde, K., Shadmehr, R., 2020. An implicit
831 memory of errors limits human sensorimotor adaptation 3, 1–38.
- 832 Awh, E., Vogel, E.K., Oh, S.H., 2006. Interactions between attention and working memory.
833 *Neuroscience* 139, 201–208. <https://doi.org/10.1016/j.neuroscience.2005.08.023>
- 834 Aydoğ, S.T., Korkusuz, P., Doral, M.N., Tetik, O., Demirel, H.A., 2006. Decrease in the numbers of
835 mechanoreceptors in rabbit ACL: The effects of ageing. *Knee Surg. Sports Traumatol.*
836 *Arthrosc.* 14, 325–329. <https://doi.org/10.1007/s00167-005-0673-2>
- 837 Bernier, P.-M., Chua, R., Bard, C., Franks, I., 2006. Updating of an internal model without
838 proprioception: a deafferentation study.
- 839 Blakemore, S., Wolpert, C.A.D., Frith, C., 2000. Why can't you tickle yourself? 11, 11–16.
- 840 Bond, K.M., Taylor, J. a, 2015. Flexible explicit but rigid implicit learning in a visuomotor adaptation
841 task. *J. Neurophysiol.* jn.00009.2015. <https://doi.org/10.1152/jn.00009.2015>
- 842 Brudner, S.N., Kethidi, N., Graeupner, D., Ivry, R.B., Taylor, X.J.A., 2016. Delayed feedback during
843 sensorimotor learning selectively disrupts adaptation but not strategy use 1499–1511.
844 <https://doi.org/10.1152/jn.00066.2015>
- 845 Christou, A.I., Miall, R.C., McNab, F., Galea, J.M., 2016. Individual differences in explicit and implicit
846 visuomotor learning and working memory capacity. *Sci. Rep.* 6, 36633.
847 <https://doi.org/10.1038/srep36633>
- 848 Cressman, E.K., Henriques, D.Y.P., 2011. Motor adaptation and proprioceptive recalibration. *Prog.*
849 *Brain Res.* 191, 91–9. <https://doi.org/10.1016/B978-0-444-53752-2.00011-4>
- 850 Cressman, E.K., Salomonczyk, D., Henriques, D.Y.P., 2010. Visuomotor adaptation and proprioceptive
851 recalibration in older adults. *Exp. Brain Res.* 205, 533–544. [https://doi.org/10.1007/s00221-](https://doi.org/10.1007/s00221-010-2392-2)
852 [010-2392-2](https://doi.org/10.1007/s00221-010-2392-2)
- 853 Darainy, M., Vahdat, S., Ostry, D.J., 2013. Perceptual learning in sensorimotor adaptation 1, 2152–
854 2162. <https://doi.org/10.1152/jn.00439.2013>

- 855 Deravet, N., Blohm, G., Orban de Xivry, J.-J., Lefèvre, P., 2018. Weighted integration of short-term
856 memory and sensory signals in the oculomotor system. *J. Vis.* 18, 16.
857 <https://doi.org/10.1167/18.5.16>
- 858 Dukelow, S.P., Herter, T.M., Moore, K.D., Demers, M.J., Glasgow, J.I., Bagg, S.D., Norman, K.E., Scott,
859 S.H., 2010. Quantitative Assessment of Limb Position Sense Following Stroke.
860 <https://doi.org/10.1177/1545968309345267>
- 861 Ernst, M., Banks, M.S., 2002. Humans integrate visual and haptic information in a statistically optimal
862 fashion. *Nature* 415, 429–433.
- 863 Fernández-Ruiz, J., Hall, C., Vergara, P., Díaz, R., 2000. Prism adaptation in normal aging: Slower
864 adaptation rate and larger aftereffect. *Cogn. Brain Res.* 9, 223–226.
865 [https://doi.org/10.1016/S0926-6410\(99\)00057-9](https://doi.org/10.1016/S0926-6410(99)00057-9)
- 866 Flanagan, J.R., Beltzner, M.A., 2000. Independence of perceptual and sensorimotor predictions in the
867 size–weight illusion. *Nat. Neurosci.* 3, 737–741. <https://doi.org/10.1038/76701>
- 868 Folstein, M., Folstein, S., McHugh, P., 1975. “MINI-MENTAL STATE” A practical state method for
869 grading the cognitive state of patients for the clinician. *J. Psychiatr. Res.* 12, 189–198.
- 870 Gastrock, R.Q., Modchalingam, S., Hart, B.M., Henriques, D.Y.P., 2020. External error attribution
871 dampens efferent-based predictions but not proprioceptive changes in hand localization.
872 *bioRxiv* 2020.02.05.936062. <https://doi.org/10.1101/2020.02.05.936062>
- 873 Gazzaley, A., Nobre, A.C., 2012. Top-down modulation: bridging selective attention and working
874 memory. *Trends Cogn. Sci.* 16, 129–35. <https://doi.org/10.1016/j.tics.2011.11.014>
- 875 Ghez, C., Gordon, J., Ghilardi, M.F., Christakos, C.N., Cooper, S.E., 1990. Roles of proprioceptive input
876 in the programming of arm trajectories. *Cold Spring Harb. Symp. Quant. Biol.* 55, 837–847.
877 <https://doi.org/10.1101/SQB.1990.055.01.079>
- 878 Goble, D.J., Coxon, J.P., Wenderoth, N., Van Impe, A., Swinnen, S.P., 2009. Proprioceptive sensibility
879 in the elderly: Degeneration, functional consequences and plastic-adaptive processes.
880 *Neurosci. Biobehav. Rev.* 33, 271–278. <https://doi.org/10.1016/j.neubiorev.2008.08.012>
- 881 Hayashi, T., Kato, Y., Nozaki, D., 2020. Divisively Normalized Integration of Multisensory Error
882 Information Develops Motor Memories Specific to Vision and Proprioception. *J. Neurosci.* 40,
883 1560–1570. <https://doi.org/10.1523/JNEUROSCI.1745-19.2019>
- 884 Hegele, M., Heuer, H., 2013. Age-related variations of visuomotor adaptation result from both the
885 acquisition and the application of explicit knowledge. *Psychol. Aging* 28, 333–9.
886 <https://doi.org/10.1037/a0031914>
- 887 Hegele, M., Heuer, H., 2010. The impact of augmented information on visuo-motor adaptation in
888 younger and older adults. *PLoS One* 5, e12071.
889 <https://doi.org/10.1371/journal.pone.0012071>
- 890 Herter, T.M., Scott, S.H., Dukelow, S.P., 2014. Systematic changes in position sense accompany
891 normal aging across adulthood. *J. Neuroengineering Rehabil.* 1–12.
- 892 Herzfeld, D.J., Vaswani, P. a, Marko, M.K., Shadmehr, R., 2014. A memory of errors in sensorimotor
893 learning. *Science* 345, 1349–53. <https://doi.org/10.1126/science.1253138>
- 894 Heuer, H., Hegele, M., 2014. Age-related variations of visuo-motor adaptation beyond explicit
895 knowledge. *Front. Aging Neurosci.* 6, 1–12. <https://doi.org/10.3389/fnagi.2014.00152>
- 896 Heuer, H., Hegele, M., 2008. Adaptation to visuomotor rotations in younger and older adults.
897 *Psychol. Aging* 23, 190–202. <https://doi.org/10.1037/0882-7974.23.1.190>
- 898 Holland, P., Welsch, R.E., 1977. Robust regression using iteratively reweighted least-squares.
899 *Commun. Stat. - Theory Methods* 6, 813–827. <https://doi.org/10.1080/03610927708827533>
- 900 Huang, J., Gegenfurtner, K.R., Schütz, A.C., 2017. Age effects on saccadic adaptation : Evidence from
901 different paradigms reveals specific vulnerabilities 17, 1–18.
902 <https://doi.org/10.1167/17.6.9.doi>
- 903 Hutter, S.A., Taylor, J.A., 2018. Relative sensitivity of explicit re-aiming and implicit motor adaptation.
904 *J. Neurophysiol.* <https://doi.org/10.1152/jn.00283.2018>
- 905 Johnson, K.O., 2001. The roles and functions of cutaneous mechanoreceptors 455–461.

- 906 Judkins, T., Scheidt, R.A., 2014. Visuo-proprioceptive interactions during adaptation of the human
907 reach. *J. Neurophysiol.* 111, 868–887. <https://doi.org/10.1152/jn.00314.2012>
- 908 Kim, H., Morehead, J.R., Parvin, D.E., Moazzezi, R., Ivry, R.B., 2018. Invariant errors reveal limitations
909 in motor correction rather than constraints on error sensitivity. *Nat. Commun. Biol.*
910 <https://doi.org/10.1038/s42003-018-0021-y>
- 911 Kitchen, N.M., Miall, R.C., 2020. Adaptation of reach action to a novel force-field is not predicted by
912 acuity of dynamic proprioception in either older or younger adults. *bioRxiv*
913 2020.07.13.200733. <https://doi.org/10.1101/2020.07.13.200733>
- 914 Kitchen, N.M., Miall, R.C., 2018. Proprioceptive deficits in inactive older adults are not reflected in
915 fast targeted reaching movements. *Exp. Brain Res.* <https://doi.org/10.1007/s00221-018-5440-y>
- 916
- 917 Kording, K.P., Wolpert, D.M., 2004. Bayesian integration in sensorimotor learning. *Nature* 427, 244–
918 7. <https://doi.org/10.1038/nature02169>
- 919 Krampe, R.T., 2002. Aging, expertise and fine motor movement. *Neurosci. Biobehav. Rev.* 26, 769–
920 776. [https://doi.org/10.1016/S0149-7634\(02\)00064-7](https://doi.org/10.1016/S0149-7634(02)00064-7)
- 921 Marko, M.K., Haith, A.M., Harran, M.D., Shadmehr, R., 2012. Sensitivity to prediction error in reach
922 adaptation. *J. Neurophysiol.* 108, 1752–63. <https://doi.org/10.1152/jn.00177.2012>
- 923 Mathis, M.W., Mathis, A., Uchida, N., 2017. Somatosensory Cortex Plays an Essential Role in Forelimb
924 Motor Adaptation in Mice. *Neuron* 93, 1493–1503.e6.
925 <https://doi.org/10.1016/j.neuron.2017.02.049>
- 926 McNab, F., Klingberg, T., 2008. Prefrontal cortex and basal ganglia control access to working memory.
927 *Nat. Neurosci.* 11, 103–107. <https://doi.org/10.1038/nn2024>
- 928 Miall, R., Wolpert, D., 1996. Forward Models for Physiological Motor Control 9.
- 929 Miall, R.C., Kitchen, N.M., Ho, S., Hannah, N., Alix, L., Kristin, G.R., Cole, J.D., Sarlegna, F.R., 2018.
930 Proprioceptive loss and the perception, control and learning of arm movements in humans :
931 evidence from sensory neuronopathy. *Exp. Brain Res.* 236, 2137–2155.
932 <https://doi.org/10.1007/s00221-018-5289-0>
- 933 Miwa, T., Miwa, Y., Kanda, K., 1995. Dynamic and static sensitivities of muscle spindle primary
934 endings in aged rats to ramp stretch. *Neurosci. Lett.* 201, 179–182.
935 [https://doi.org/10.1016/0304-3940\(95\)12165-X](https://doi.org/10.1016/0304-3940(95)12165-X)
- 936 Morehead, J.R., Qasim, S.E., Crossley, M.J., Ivry, R., 2015. Savings upon Re-Aiming in Visuomotor
937 Adaptation. *J. Neurosci.* 35, 14386–14396. <https://doi.org/10.1523/JNEUROSCI.1046-15.2015>
- 938 Morehead, J.R., Taylor, J.A., Parvin, D., Ivry, R.B., 2017. Characteristics of Implicit Sensorimotor
939 Adaptation Revealed by Task-irrelevant Clamped Feedback. *J. Cogn. Neurosci.* 26, 194–198.
940 <https://doi.org/10.1162/jocn>
- 941 Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh inventory.
942 *Neuropsychologia* 9, 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)
- 943 Orban de Xivry, J.-J., Coppe, S., Blohm, G., Lefèvre, P., 2013. Kalman Filtering Naturally Accounts for
944 Visually Guided and Predictive Smooth Pursuit Dynamics. *J. Neurosci.* 33, 17301–17313.
- 945 Ostry, D.J., Darainy, M., Mattar, A.A.G., Wong, J., Gribble, P.L., 2010. Somatosensory plasticity and
946 motor learning. *J. Neurosci.* 30, 5384–93. <https://doi.org/10.1523/JNEUROSCI.4571-09.2010>
- 947 Parthasarathy, M., Mantini, D., Orban De Xivry, J.-J., 2020. Increased upper-limb sensory
948 attenuation with age. *bioRxiv* 2020.09.17.301739.
949 <https://doi.org/10.1101/2020.09.17.301739>
- 950 Pipereit, K., Bock, O., Vercher, J.-L., 2006. The contribution of proprioceptive feedback to
951 sensorimotor adaptation. *Exp. Brain Res.* 174, 45–52. <https://doi.org/10.1007/s00221-006-0417-7>
- 952
- 953 Rand, M.K., Heuer, H., 2020. A condition that produces sensory recalibration and abolishes
954 multisensory integration. *Cognition* 202, 104326.
955 <https://doi.org/10.1016/j.cognition.2020.104326>
- 956 Raz, N., Lindenberger, U., Rodrigue, K.M., Kennedy, K.M., Head, D., Williamson, A., Dahle, C.,
957 Gerstorff, D., Acker, J.D., 2005. Regional brain changes in aging healthy adults: General trends,

- 958 individual differences and modifiers. *Cereb. Cortex* 15, 1676–1689.
959 <https://doi.org/10.1093/cercor/bhi044>
- 960 Reuter, E.-M., Leow, L.-A., Carroll, T.J., 2020. Task feedback processing differs between young and
961 older adults in visuomotor rotation learning despite similar initial adaptation and savings.
962 *Neuroscience*. <https://doi.org/10.1016/j.neuroscience.2020.09.038>
- 963 Reuter, E.-M., Pearcey, G.E.P., Carroll, T.J., 2018. Greater neural responses to trajectory errors are
964 associated with superior force field adaptation in older adults. *Exp. Gerontol.* #pagerange#.
965 <https://doi.org/10.1016/j.exger.2018.05.020>
- 966 Sainburg, R.L., Ghilardi, M.F., Poizner, H., Ghez, C., 1995. Control of limb dynamics in normal subjects
967 and patients without proprioception. *J. Neurophysiol.* 73, 820–835.
968 <https://doi.org/10.1152/jn.1995.73.2.820>
- 969 Salomonczyk, D., Cressman, E.K., Henriques, D.Y.P., 2013. The role of the cross-sensory error signal in
970 visuomotor adaptation. *Exp. Brain Res.* 228, 313–325. [https://doi.org/10.1007/s00221-013-](https://doi.org/10.1007/s00221-013-3564-7)
971 [3564-7](https://doi.org/10.1007/s00221-013-3564-7)
- 972 Scarchilli, K., Vercher, J.L., Gauthier, G.M., Cole, J., 1999. Does the oculo-manual co-ordination
973 control system use an internal model of the arm dynamics? *Neurosci. Lett.* 265, 139–142.
974 [https://doi.org/10.1016/S0304-3940\(99\)00224-4](https://doi.org/10.1016/S0304-3940(99)00224-4)
- 975 Scheidt, R.A., Conditt, M.A., Secco, E.L., Mussa-Ivaldi, F.A., 2005. Interaction of visual and
976 proprioceptive feedback during adaptation of human reaching movements. *J. Neurophysiol.*
977 93, 3200–3213. <https://doi.org/10.1152/jn.00947.2004>
- 978 Schween, R., Hegele, M., 2017. Feedback delay attenuates implicit but facilitates explicit adjustments
979 to a visuomotor rotation. *Neurobiol. Learn. Mem.* 140, 124–133.
980 <https://doi.org/10.1016/j.nlm.2017.02.015>
- 981 Seidler, R.D., 2007. Aging affects motor learning but not savings at transfer of learning. *Learn. Mem.*
982 *Cold Spring Harb. N* 14, 17–21. <https://doi.org/10.1101/lm.394707>
- 983 Seidler, R.D., 2006. Differential effects of age on sequence learning and sensorimotor adaptation.
984 *Brain Res. Bull.* 70, 337–346. <https://doi.org/10.1016/j.brainresbull.2006.06.008>
- 985 Sexton, B.M., Liu, Y., Block, H.J., 2019. Increase in weighting of vision vs. proprioception associated
986 with force field adaptation. *Sci. Rep.* 9, 1–13. <https://doi.org/10.1038/s41598-019-46625-7>
- 987 Shadmehr, R., Smith, M. a, Krakauer, J.W., 2010. Error correction, sensory prediction, and adaptation
988 in motor control. *Annu. Rev. Neurosci.* 33, 89–108. [https://doi.org/10.1146/annurev-neuro-](https://doi.org/10.1146/annurev-neuro-060909-153135)
989 [060909-153135](https://doi.org/10.1146/annurev-neuro-060909-153135)
- 990 Shaffer, S.W., Harrison, A.L., 2007. Aging of the Somatosensory System: A Translational Perspective.
991 *Phys. Ther.* 87, 193–207. <https://doi.org/10.2522/ptj.20060083>
- 992 Swash, M., Fox, K.P., 1972. The effect of age on human skeletal muscle studies of the morphology
993 and innervation of muscle spindles. *J. Neurol. Sci.* 16, 417–432.
994 [https://doi.org/10.1016/0022-510X\(72\)90048-2](https://doi.org/10.1016/0022-510X(72)90048-2)
- 995 Taylor, J.A., Ivry, R.B., 2011. Flexible Cognitive Strategies during Motor Learning. *PLoS Comput. Biol.*
996 7, e1001096. <https://doi.org/10.1371/journal.pcbi.1001096>
- 997 Taylor, M.M., Creelman, C.D., 1967. PEST : Efficient Estimates on Probability Functions 782, 782–787.
998 <https://doi.org/10.1121/1.1910407>
- 999 Tsay, J.S., Kim, H.E., Parvin, D.E., Stover, A.R., Ivry, R.B., 2020. Individual differences in proprioception
1000 predict the extent of implicit sensorimotor adaptation. *bioRxiv* 2020.10.03.324855.
1001 <https://doi.org/10.1101/2020.10.03.324855>
- 1002 Tseng, Y., Diedrichsen, J., Krakauer, J.W., Shadmehr, R., Bastian, A.J., 2007. Sensory Prediction Errors
1003 Drive Cerebellum-Dependent Adaptation of Reaching 54–62.
1004 <https://doi.org/10.1152/jn.00266.2007>.
- 1005 Vachon, C.M., Modchalingam, S., Hart, B.M. t, Henriques, D.Y.P., 2020. The effect of age on
1006 visuomotor learning processes. *PLOS ONE* 15, e0239032.
1007 <https://doi.org/10.1371/journal.pone.0239032>
- 1008 van Beers, R.J., Sittig, a C., Gon, J.J., 1999. Integration of proprioceptive and visual position-
1009 information: An experimentally supported model. *J. Neurophysiol.* 81, 1355–64.

- 1010 van Beers, R.J., Wolpert, D.M., Haggard, P., 2002. When feeling is more important than seeing in
1011 sensorimotor adaptation. *Curr. Biol.* 12, 834–837.
- 1012 Vandevorde, K., Orban de Xivry, J.-J., 2020. Why is the explicit component of motor adaptation
1013 limited in elderly adults? *J. Neurophysiol.* 124, 152–167.
1014 <https://doi.org/10.1152/jn.00659.2019>
- 1015 Vandevorde, K., Orban de Xivry, J.-J., 2019. Internal model recalibration does not deteriorate with
1016 age while motor adaptation does. *Neurobiol. Aging* 80, 138–153.
1017 <https://doi.org/10.1016/j.neurobiolaging.2019.03.020>
- 1018 Verrillo, R.T., Bolanowski, S.J., Gescheider, G.A., 2002. Effect of aging on the subjective magnitude of
1019 vibration. *Somatosens. Mot. Res.* 19, 238–244.
1020 <https://doi.org/10.1080/0899022021000009161>
- 1021 Walhovd, K.B., Westlye, L.T., Amlien, I., Espeseth, T., Reinvang, I., Raz, N., Agartz, I., Salat, D.H.,
1022 Greve, D.N., Fischl, B., Dale, A.M., Fjell, A.M., 2011. Consistent neuroanatomical age-related
1023 volume differences across multiple samples. *NBA* 32, 916–932.
1024 <https://doi.org/10.1016/j.neurobiolaging.2009.05.013>
- 1025 Watson, A.B., Pelli, D.G., 1983. QUEST : A Bayesian adaptive psychometric method 33, 113–120.
- 1026 Wei, K., Kording, K.P., 2009. Relevance of error: what drives motor adaptation? *J. Neurophysiol.* 101,
1027 655–64. <https://doi.org/10.1152/jn.90545.2008>
- 1028 Wolpe, N., Ingram, J.N., Tsvetanov, K.A., Geerligs, L., Kievit, R.A., Henson, R.N., Wolpert, D.M., Tyler,
1029 L.K., Brayne, C., Bullmore, E., Calder, A., Cusack, R., Dalgleish, T., Duncan, J., Matthews, F.E.,
1030 Marslen-Wilson, W., Shafto, M.A., Campbell, K., Cheung, T., Davis, S., McCarrey, A., Mustafa,
1031 A., Price, D., Samu, D., Taylor, J.R., Treder, M., van Belle, J., Williams, N., Bates, L., Emery, T.,
1032 Erzinçlioglu, S., Gadie, A., Gerbase, S., Georgieva, S., Hanley, C., Parkin, B., Troy, D., Auer, T.,
1033 Correia, M., Gao, L., Green, E., Henriques, R., Allen, J., Amery, G., Amunts, L., Barcroft, A.,
1034 Castle, A., Dias, C., Dowrick, J., Fair, M., Fisher, H., Goulding, A., Grewal, A., Hale, G., Hilton,
1035 A., Johnson, F., Johnston, P., Kavanagh-Williamson, T., Kwasniewska, M., McMinn, A.,
1036 Norman, K., Penrose, J., Roby, F., Rowland, D., Sargeant, J., Squire, M., Stevens, B., Stoddart,
1037 A., Stone, C., Thompson, T., Yazlik, O., Barnes, D., Dixon, M., Hillman, J., Mitchell, J., Willis, L.,
1038 Rowe, J.B., 2016. Ageing increases reliance on sensorimotor prediction through structural
1039 and functional differences in frontostriatal circuits. *Nat. Commun.* 7, 13034.
1040 <https://doi.org/10.1038/ncomms13034>
- 1041 Wolpert, D.M., Ghahramani, Z., Jordan, M.I., 1995. An internal model for sensorimotor integration.
1042 *Science* 269, 1880–1882. <https://doi.org/10.1126/science.7569931>
- 1043 Yan, J.H., Thomas, J.R., Stelmach, G.E., 1998. Aging and Rapid Aiming Arm Movement Control
1044 Movement Control. *Exp. Aging Res.* 24, 155–168. <https://doi.org/10.1080/036107398244292>
1045