

1 Aging exerts a limited influence on the perception of self- 2 generated and externally generated touch

3 Lili Timar¹, Xavier Job¹, Jean-Jacques Orban de Xivry^{2,3}, Konstantina Kilteni^{1*}

4 ¹Department of Neuroscience, Karolinska Institutet, Stockholm, Sweden

5 ²Department of Movement Sciences, KU Leuven, Leuven, Belgium

6 ³KU Leuven Brain Institute, KU Leuven, Leuven, Belgium

7 *Correspondence and requests for materials should be addressed to konstantina.kilteni@ki.se

8 Abstract

9 Touch generated by our voluntary movements is attenuated both at the perceptual and neural
10 level compared to touch of the same intensity delivered to our body by another person or
11 machine. This somatosensory attenuation phenomenon is considered to rely on the integration
12 of somatosensory input and predictions about the somatosensory consequences of our actions.
13 Previous studies have reported increased somatosensory attenuation in elderly people,
14 proposing an overreliance on sensorimotor predictions to compensate for age-related declines
15 in somatosensory perception; however, recent results have challenged this relationship. In a
16 preregistered study, we used a force-discrimination task to assess whether aging increases
17 somatosensory attenuation and whether this increase is explained by decreased somatosensory
18 precision in elderly individuals. Although we observed significant somatosensory attenuation
19 in 94% of our sample (n = 108, 21–77 years old) regardless of age, we did not find a significant
20 increase in somatosensory attenuation in our elderly participants (65–77 years old) unless we
21 included only the oldest subset (69–77 years old). Moreover, we did not observe a significant
22 age-related decline in somatosensory precision or a significant relationship of age with
23 somatosensory attenuation. Together, our results suggest that aging exerts a limited influence
24 on the perception of self-generated and externally generated touch and prompt reconsideration
25 of the proposed direct relationship between somatosensory precision and attenuation in elderly
26 individuals.

27 Keywords

28 aging; somatosensory attenuation; somatosensory precision; sensorimotor predictions; forward
29 model

30 New and Noteworthy

31 Self-generated touch is attenuated compared to externally generated touch of identical
32 intensity. This somatosensory attenuation has been previously shown to be increased in elderly
33 participants, but it remains unclear whether it is related to age-related somatosensory decline.
34 In our preregistered study, we observed increased somatosensory attenuation in the oldest
35 subset of participants (≥ 69 years), but we found no evidence of an age-related decline in
36 somatosensory function or a relationship of age with somatosensory attenuation. We propose

37 that aging exerts a limited influence on the perception of self-generated and externally
38 generated touch.

39 Introduction

40 Aging is associated with widespread brain changes (Raz et al. 2005; Zhao et al. 2019; Ziegler
41 et al. 2012) that affect both motor (Michely et al. 2018; Solesio-Jofre et al. 2014; Wang et al.
42 2019; Zapparoli et al. 2022) and somatosensory systems (Brodoehl et al. 2013; Hagiwara et al.
43 2014; McIntyre et al. 2021; Wickremaratchi and Llewelyn 2006). In terms of motor
44 performance, previous research has found that aging impairs the execution of voluntary
45 movements (such as grasping), manual dexterity (such as grip force magnitude) (Diermayr et
46 al. 2011), balance (L. Sturnieks et al. 2008), and motor learning (Koenraad Vandevoorde and
47 Orban De Xivry 2020; Vandevoorde and Orban de Xivry 2019; Wolpe et al. 2020). In addition,
48 aging was shown to negatively influence somatosensory functioning, with multiple studies
49 reporting an age-related decline (Bowden and McNulty 2013; Deflorio et al. 2022; Gescheider
50 et al. 1994).

51 Motor control is largely dependent on the integration of motor signals with somatosensory
52 information. A classic phenomenon related to this sensorimotor integration is somatosensory
53 attenuation, which refers to perceiving touches that are produced by our own (voluntary)
54 movements as less intense than touches of the same physical intensity that are externally
55 generated (Bays and Wolpert 2008; Blakemore et al. 2000b; Kilteni 2023). For example,
56 behavioral studies have shown that self-generated strokes, forces and taps applied to our left
57 hand by our right hand are perceived as weaker than the same touches applied to our left hand
58 by another person or a machine (Asimakidou et al. 2022; Bays et al. 2005, 2006; Blakemore et
59 al. 1999a; Job and Kilteni 2023; Kilteni et al. 2018, 2019, 2020, 2021; Kilteni and Ehrsson
60 2017a, 2017b, 2020, 2022; Shergill et al. 2003). Similarly, neuroimaging studies have shown
61 that self-generated touches elicit reduced activity in the primary (Hesse et al. 2010; Kilteni et
62 al. 2022) and secondary somatosensory cortices (Blakemore et al. 1998; Kilteni and Ehrsson
63 2020; Shergill et al. 2013) as well as in the cerebellum (Blakemore et al. 1999b; Kilteni and
64 Ehrsson 2020) compared to externally generated touches of identical intensity. Somatosensory
65 attenuation is considered to facilitate differentiation between self-generated and externally
66 generated sensations (Frith 2012) and to contribute to establishing and maintaining our sense
67 of self by allowing us to separate our actions from those of others (Corlett et al. 2019; Frith
68 2005a). Furthermore, it is considered one of the reasons that humans are unable to tickle
69 ourselves (Blakemore et al. 2000b; Weiskrantz et al. 1971).

70 Computational motor control theories posit that somatosensory attenuation arises from the
71 brain's predictions about the sensory consequences of our movements. Accordingly, during a
72 voluntary movement, the brain uses an internal forward model together with a copy of the
73 motor command ("efference copy") to predict the sensory feedback of the movement (Franklin
74 and Wolpert 2011; McNamee and Wolpert 2019; Wolpert and Flanagan 2001). These
75 predictions allow the brain to estimate the expected sensory feedback without relying on the
76 actual sensory feedback, which suffers from intrinsic delays (Bays and Wolpert 2008;
77 Davidson and Wolpert 2005; Franklin and Wolpert 2011; Kawato 1999; Shadmehr and
78 Krakauer 2008), and to integrate it with the received sensory signals to improve the estimation
79 of the state of the body (Shadmehr and Krakauer 2008). Action prediction signals also serve to
80 attenuate the expected self-generated sensations (Bays et al. 2006; Job and Kilteni 2023),
81 thereby increasing the salience and prioritizing the processing of unexpected externally

82 generated sensations that might be more behaviorally relevant (Bays and Wolpert 2008;
83 Blakemore et al. 2000b; Shergill et al. 2003; Wolpert and Flanagan 2001). Within a Bayesian
84 integration framework, somatosensory attenuation relies on the integration of the forward
85 model's predictions and the somatosensory information, with both sources of information
86 weighted based on their relative reliability (Ernst and Banks 2002; Körding et al. 2004).
87 Interestingly, alterations in this integration of predictions and sensory information have been
88 reported in several clinical and neurobiological models of psychosis spectrum disorders, such
89 as schizophrenia (Blakemore et al. 2000a, 2002; Corlett et al. 2019; Frith 2005b, 2012; Frith et
90 al. 2000; Shergill et al. 2005, 2014) and schizotypy (Asimakidou et al. 2022), as well as
91 functional movement disorders (Pareés et al. 2014) and Parkinson's disease (Wolpe et al.
92 2018).

93 Aberrant somatosensory attenuation has also been reported in elderly participants compared to
94 young participants in two different studies (Parthasharathy et al. 2022; Wolpe et al. 2016).
95 Specifically, when asked to match externally generated forces applied to their finger with self-
96 produced forces, Wolpe et al. (2016) observed that older adults (65–88 years old) applied
97 stronger self-produced forces than younger adults (18–39 years old), suggesting a greater
98 attenuation of self-generated sensations with aging. Additionally, older adults were less precise
99 than younger adults in distinguishing the different forces, indicating a negative impact of age
100 on somatosensory perception; the decreased force sensitivity was proportional to their
101 increased attenuation. Based on these findings, the authors interpreted increased somatosensory
102 attenuation in elderly individuals as decreased reliance on somatosensory information due to
103 age-related reductions in somatosensory precision that, in turn, result in an increased reliance
104 on sensorimotor predictions (consistent with Bayesian integration). On the other
105 hand, Parthasharathy and colleagues (2022), using the same task but with the arm instead of
106 the hand, also reported increased somatosensory attenuation in older adults (55–75 years old)
107 compared to young adults (18–35 years old), similar to Wolpe et al. (2016), but found no
108 evidence of decreased somatosensory precision in older adults, suggesting that somatosensory
109 attenuation and precision might not be as closely related as previously suggested.

110 Here, we reinvestigated the role of aging in somatosensory attenuation and its relationship with
111 somatosensory precision across a wide age range (21–77 years). Specifically, we tested
112 whether a decline in somatosensory precision explains the effects of increased somatosensory
113 attenuation with aging, as proposed by Wolpe et al. (2016), or if the two are unrelated, as
114 suggested by Parthasarathy et al.(2022). The two previous studies used the force-matching task
115 (Shergill et al. 2003) to quantify somatosensory attenuation, in which the participants receive
116 an externally generated force on their relaxed left index finger by a motor and are subsequently
117 asked to match this reference force. In the control condition, participants match the reference
118 force by moving a joystick or slider that indirectly controls the force applied by the motor on
119 their finger (slider condition). Several behavioral studies have shown that in this condition,
120 participants precisely match the required forces, thus showing accurate somatosensory
121 perception(Kilteni and Ehrsson 2017a, 2017b; Kilteni and Henrik Ehrsson 2020; Shergill et al.
122 2003; Wolpe et al. 2016). In contrast, in the experimental condition, when participants matched
123 the reference force by directly pressing with their right index finger against their left one via a
124 force sensor (direct condition), they overestimated the required forces and systematically

125 produced stronger forces (Kilteni and Henrik Ehrsson 2020; Shergill et al. 2003; Wolpe et al.
126 2016). This suggests that participants attenuate their (directly) self-generated forces based on
127 motor commands and increase the strength of self-produced forces to compensate for this
128 somatosensory attenuation.

129 In the present study, we chose not to include the force-matching task and instead used the force-
130 discrimination task, a well-established psychophysical test that has been previously used to
131 assess somatosensory attenuation (Asimakidou et al. 2022; Bays et al. 2005, 2006; Job and
132 Kilteni 2023; Kilteni 2023; Kilteni et al. 2019, 2020, 2021, 2022; Kilteni and Ehrsson 2022).
133 In the force-discrimination task, participants receive two forces on their finger and are asked
134 to indicate which force felt stronger. We chose the force-discrimination task instead of the
135 force-matching task for three reasons. First, in contrast to the direct and slider conditions of the
136 force-matching task, which require participants to move, the force-discrimination task allows
137 a more accurate quantification of the perception of self-generated and externally generated
138 forces because it includes a control condition of pure externally generated touch in the absence
139 of any movement (no efference copy). Second, the force-discrimination task allows the
140 psychophysical quantification of somatosensory precision for self-generated and externally
141 generated stimuli separately. Third, elderly populations are known to have motor deficits, and
142 their perception in the force-matching task is assessed with a motor response (*i.e.*, pressing to
143 match a particular force or operating a joystick). Thus, another advantage of the force-
144 discrimination task is that the perceptual report (*i.e.*, indicating which of two forces felt
145 stronger) does not rely on motor abilities to the same extent. Moreover, given that both the
146 force-matching task and the force-discrimination task involve the use of working memory to
147 remember the forces to match (force-matching task) or judge them (force-discrimination task),
148 we additionally assessed tactile working memory in our study for the first time to rule out the
149 possibility that the increased somatosensory attenuation observed in older adults in the two
150 previous studies was simply due to a decline in their tactile working memory.

151 **Materials and Methods**

152 **Preregistration**

153 The methods, hypotheses and analyses of the study were preregistered (<https://osf.io/8u7by>).
154 All analyses included in the preregistration are indicated as “*preregistered analyses*” in the
155 Results section. Any additional analyses that were not included in the preregistration are clearly
156 indicated in the manuscript as “*supplementary analyses*” in the Results section.

157 **Participants**

158 Data from one hundred and eight (108) participants were included in the present study. These
159 participants were divided into the *young* (n = 36, age: range = 21–33; mean ± SD = 26 ± 3.85
160 years; 30 right-handed, 4 left-handed, 2 ambidextrous), *middle-aged* (n = 36, age: range = 43–
161 56; mean ± SD = 48.6 ± 3.77 years; 30 right-handed, 3 left-handed, 3 ambidextrous) and *elderly*
162 groups (n = 36, age: range = 65–77 years; mean ± SD = 69.6 ± 3.59 years; 35 right-handed, 1
163 left-handed). Each age group had a balanced sex ratio, consisting of 18 female and 18 male
164 subjects. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield 1971).
165 The sample size was based on a previous study assessing somatosensory attenuation and
166 precision across similar age groups (Parthasharathy et al. 2022). All participants reported
167 having normal or corrected-to-normal visual acuity, were healthy (without current or previous
168 neurological or psychiatric disorders) and were not taking any medication to treat such
169 conditions.

170 All participants provided written informed consent. The study lasted approximately 60 minutes
171 and was approved by the Swedish Ethical Review Authority (application 2020-03186,
172 amendment 2021-06235).

173 **Screening methods and exclusion criteria**

174 *Cognitive function*

175 All elderly participants were tested for mild cognitive impairment, defined as greater cognitive
176 impairment than is expected for one's age. We used the Montreal Cognitive Assessment
177 (MoCA version 8.3) (Nasreddine et al. 2005), which assesses cognitive function in several
178 domains, including attention/working memory, executive function, episodic memory,
179 language, and visuospatial skills; this assessment has been validated for use with individuals
180 between 55 and 85 years old (Nasreddine et al. 2005). In the present study, the MoCA was used
181 to screen elderly participants and ensure that they could understand and follow experimental
182 instructions. Scoring of each individual and correction for low education level were performed
183 according to the instructions. The test was conducted in the native language of the participant
184 by a certified experimenter who completed the necessary training to carry out and score the test
185 (<https://www.mocatest.org/training-certification/>). Following the standard cutoff score used,
186 we included only elderly individuals with a MoCA score of 26 or higher.

187 *Tactile working memory*

188 All participants were assessed for tactile working memory (WM) to ensure that they could
189 reliably remember at least two brief forces applied to their fingers in a short period of time, as
190 required by the force-discrimination task (see below). We used the working memory task
191 introduced and described by Heled et al. (2021). During the task, the participants comfortably
192 sat in a chair with their eyes closed and placed four fingers of each hand on the upper row of a
193 QWERTY keyboard (right hand fingers on ‘Q’, ‘W’, ‘E’, ‘R’ keys and left hand fingers on
194 ‘U’, ‘I’, ‘O’, ‘P’ keys). Next, the experimenter lightly touched the participant’s fingers,
195 between the second and third knuckle, with the back of a pencil for one second each, in a
196 specific sequence. Participants were then asked to repeat the sequence back, in the same order
197 as it was presented, by pushing down on the keys with the fingers that had been touched
198 (**Supplementary Figure S1**). One elderly participant had difficulties with the keyboard, and
199 he provided the answers verbally by naming the fingers instead of tapping on the keys. The test
200 started with three 2-finger sequence trials. If at least one of the three sequences was correctly
201 reproduced, then the next sequence was increased in length by one, up to sequences 9 fingers
202 in length. Each sequence length included three trials: one trial on the left hand only, one on the
203 right hand only, and one on both hands. The task ended if participant made three consecutive
204 mistakes within the same sequence length or when the ninth sequence was successfully
205 recalled. We calculated the longest sequence that the participant could recall without a mistake
206 (*longest sequence recalled*; score range: 0–9) and the number of correct answers given
207 (*maximum WM score*; score range: 0–24). We included individuals who could recall sequences
208 of at least two fingers (*longest sequence recalled* ≥ 2), given that the force-discrimination task
209 included two tactile stimuli.

210 *Exclusion of participants*

211 In total, eighteen (18) participants were excluded: fifteen elderly participants who did not reach
212 the MoCA cutoff score, one middle-aged participant who could not perform the working
213 memory task, one middle-aged participant who experienced technical issues, and finally, one
214 middle-aged participant who revealed that they took medication after being tested. These
215 excluded individuals were replaced by an equal number of new participants to reach the target
216 sample size (108).

217 **Psychophysical task**

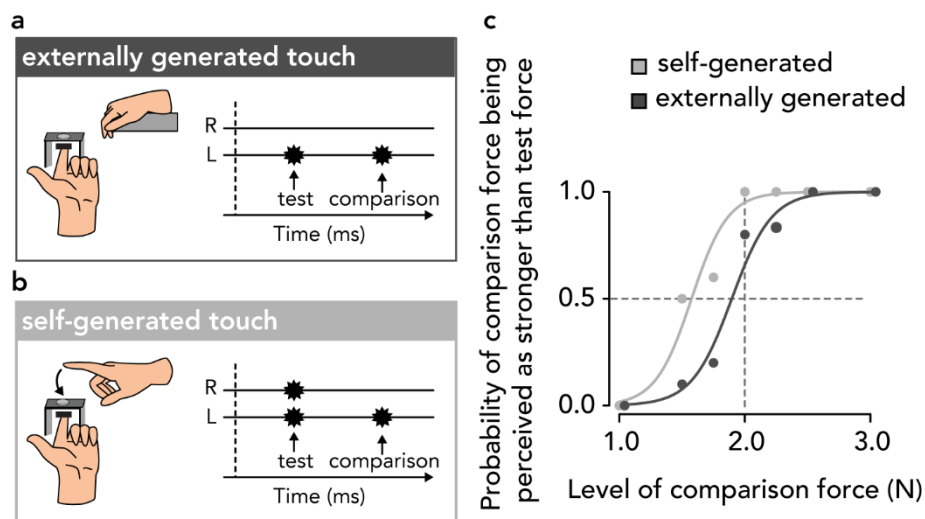
218 The psychophysical task was a two-alternative forced choice (2AFC) force-discrimination task
219 that has been used by numerous studies investigating somatosensory attenuation (Asimakidou
220 et al. 2022; Bays et al. 2005, 2006; Job and Kilteni 2023; Kilteni 2023; Kilteni et al. 2020,
221 2021, 2022; Kilteni and Ehrsson 2022).

222 Participants rested their left hands palm up with their index fingers on a molded support and
223 their right hands palm down on top of a set of sponges. A vacuum pillow (Germa protec, AB
224 Germa) was provided to support the participants’ left arm and increase their comfort. Every
225 trial started with an auditory tone. Next, a DC electric motor (Maxon EC Motor EC 90 flat;
226 manufactured in Switzerland) delivered two brief (100-ms) forces to the pulp of participants’
227 left index finger through a cylindrical probe (25 mm in height) with a flat aluminum surface

228 (20 mm in diameter) attached to the motor's lever. Participants then verbally indicated which
229 force felt stronger, the first (*test* force) or the second (*comparison* force). The interstimulus
230 interval varied randomly between 500 ms and 800 ms. The intensity of the *test* force was set to
231 2 N, while the *comparison* force pseudorandomly varied among seven possible intensities (1,
232 1.5, 1.75, 2, 2.25, 2.5, or 3 N). A force sensor (FSG15N1A, Honeywell Inc.; diameter, 5 mm;
233 minimum resolution, 0.01 N; response time, 1 ms; measurement range, 0–15 N) was placed
234 within the cylindrical probe to record the forces exerted on the left index finger. A force of 0.1
235 N was constantly applied to the participant's left index finger to ensure accurate force
236 intensities.

237 There were two experimental conditions. In the *externally generated touch* condition (**Figure**
238 **1a**), the participants relaxed both their hands, and the *test* force was delivered automatically
239 800 ms after the auditory tone. In the *self-generated touch* condition (**Figure 1b**), the
240 participants were instructed to tap with their right index finger on a force sensor (identical
241 specifications as above) placed on top of, but not in contact with, their left index finger. The
242 participants' tap on the force sensor triggered the *test* force on their left index finger. Each
243 condition consisted of 70 trials; all seven intensities of the *comparison* force were presented
244 ten times (7×10) per condition, resulting in a total of 140 trials per participant. The order of the
245 intensities was pseudorandomized, and the order of the conditions was counterbalanced across
246 participants.

247 White noise was played through a pair of headphones to mask any sounds made by the motor.
248 During the experiment, the participants' left index finger was occluded from vision, and they
249 were asked to focus on a fixation cross placed on the wall approximately 80 cm in front of
250 them.



252 **Figure 1. The force-discrimination task.** In both conditions, the participants experienced two
253 forces on the pulp of their left index finger, the *test* force and the *comparison* force, and verbally
254 indicated which force felt stronger. **(a)** In the *externally generated touch* condition, the
255 participants relaxed both their hands and received the *test* and the *comparison* forces
256 automatically on the pulp of their left index finger. **(b)** In the *self-generated touch* condition,
257 the participants triggered the *test* force on the left index finger by actively tapping on a force

258 sensor with their right index finger placed above their left finger. Next, they received the
259 *comparison* force. (c) Responses and fitted logistic models of the responses of one participant
260 in the two experimental conditions. The leftward shift of the light gray curve with respect to
261 the dark gray one indicates that the *test* force in the *self-generated touch* condition felt weaker
262 compared to that in the *externally generated touch* condition.

263 Psychophysical fit

264 In each condition, the participant's responses were fitted with a generalized linear model using
265 a *logit* link function (Figure 1c) (Equation 1):

266

$$267 \quad p = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}} \text{ (Equation 1)}$$

268 Two parameters of interest were extracted. First, the point of subjective equality ($PSE = -\frac{\beta_0}{\beta_1}$)
269 represents the intensity at which the *test* force felt as strong as the *comparison* force ($p = 0.5$)
270 and thus quantifies the participants' perceived intensity of the *test* force. Subsequently,
271 somatosensory attenuation was calculated as the difference between the PSEs of the *externally*
272 *generated* and *self-generated* touch conditions ($PSE_{external} - PSE_{self}$) (Asimakidou et al. 2022;
273 Job and Kilteni 2023; Kilteni et al. 2020, 2022; Kilteni and Ehrsson 2022). Second, the *just*
274 *noticeable difference* ($JND = \frac{\log(3)}{\beta_1}$) reflects the participants' sensitivity in the psychophysical
275 task and thus quantifies their somatosensory precision in each condition, corresponding to the
276 difference between the thresholds at $p = 0.5$ and $p = 0.75$.

277

278 Before fitting the responses, the *comparison* forces were binned to the nearest of the seven
279 possible force intensities (1, 1.5, 1.75, 2, 2.25, 2.5, or 3 N). After the data collection, 60 out of
280 15120 (0.4%) trials were rejected: 42 trials (0.28%) were rejected because the intensity of the
281 *test* force (2 N) was not applied accurately (*test* force < 1.85 N or *test* force > 2.15 N), and 18
282 trials (0.12%) were rejected because there were missing responses.

283 Additional measures

284 As secondary variables, we further recorded (a) the peak active forces the participants applied
285 to the force sensor with their right index finger (*peak force*), (b) the time it took for the
286 participants to reach the peak force after the beginning of the trial (*time to peak force*), and (c)
287 the movements of their right index finger as registered using a Micro Sensor 1.8 attached to a
288 Polhemus Liberty electromagnetic tracker (<https://polhemus.com/motion-tracking/all-trackers/liberty>). If somatosensory attenuation is increased in *elderly* participants compared to
289 *younger* participants, as we expected, these additional measures could be used to explore the
290 relationships of age with forces, timing, and kinematics together with attenuation. Due to
291 technical reasons, the movements of the right index finger were not correctly registered; thus,
292 supplementary analyses were performed with only the active peak forces and their times.

294 Hypotheses

295 We tested four preregistered experimental hypotheses using the collected data. First, we
296 expected to replicate the classic somatosensory attenuation phenomenon in our sample by
297 finding that the PSEs in the *self-generated touch* condition were significantly lower than the
298 PSEs in the *externally generated touch* condition, regardless of age group (H1). Second, given
299 earlier studies reporting a decline in somatosensory functioning (Bowden and McNulty 2013;
300 Deflorio et al. 2022; Gescheider et al. 1994; Humes et al. 2009; Stevens and Cruz 1996) and a
301 reduction in the density of cutaneous mechanoreceptors with age (García-Piqueras et al. 2019)
302 (see also (Lin et al. 2004)), we hypothesized that JND values in the *externally generated touch*
303 condition (*i.e.*, $JND_{external}$) would be significantly higher in *elderly* participants than in *young*
304 and *middle-aged* participants (H2). Third, given the two previous studies reporting increased
305 attenuation in older participants (Parthasharathy et al. 2022; Wolpe et al. 2016), we expected
306 to find increased somatosensory attenuation in *elderly* participants compared with *younger*
307 participants (H3). Finally, we assessed the proposal of Wolpe et al. (2016) that decreased
308 somatosensory precision drives the increased attenuation in *elderly* participants by testing
309 whether somatosensory precision is a significant positive predictor of somatosensory
310 attenuation (H4).

311 **Statistical analysis**

312 Data were analyzed in R (version 4.2.0) (R Core Team 2022) and JASP (version 0.16.4) (JASP
313 Team 2022). The normality of the data was assessed with the Shapiro–Wilk test. Planned
314 comparisons were performed using parametric (paired or independent-sample t tests) or
315 nonparametric (Wilcoxon signed-rank and Wilcoxon rank sum) tests depending on the
316 normality of variable distributions. A Welch t test was used if the variances of the compared
317 distributions were unequal according to Levene’s test. For every statistical comparison, we
318 report the corresponding statistic, the 95% confidence intervals (CI^{95}) and the effect size
319 (Cohen’s d or the matched rank-biserial correlation (r_{rb}), depending on the distribution
320 normality). We also performed a Bayesian factor (BF) analysis (default Cauchy priors with a
321 scale of 0.707) for the statistical tests of interest reporting nonsignificant differences to provide
322 information about the level of support for the null hypothesis compared to the alternative
323 hypothesis. Spearman correlation coefficients were calculated for nonnormally distributed
324 data. Finally, for regression analysis, a robust linear regression was performed to reduce the
325 impact of outlier observations.

326
327 Our four preregistered hypotheses were directional (<https://osf.io/8u7by>); thus, all statistical
328 comparisons concerning these hypotheses were one-tailed. All other comparisons concerning
329 secondary variables or variables for which we did not have a specific hypothesis were two-
330 tailed. For every statistical test, we clearly report whether the performed test was one-tailed or
331 two-tailed. However, the main results remained the same regardless of whether we performed
332 one-tailed or two-tailed tests. Finally, regarding multiple comparisons among the three age
333 groups, we corrected the p values using the false discovery rate (FDR). Corrected p values are
334 thus denoted as “ FDR -corrected” throughout.

335 **Results**

336

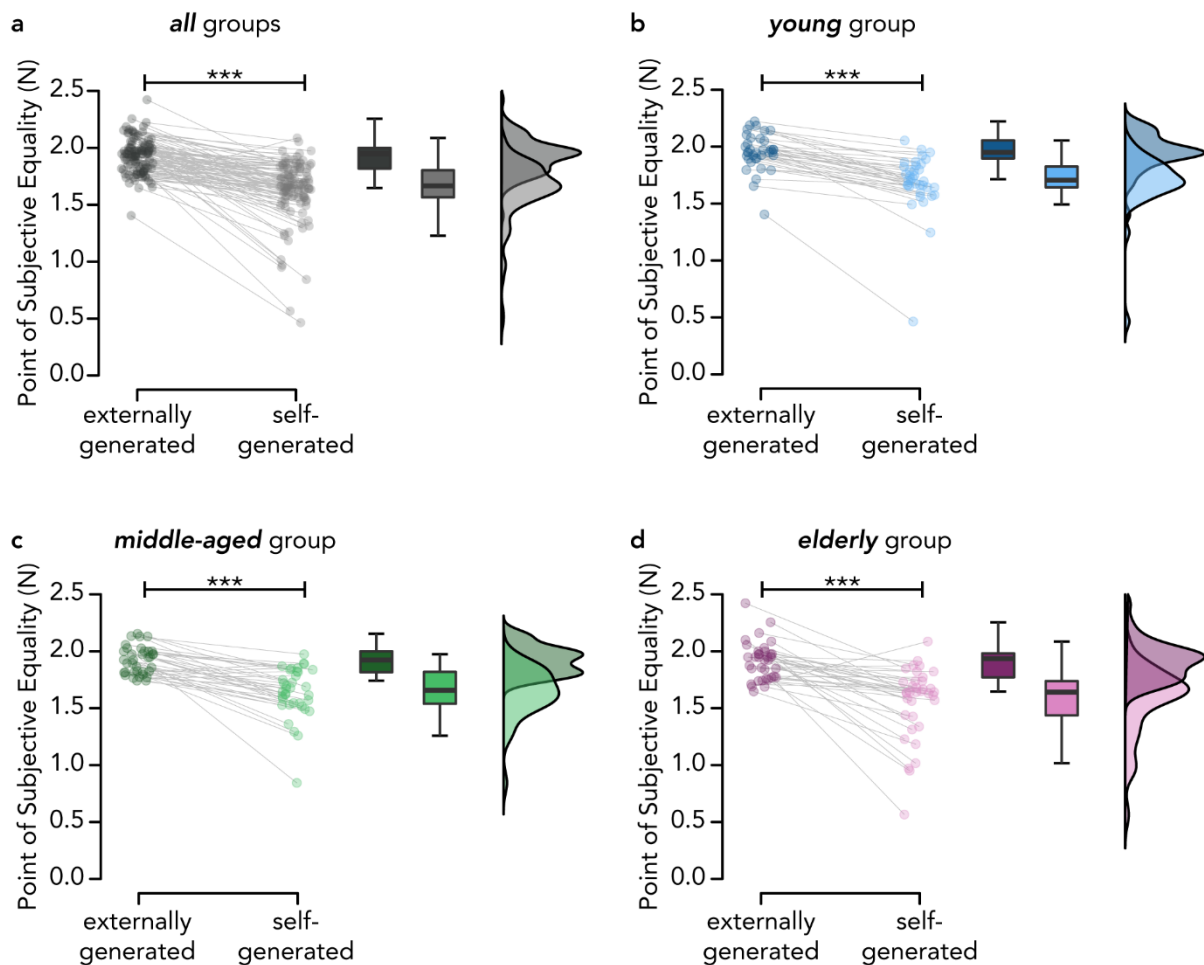
337 As stated in our inclusion criteria, we first ensured that our elderly participants showed no
338 signs of mild cognitive impairment and that all participants could retain at least two tactile
339 stimuli applied to their fingers in their working memory (**Supplementary Text S1, Figure**
340 **S2**).

341 ***Somatosensory attenuation – preregistered analysis***

342 Our first hypothesis was that PSEs in the *self-generated touch* condition would be
343 significantly lower than the PSEs in the *externally generated touch* condition, regardless of
344 age group. Supporting our first hypothesis (H1), the PSEs in the *self-generated touch*
345 condition were significantly lower than those in the *externally generated touch* condition
346 across the entire sample ($n = 108$): Wilcoxon sign-rank test, $W = 112$, $p < .001$, $CI^{95} = [-\infty, -$
347 $0.231]$, $r_{rb} = -0.962$, one-tailed (**Figure 2a, Supplementary Figures S3-S5**). This pattern was
348 observed in 102 out of 108 (94%) participants and indicates that self-generated forces are
349 robustly attenuated compared to externally generated forces of equal intensity, in line with
350 several previous studies (Asimakidou et al. 2022; Bays et al. 2005, 2006; Kilteni et al. 2019,
351 2020, 2021, 2022; Kilteni and Ehrsson 2022).

352 ***Somatosensory attenuation – supplementary analysis***

353 Additional supplementary analyses showed that the attenuation effect was observed in every
354 age group: PSEs in the *self-generated touch* condition were significantly lower than those in
355 the *externally generated touch* condition within the *young* ($W = 0$, $p < .001$, $CI^{95} = [-\infty, -0.2]$,
356 $r_{rb} = -1.0$, one-tailed) (**Figure 2b**), *middle-aged* ($W = 10$, $p < .001$, $CI^{95} = [-\infty, -0.205]$, $r_{rb} = -$
357 0.97 , one-tailed) (**Figure 2c**) and *elderly* groups ($W = 26$, $p < .001$, $CI^{95} = [-\infty, -0.225]$, $r_{rb} = -$
358 0.922 , one-tailed) (**Figure 2d**).



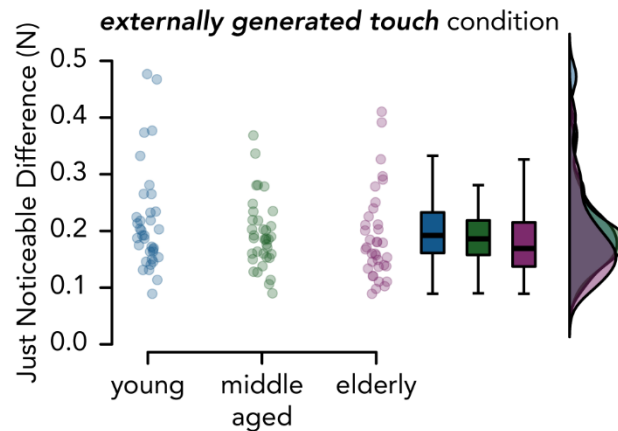
359

360 **Figure 2. Somatosensory attenuation across age groups.** (a) Across all age groups (pooled
 361 data; $n = 108$), self-generated touches were perceived as significantly weaker than externally
 362 generated touches of identical intensity. The same effect was found separately for the *young*
 363 (b), *middle-aged* (c), and *elderly* groups (d) ($n = 36$ for each group). The boxplots display the
 364 median and interquartile ranges of the PSEs in the *externally generated* and *self-generated*
 365 *touch* conditions per age group. Markers denote the PSE values for each participant, and
 366 raincloud plots show the distribution of the data. Line plots illustrate the PSE differences
 367 between the *externally generated* and *self-generated touch* conditions for each participant (***)
 368 $p < .001$).

369 ***Ageing and somatosensory precision – preregistered analysis***

370 Second, we hypothesized that JND values in the *externally generated touch* condition (*i.e.*,
 371 $JND_{external}$) would be significantly higher for *elderly* participants than for *young* and *middle-*
 372 *aged* participants. Contrary to our hypothesis (H2), we did not find an increase in the JND
 373 values in the *elderly* group compared to the *young group* ($W = 514$, *FDR*-corrected $p = 0.935$,
 374 $CI^{95} = [-0.048, \infty]$, $r_{rb} = -0.207$, one-tailed) group. The Bayesian analysis provided moderate
 375 evidence of an absence of impairment in somatosensory precision between the *elderly* and
 376 *young* groups ($BF_{0+} = 9.351$). No differences were observed between the *elderly* and *middle-*
 377 *aged* groups ($W = 564$, *FDR*-corrected $p = 0.935$, $CI^{95} = [-0.035, \infty]$, $r_{rb} = -0.130$, one-tailed)
 378 and the Bayesian analysis again provided moderate support for the absence of difference (BF_{0+}

379 = 6.665). Finally, the JND values of the *middle-aged* group did not significantly differ from
380 those of the *young* group ($W = 581.5$, FDR -corrected $p = 0.935$, $CI^{95} = [-0.033, \infty]$, $r_{rb} = -0.103$,
381 $BF_{0+} = 7.245$, one-tailed) (**Figure 3**).



382

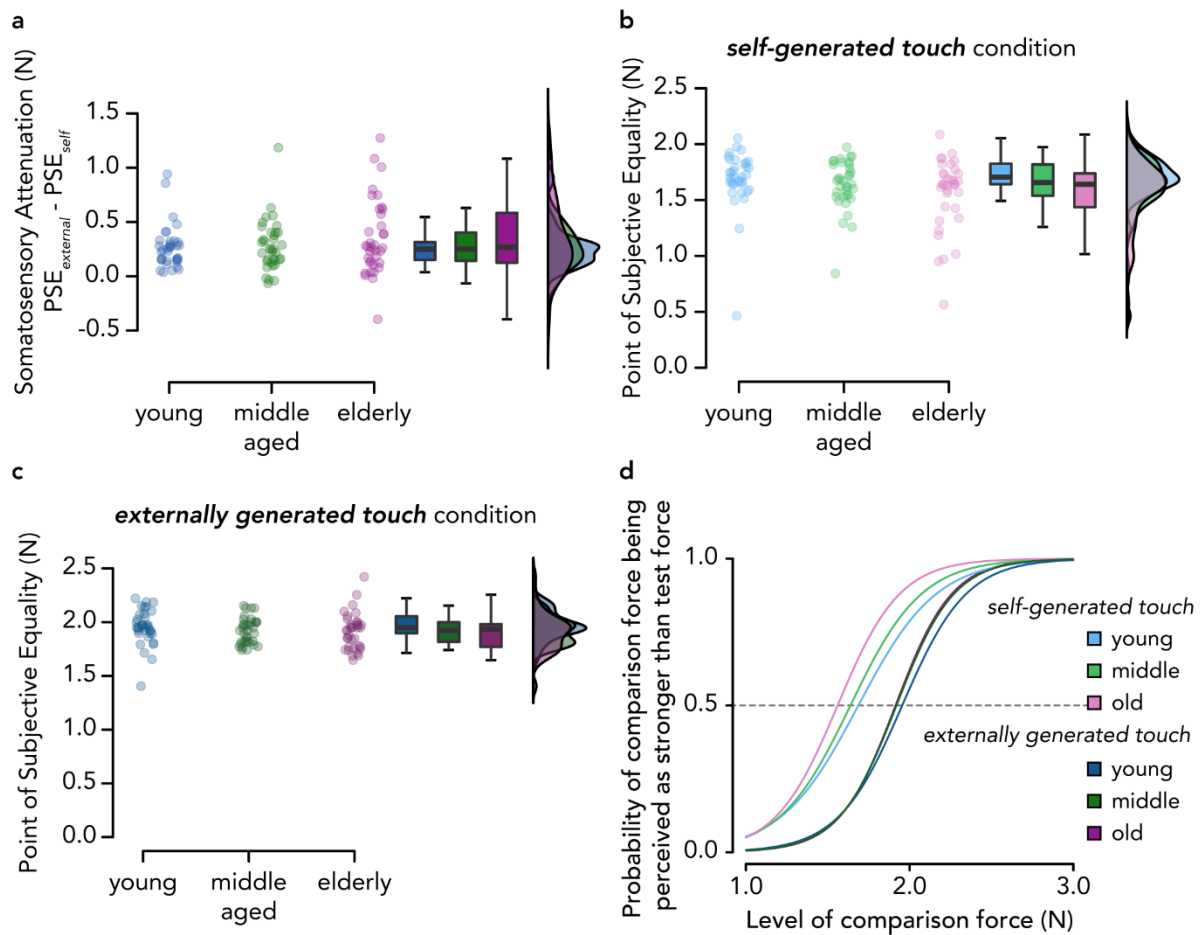
383 **Figure 3. Somatosensory precision across age groups.** JND values in the *externally*
384 *generated touch* condition across the three age groups. There were no significant differences
385 among the three groups, and the Bayesian analyses supported the absence of differences. The
386 boxplots display the median and interquartile ranges, and the dots represent the individual
387 participant values. Raincloud plots show the distribution of the data.

388 *Aging and somatosensory precision – supplementary analysis*

389 In a non-preregistered (supplementary) post hoc analysis, we explored whether somatosensory
390 impairment was more pronounced in the oldest of our *elderly* participants. To this end, we
391 performed the same analysis as above, but we split the *elderly* group (65–77 years of age) at
392 its median age and compared the oldest *elderly* 69+ participants ($n = 18$, $age = 69–77$ years)
393 to the *young* group. Once again, we did not detect any somatosensory impairment in the *elderly*
394 69+ participants compared to the *young* participants ($W = 220$, $p = 0.973$, $CI^{95} = [-0.059, \infty]$,
395 $r_{rb} = -0.321$, one-tailed, $BF_{0+} = 7.874$) (**Supplementary Figure S6**). If anything, the pattern
396 suggested similar if not better somatosensory precision in the *elderly* 69+ participants
397 compared to the *young* participants.

398 *Aging and somatosensory attenuation – preregistered analysis*

399 To test our third hypothesis, we examined whether the magnitude of somatosensory attenuation
400 was greater in the *elderly* group than in the other two groups, as previously shown
401 (Parthasharathy et al. 2022; Wolpe et al. 2016). Contrary to our hypothesis (H3), we did not
402 observe any significant increase in the magnitude of somatosensory attenuation between the
403 *elderly* group and the *young* group ($W = 710$, FDR -corrected $p = 0.368$, $CI^{95} = [-0.037, \infty]$, r_{rb}
404 $= 0.096$, one-tailed) or the *middle-aged* group ($W = 712$, $p = FDR$ -corrected 0.368, $CI^{95} = [-$
405 $0.057, \infty]$, $r_{rb} = 0.099$, one-tailed), nor between the *middle-aged* and *young* groups ($W = 673$,
406 FDR -corrected $p = 0.392$, $CI^{95} = [-0.057, \infty]$, $r_{rb} = 0.039$, one-tailed) (**Figure 4a**). The Bayesian
407 analysis provided weak/moderate evidence of a similar magnitude of attenuation across all
408 three age groups (*elderly* compared to *young*: $BF_{0+} = 2.716$; *elderly* compared to *middle-aged*:
409 $BF_{0+} = 2.072$; *middle-aged* compared to *young*: $BF_{0+} = 3.896$).



410

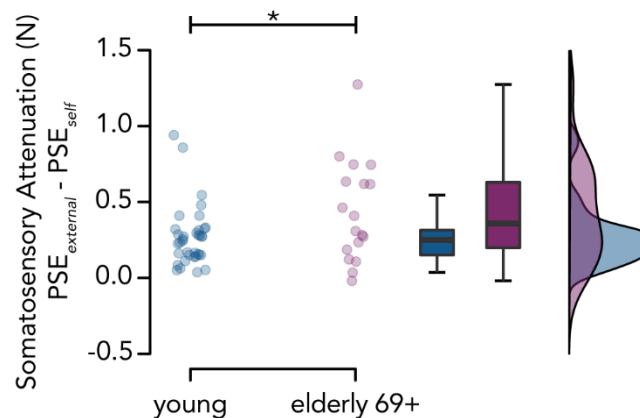
411 **Figure 4. Somatosensory attenuation across age groups.** (a) Somatosensory attenuation
 412 ($PSE_{external} - PSE_{self}$) across the three age groups. No significant increase in somatosensory
 413 attenuation was observed in the *elderly* group compared to the *middle-aged* and *young* groups
 414 or between the *middle-aged* group and the *young* group. (b-c) The *elderly* group perceived their
 415 self-generated touches as significantly weaker than the *young* group (b), but a similar trend was
 416 observed for externally generated touches (c), indicating weaker somatosensory perception in
 417 elderly participants in general. (d) Mean psychometric curves for each age group and
 418 experimental condition according to the mean PSE and JND values. A leftward shift of the
 419 curve in the *self-generated touch* condition compared to the *externally generated touch*
 420 condition indicates somatosensory attenuation. The curves for the *externally generated touch*
 421 condition overlap for the *middle-aged* and *elderly* participants.

422 *Aging and somatosensory attenuation – supplementary analyses*

423 First, to further explore this absence of increased attenuation in the *elderly* participants, we
 424 performed two additional non-preregistered analyses to test whether the participants'
 425 perception differed in the *self-generated* and *externally generated touch* conditions within each
 426 age group. As seen in the boxplots of **Figure 4b-c** and the group model fits in **Figure 4d**, the
 427 PSEs in both the *self-generated touch* and *externally generated touch* conditions decreased as
 428 a function of aging, which could effectively explain why we did not observe significant changes
 429 in the magnitude of somatosensory attenuation (*i.e.*, no PSE difference between the two
 430 conditions).

431 However, there were no significant differences among groups in either the *self-generated touch*
432 condition (*elderly* vs. *young* group, $W = 456.5$, *FDR-corrected* $p = 0.093$, $CI^{95} = [-0.195, -$
433 $0.007]$, $r_{rb} = -0.296$, $BF_{01} = 0.736$, two-tailed; *elderly* vs. *middle-aged*, $W = 585.5$, *FDR-*
434 *corrected* $p = 0.485$, $CI^{95} = [-0.155, 0.057]$, $r_{rb} = -0.096$, $BF_{01} = 3.161$, two-tailed; *middle-aged*
435 vs. *young*, $W = 527.5$, *FDR-corrected* $p = 0.265$, $CI^{95} = [-0.137, 0.025]$, $r_{rb} = -0.186$, $BF_{01} =$
436 1.788 two-tailed) or the *externally generated touch* condition (*elderly* vs. *young* group, $W =$
437 519 , *FDR-corrected* $p = 0.304$, $CI^{95} = [-0.133, 0.024]$, $r_{rb} = -0.199$, $BF_{01} = 1.995$, two-tailed;
438 *elderly* vs. *middle-aged*, $t(70) = -0.153$, *FDR-corrected* $p = 0.879$, $CI^{95} = [-0.073, 0.063]$, $d = -$
439 0.036 , $BF_{01} = 4.073$, two-tailed; *middle-aged* vs. *young*, $W = 534.5$, *FDR-corrected* $p = 0.304$,
440 $CI^{95} = [-0.122, 0.025]$, $r_{rb} = -0.175$, $BF_{01} = 1.990$, two-tailed).

441 Second, we performed the same non-preregistered post hoc analysis used to test Hypothesis 2
442 for Hypothesis 3 to assess whether increased somatosensory attenuation would be more
443 pronounced in the oldest of our *elderly* participants. As before, we split the elderly group (age
444 range: 65–77 years) at the median age of our elderly participants, and we compared the *elderly*
445 69+ participants ($n = 18$, age = 69–77 years) to the *young* group. Indeed, we observed that
446 somatosensory attenuation was significantly higher in the *elderly 69+* group than in the *young*
447 group ($W = 415$, $p = 0.049$, $CI^{95} = [0.001, \infty]$, $r_{rb} = 0.281$, one-tailed) (**Figure 5**).



448

449 **Figure 5. Somatosensory attenuation in young and elderly 69+ participants.** We observed
450 greater somatosensory attenuation in the *elderly 69+* group ($n = 18$) than in the *young* group (n
451 $= 36$).

452 *Somatosensory attenuation, aging, and somatosensory precision – preregistered analysis*

453 Finally, to test our fourth and final hypothesis, we investigated whether the magnitude of
454 somatosensory attenuation is related to the somatosensory precision of externally generated
455 touch by testing whether somatosensory precision is a significant positive predictor of
456 somatosensory attenuation, as previously suggested (Wolpe et al. 2016). To this end, we
457 constructed a robust linear regression model using somatosensory precision as a regressor of
458 somatosensory attenuation as well as age group (*young*, *middle-aged*, *old*) and their interaction.
459 We chose a robust linear regression model rather than a linear regression model to decrease the
460 effect of outliers. None of the regressor coefficients or their interaction were significant (all p
461 values > 0.67 , $R^2 = 0.005$). In line with our above results, somatosensory precision was not a

462 predictor of somatosensory attenuation, and somatosensory precision and age did not exert a
463 joint effect on the degree of somatosensory attenuation.

464 *Additional measures*

465 Finally, there were no significant differences in the magnitude of the active forces the
466 participants applied or in the time it took them to apply the forces among age groups, and there
467 was no significant relationship between these measures and somatosensory attenuation
468 (**Supplementary Text S2, Supplementary Figure S7**).

469 Discussion

470 The present study investigated how aging impacts somatosensory attenuation and
471 somatosensory precision, with the aim of resolving previous contradictory results regarding the
472 underlying mechanisms of age-related changes in somatosensory attenuation (Parthasharathy
473 et al. 2022; Wolpe et al. 2016).

474 Our first analysis replicated the somatosensory attenuation phenomenon across our entire
475 sample. Specifically, the prevalence of somatosensory attenuation was high (94% of the 108
476 participants showed this effect), in line with studies using similar (Asimakidou et al. 2022) or
477 larger sample sizes (Wolpe et al. 2016). The attenuation effect was detected in each individual
478 age group: *young*, *middle-aged*, and *elderly* participants exhibited significant somatosensory
479 attenuation of self-generated forces compared to externally generated forces of the same
480 intensity. These results therefore extend those of earlier studies (Parthasharathy et al. 2022;
481 Wolpe et al. 2016), including the use of the force-discrimination task to psychophysically
482 quantify somatosensory attenuation.

483 Contrary to our hypothesis and to previous evidence showing a decline in somatosensory
484 precision with aging (Bowden and McNulty 2013; Deflorio et al. 2022; Gescheider et al. 1994;
485 Humes et al. 2009; Stevens and Cruz 1996), we did not find that *elderly* participants were worse
486 than *young* participants in discriminating forces. Furthermore, this absence of decline was
487 supported by our Bayesian analysis. Although this result is surprising, several factors could
488 account for this lack of somatosensory decline with aging. First, it could be argued that our
489 psychophysical task (force discrimination) was not sensitive enough to capture potentially
490 small differences in precision among age groups. However, we consider this unlikely since we
491 have previously used this task to detect differences in somatosensory precision (Kilteni and
492 Ehrsson 2022); moreover, as shown in **Figure 3** and **Figure S6**, our *elderly* participants
493 demonstrated (albeit not significantly) better performance than the *young* participants, as also
494 found by Parthasharathy et al. (2022). Second, our participants may not have been old enough
495 to manifest somatosensory deficits. For example, Bowden and McNulty (2013) showed
496 significantly elevated tactile thresholds at the tip of the index finger for only adults above 80
497 years old. Moreover, by combining different tests of somatosensory function, these authors
498 concluded that the decline in cutaneous sensation becomes faster after the age of 60 years in
499 males and 70 years in females. However, we also consider this interpretation unlikely, as we
500 did not observe somatosensory deficits even when comparing the *young* group to the oldest
501 subset of participants from our *elderly* group (individuals ≥ 69 years old), who were
502 predominantly male and thus should have exhibited greater somatosensory deficits. However,
503 in addition to their chronological age, we should mention that all our *elderly* participants were
504 screened to prevent the presence of mild cognitive decline. Since sensorimotor and cognitive
505 deficits are comorbid in older adults, and cognitive decline is linked with deficits in sensory
506 function (Ghisletta and Lindenberger 2005; Li and Lindenberger 2002; Lindenberger and
507 Baltes 1994; Roberts and Allen 2016; Rong et al. 2020), one possibility is that our screened
508 elderly sample was skewed toward individuals with better cognitive and sensory abilities than
509 the elderly samples of previous studies. Relatedly, another possibility is that our older sample
510 might have used remaining intact cognitive processes to compensate for any age-related

511 somatosensory decline and perform at a similar level as younger adults (Roberts and Allen
512 2016).

513 An alternative explanation for the lack of somatosensory deficits with aging could be that
514 somatosensory decline is minimal and/or not always present in elderly participants (Heft and
515 Robinson 2017). It is interesting to note that age-related somatosensory deficits are less
516 systematically reported than visual or auditory deficits (Heft and Robinson 2014, 2017), do not
517 necessarily co-occur with deficits in other sensory modalities (Cavazzana et al. 2018), and can
518 highly depend on the sex of the participants, the stimulation site and assessment method
519 (Bowden and McNulty 2013). In contrast to studies reporting somatosensory decline, other
520 studies report minimal or even no somatosensory changes between young and old participants.
521 For example, in a fine texture-discrimination task, Skedung et al. (2018) reported lower
522 discrimination capacity in the elderly group (aged 67–85 years) than the young group (aged
523 19–25 years), with 13 out of 30 elderly participants (43%) nevertheless performing equally as
524 well as the young participants. Older participants (mean age = 63 years) were shown to have
525 similar haptic thresholds for detection and discrimination as younger participants (mean age =
526 28 years) (Konczak et al. 2012), and chronological age (50–100 years) was not found to
527 significantly correlate with tactile measures (Cavazzana et al. 2018). Additionally, in a pressure
528 sensitivity task, Tremblay et al. (2005) observed that older (60–86 years) participants'
529 sensitivity to minimal pressure was highly functional, even if it was reduced compared to that
530 of younger participants (aged 19–32 years). Similar to our results, Parthasharathy et al. (2022)
531 reported that older participants reproduced the forces more accurately in the slider condition of
532 the force-matching task than young participants. Overall, it could be that somatosensory
533 function shows minimal to small declines with age (Heft and Robinson 2014), similar to
534 proprioception, which shows a small, if nonnegligible, age-related decline (Djajadikarta et al.
535 2020; Herter et al. 2014; Kitchen and Miall 2021; Roberts and Allen 2016).

536 Finally, it is also possible that pressure/force perception in elderly individuals is more resistant
537 to age-related decline than other types of tactile functioning. Interestingly, most of the studies
538 showing large declines in somatosensory sensitivity with aging used texture discrimination,
539 spatial acuity or vibrotactile tasks (Gescheider et al. 1994; Skedung et al. 2018; Stevens and
540 Cruz 1996), but less consistent findings were shown for pressure/force perception
541 (Parthasharathy et al. 2022; Tremblay et al. 2005; Wolpe et al. 2016). This might not be
542 surprising, as different assessments of somatosensory functioning might stimulate distinct
543 classes of mechanoreceptors that may be differentially affected by aging (García-Piqueras et
544 al. 2019).

545 In contrast to our hypothesis, we did not find significantly higher somatosensory attenuation in
546 the elderly group than in the younger groups, as reported by Wolpe et al. (2016) and
547 Parthasharathy (2022). Although, as seen in **Figure 4b**, *elderly* participants tended to perceive
548 their self-generated touches as weaker than younger participants, the same pattern was
549 observed for externally generated touches (**Figure 4c**). We speculate that increased attenuation
550 might be pronounced in the oldest of our participants, as Wolpe et al. (2016) found a sharp
551 increase in attenuation at the higher end of their age group, suggesting a rapid increase in the
552 attenuation of self-generated forces in individuals in their late 70s and 80 years or older, rather

553 than a linear relationship with age. Indeed, when we compared the oldest subset of our elderly
554 participants (aged ≥ 69 years) to the *young* group, we did observe significantly higher
555 attenuation in line with previous studies (Parthasharathy et al. 2022; Wolpe et al. 2016), albeit
556 statistically marginal ($p = 0.049$). Therefore, according to our data and methods, the increase
557 in somatosensory attenuation seems to require older samples than previously suggested.

558 Finally, across our sample, we did not find any significant relationship between somatosensory
559 attenuation and somatosensory precision. This is in agreement with our previous findings
560 reporting no significant relationship between perceived somatosensory precision and
561 somatosensory magnitude (Kilteni and Ehrsson 2022). According to the Bayesian integration
562 framework, the age-related increase in somatosensory attenuation is caused by increased
563 weighting of the internal models' predictions and decreased weighting of sensory information
564 (Wolpe et al. 2016). Given that the internal model is thought to remain intact with aging (Heuer
565 et al. 2011; Vandevorde and Orban de Xivry 2019), somatosensory decline should lead to
566 increased somatosensory attenuation. Since we did not observe any somatosensory decline in
567 our *elderly* participants, we might not have recruited a sample with enough variability to detect
568 such a relationship. Nevertheless, since we showed significantly higher somatosensory
569 attenuation in our oldest participants without concomitant somatosensory declines, our results
570 indicate that somatosensory attenuation and precision might not be strictly linked in elderly
571 individuals, in line with (Parthasharathy et al. 2022) but in contrast to (Wolpe et al. 2016).

572 **Conclusions**

573 Overall, the results of our preregistered study suggest that aging exerts a limited influence on
574 the perception of self-generated and externally generated touch. First, using a force-
575 discrimination task, we observed significant somatosensory attenuation in 94% of our sample,
576 regardless of age, extending previous findings by using different psychophysical measures
577 (Parthasharathy et al. 2022; Wolpe et al. 2016). Second, contrary to the two preceding studies, we
578 did not find increased attenuation in our elderly group (aged 65–77 years); however, we
579 observed this phenomenon when we compared the oldest subset of our elderly group (aged ≥ 69
580 years) to the young group (aged 21–33 years). Hence, our findings suggest that an increase in
581 somatosensory attenuation might be more pronounced in samples older than 70 years. Last, we
582 did not find an age-related decline in somatosensory precision or any indication that such a
583 decline is related to increased somatosensory attenuation. This finding calls into question
584 whether deficits in somatosensory precision play an important role in the age-related increase
585 in somatosensory attenuation, as previously suggested.

586 **Author Contributions**

587 All authors contributed to conceiving and designing the experiment. L.T. collected the data.
588 L.T. and K.K. conducted the statistical analysis. L.T., X.J., K.K. and J.-J.O. wrote the
589 manuscript.

590 **Acknowledgments**

591 Lili Timar, Xavier Job and Konstantina Kilteni were supported by the Swedish Research
592 Council (VR Starting Grant 2019-01909 to K.K.). Experiment costs were covered by the same
593 project.

594 **Disclosures**

595 The authors declare that they have no conflicts of interest, financial or otherwise.

596 **References**

- 597 **Asimakidou E, Job X, Kilteni K.** The positive dimension of schizotypy is associated with a reduced
598 attenuation and precision of self-generated touch. *Schizophrenia* 8, 2022.
- 599 **Bays PM, Flanagan JR, Wolpert DM.** Attenuation of self-generated tactile sensations is predictive,
600 not postdictive. *PLoS Biol* 4: 281–284, 2006.
- 601 **Bays PM, Wolpert DM.** Predictive attenuation in the perception of touch. In: *Sensorimotor*
602 *Foundations of Higher Cognition*, edited by Haggard EP, Rosetti Y, Kawato M. Oxford University
603 Press, 2008, p. 339–358.
- 604 **Bays PM, Wolpert DM, Flanagan JR.** Perception of the consequences of self-action is temporally
605 tuned and event driven. *Current Biology* 15: 1125–1128, 2005.
- 606 **Blakemore S-J, Frith CD, Wolpert DM.** Spatio-Temporal Prediction Modulates the Perception of Self-
607 Produced Stimuli. *J Cogn Neurosci* 551–559, 1999a.
- 608 **Blakemore S-J, Smith " J, Steel R, Johnstone EC, Frith CD.** *The perception of self-produced*
609 *sensory stimuli in patients with auditory hallucinations and passivity experiences : evidence for a*
610 *breakdown in self-monitoring.* 2000a.
- 611 **Blakemore S-J, Wolpert D, Frith C.** Why can't you tickle yourself? *Neuroreport* 11: R11–R16, 2000b.
- 612 **Blakemore S-J, Wolpert DM, Frith CD.** Central cancellation of self-produced tickle sensation. *Nat*
613 *Neurosci* 1: 635–640, 1998.
- 614 **Blakemore S-J, Wolpert DM, Frith CD.** The Cerebellum Contributes to Somatosensory Cortical
615 Activity during Self-Produced Tactile Stimulation. *Neuroimage* 10: 448–459, 1999b.
- 616 **Blakemore S-J, Wolpert DM, Frith CD.** Abnormalities in the awareness of action. *Trends Cogn Sci* 6:
617 237–242, 2002.
- 618 **Bowden JL, McNulty PA.** Age-related changes in cutaneous sensation in the healthy human hand.
619 *Age (Omaha)* 35: 1077–1089, 2013.
- 620 **Brodoehl S, Klingner C, Stieglitz K, Witte OW.** Age-related changes in the somatosensory processing
621 of tactile stimulation-An fMRI study. *Behavioural Brain Research* 238: 259–264, 2013.
- 622 **Cavazzana A, Röhrborn A, Garthus-Niegel S, Larsson M, Hummel T, Croy I.** Sensory-specific
623 impairment among older people. An investigation using both sensory thresholds and subjective
624 measures across the five senses. *PLoS One* 13, 2018.
- 625 **Corlett PR, Horga G, Fletcher PC, Alderson-Day B, Schmack K, Powers AR.** Hallucinations and Strong
626 Priors. *Trends Cogn Sci* 23Elsevier Ltd: 114–127, 2019.
- 627 **Davidson PR, Wolpert DM.** Widespread access to predictive models in the motor system: A short
628 review. *J Neural Eng* 22005.
- 629 **Deflorio D, Di Luca M, Wing AM.** Skin properties and afferent density in the deterioration of tactile
630 spatial acuity with age. *Journal of Physiology* 0: 1–17, 2022.
- 631 **Diermayr G, McIsaac TL, Gordon AM.** Finger force coordination underlying object manipulation in
632 the elderly - A mini-review. *Gerontology* 57: 217–227, 2011.

- 633 **Djajadikarta ZJ, Gandevia SC, Taylor JL.** Age has no effect on ankle proprioception when movement
634 history is controlled. *J Appl Physiol* 128: 1365–1372, 2020.
- 635 **Ernst MO, Banks MS.** Humans integrate visual and haptic information in a statistically optimal
636 fashion. *Vision Science Program/School of Optometry, University of California, Berkeley* 94720-2020,
637 USA 415: 429–433, 2002.
- 638 **Franklin DW, Wolpert DM.** Computational mechanisms of sensorimotor control. *Neuron* 72: 425–
639 442, 2011.
- 640 **Frith C.** The self in action: Lessons from delusions of control. *Conscious Cogn* 14: 752–770, 2005a.
- 641 **Frith C.** The neural basis of hallucinations and delusions. *C R Biol* 328: 169–175, 2005b.
- 642 **Frith C.** Explaining delusions of control: The comparator model 20years on. *Conscious Cogn* 21: 52–
643 54, 2012.
- 644 **Frith CD, Blakemore S-J, Wolpert DM.** Abnormalities in the awareness and control of action. *Philos*
645 *Trans R Soc Lond B Biol Sci* 355: 1771–1788, 2000.
- 646 **García-Piqueras J, García-Mesa Y, Cárcaba L, Feito J, Torres-Parejo I, Martín-Biedma B, Cobo J,**
647 **García-Suárez O, Vega JA.** Ageing of the somatosensory system at the periphery: age-related
648 changes in cutaneous mechanoreceptors. *J Anat* 234: 839–852, 2019.
- 649 **Gescheider GA, Beiles EJ, Checkosky CM, Bolanowski SJ, Verrillo RT.** The effects of aging on
650 information-processing channels in the sense of touch: II. Temporal summation in the p channel.
651 *Somatosens Mot Res* 11: 359–365, 1994.
- 652 **Ghisletta P, Lindenberger U.** Exploring structural dynamics within and between sensory and
653 intellectual functioning in old and very old age: Longitudinal evidence from the Berlin Aging Study.
654 *Intelligence* 33: 555–587, 2005.
- 655 **Hagiwara K, Ogata K, Okamoto T, Uehara T, Hironaga N, Shigeto H, Kira J ichi, Tobimatsu S.** Age-
656 related changes across the primary and secondary somatosensory areas: An analysis of
657 neuromagnetic oscillatory activities. *Clinical Neurophysiology* 125: 1021–1029, 2014.
- 658 **Heft MW, Robinson ME.** Age differences in suprathreshold sensory function. *Age (Omaha)* 36: 1–8,
659 2014.
- 660 **Heft MW, Robinson ME.** Somatosensory function in old age. *J Oral Rehabil* 44Blackwell Publishing
661 Ltd: 327–332, 2017.
- 662 **Heled E, Rotberg S, Yavich R, Hoofien AD.** Introducing the Tactual Span: A New Task for Assessing
663 Working Memory in the Teactile Modality. *Assessment* 28: 1018–1031, 2021.
- 664 **Herter TM, Scott SH, Dukelow SP.** Systematic changes in position sense accompany normal aging
665 across adulthood. *J Neuroeng Rehabil* 11: 1–12, 2014.
- 666 **Hesse MD, Nishitani N, Fink GR, Jousmäki V, Hari R.** Attenuation of somatosensory responses to
667 self-produced tactile stimulation. *Cerebral Cortex* 20: 425–432, 2010.
- 668 **Heuer H, Hegele M, Sülzenbrück S.** Implicit and explicit adjustments to extrinsic visuo-motor
669 transformations and their age-related changes. *Hum Mov Sci* 30: 916–930, 2011.

- 670 **Humes LE, Busey TA, Craig JC, Kewley-Port D.** The effects of age on sensory thresholds and temporal
671 gap detection in hearing, vision, and touch. *Atten Percept Psychophys* 71: 1439–1459, 2009.
- 672 **JASP Team.** JASP (Version 0.16.3)[Computer software]. 2022.
- 673 **Job X, Kilteni K.** Action does not enhance but attenuates predicted touch. *bioRxiv*
674 2023.04.03.535383, 2023.
- 675 **Kawato M.** Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9: 718–
676 727, 1999.
- 677 **Kilteni K.** Somatosensory Research Methods. New York, NY: Springer US, 2023.
- 678 **Kilteni K, Andersson BJ, Houborg C, Ehrsson HH.** Motor imagery involves predicting the sensory
679 consequences of the imagined movement. *Nat Commun* 9: 1617, 2018.
- 680 **Kilteni K, Ehrsson HH.** Sensorimotor predictions and tool use: Hand-held tools attenuate self-touch.
681 *Cognition* 165: 1–9, 2017a.
- 682 **Kilteni K, Ehrsson HH.** Body ownership determines the attenuation of self-generated tactile
683 sensations. *Proceedings of the National Academy of Sciences* 114: 8426–8431, 2017b.
- 684 **Kilteni K, Ehrsson HH.** Functional Connectivity between the Cerebellum and Somatosensory Areas
685 Implements the Attenuation of Self-Generated Touch. *The Journal of Neuroscience* 40: 894–906,
686 2020.
- 687 **Kilteni K, Ehrsson HH.** Predictive attenuation of touch and tactile gating are distinct perceptual
688 phenomena. *iScience* 25: 104077, 2022.
- 689 **Kilteni K, Engeler P, Boberg I, Maurex L, Ehrsson HH.** No evidence for somatosensory attenuation
690 during action observation of self-touch. *European Journal of Neuroscience* 54: 6422–6444, 2021.
- 691 **Kilteni K, Engeler P, Ehrsson HH.** Efference Copy Is Necessary for the Attenuation of Self-Generated
692 Touch. *iScience* 23: 100843, 2020.
- 693 **Kilteni K, Henrik Ehrsson H.** Functional connectivity between the cerebellum and somatosensory
694 areas implements the attenuation of self-generated touch. *Journal of Neuroscience* 40: 894–906,
695 2020.
- 696 **Kilteni K, Houborg C, Ehrsson HH.** Rapid learning and unlearning of predicted sensory delays in self-
697 generated touch. *Elife* 8: 1–17, 2019.
- 698 **Kilteni K, Houborg C, Ehrsson HH.** Brief temporal perturbations in somatosensory reafference
699 disrupt perceptual and neural attenuation and increase supplementary motor-cerebellar
700 connectivity. *bioRxiv* 2022.11.25.517892, 2022.
- 701 **Kitchen NM, Miall RC.** Adaptation of reach action to a novel force-field is not predicted by acuity of
702 dynamic proprioception in either older or younger adults. *Exp Brain Res* 239: 557–574, 2021.
- 703 **Koenraad Vandevoorde X, Orban De Xivry J-J.** Why is the explicit component of motor adaptation
704 limited in elderly adults? *J Neurophysiol* 124: 152–167, 2020.
- 705 **Konczak J, Sciutti A, Avanzino L, Squeri V, Gori M, Masia L, Abbruzzese G, Sandini G.** Parkinson’s
706 disease accelerates age-related decline in haptic perception by altering somatosensory integration.
707 *Brain* 135: 3371–3379, 2012.

- 708 **Körding KP, Ku SP, Wolpert DM.** Bayesian integration in force estimation. *J Neurophysiol* 92: 3161–
709 3165, 2004.
- 710 **L. Sturnieks D, St George R, R. Lord S.** Balance disorders in the elderly. *Neurophysiologie Clinique* 38:
711 467–478, 2008.
- 712 **Li KZH, Lindenberger U.** Relations between aging sensory/sensorimotor and cognitive functions.
713 *Neurosci Biobehav Rev* 777–783, 2002.
- 714 **Lin WM, Hsieh ST, Chang YC.** Effects of aging on human skin innervation. *Neuroreport* 15: 149–153,
715 2004.
- 716 **Lindenberger U, Baltes PB.** Sensory functioning and intelligence in old age: A strong connection.
717 *Psychol Aging* 9: 339–355, 1994.
- 718 **McIntyre S, Nagi SS, McGlone F, Olausson H.** The Effects of Ageing on Tactile Function in Humans.
719 *Neuroscience* 464: 53–58, 2021.
- 720 **McNamee D, Wolpert DM.** Internal Models in Biological Control. *Annu Rev Control Robot Auton Syst*
721 339–364, 2019.
- 722 **Michely J, Volz LJ, Hoffstaedter F, Tittgemeyer M, Eickhoff SB, Fink GR, Grefkes C.** Network
723 connectivity of motor control in the ageing brain. *Neuroimage Clin* 18: 443–455, 2018.
- 724 **Nasreddine ZS, Phillips NA, Bédirian V, Charbonneau S, Whitehead V, Collin I, Cummings JL,
725 Chertkow H.** The Montreal Cognitive Assessment, MoCA: A brief screening tool for mild cognitive
726 impairment. *J Am Geriatr Soc* 53: 695–699, 2005.
- 727 **Oldfield RC.** *THE ASSESSMENT AND ANALYSIS OF HANDEDNESS: THE EDINBURGH INVENTORY.*
728 Pergamon Press, 1971.
- 729 **Pareés I, Brown H, Nuruki A, Adams RA, Davare M, Bhatia KP, Friston K, Edwards MJ.** Loss of
730 sensory attenuation in patients with functional (psychogenic) movement disorders. *Brain* 137: 2916–
731 2921, 2014.
- 732 **Parthasarathy M, Mantini D, Orban de Xivry JJ.** Increased upper-limb sensory attenuation with
733 age. *J Neurophysiol* 127: 474–492, 2022.
- 734 **R Core Team.** R: A Language and Environment for Statistical Computing. 2022.
- 735 **Raz N, Lindenberger U, Rodrigue KM, Kennedy KM, Head D, Williamson A, Dahle C, Gerstorf D,
736 Acker JD.** Regional brain changes in aging healthy adults: General trends, individual differences and
737 modifiers. *Cerebral Cortex* 15: 1676–1689, 2005.
- 738 **Roberts KL, Allen HA.** Perception and cognition in the ageing brain: A brief review of the short- and
739 long-term links between perceptual and cognitive decline. *Front Aging Neurosci* 8: 1–7, 2016.
- 740 **Rong H, Lai X, Jing R, Wang X, Fang H, Mahmoudi E.** Association of Sensory Impairments With
741 Cognitive Decline and Depression Among Older Adults in China. *JAMA Netw Open* 3: e2014186,
742 2020.
- 743 **Shadmehr R, Krakauer JW.** A computational neuroanatomy for motor control. *Exp Brain Res* 185:
744 359–381, 2008.

- 745 **Shergill SS, Bays PM, Frith CD, Wolpert DM.** Two eyes for an eye: the neuroscience of force
746 escalation. *Science* 301: 187, 2003.
- 747 **Shergill SS, Samson G, Bays PM, Frith CD, Wolpert DM.** Evidence for sensory prediction deficits in
748 schizophrenia. *American Journal of Psychiatry* 162: 2384–2386, 2005.
- 749 **Shergill SS, White TP, Joyce DW, Bays PM, Wolpert DM, Frith CD.** Modulation of somatosensory
750 processing by action. *Neuroimage* 70: 356–362, 2013.
- 751 **Shergill SS, White TP, Joyce DW, Bays PM, Wolpert DM, Frith CD.** Functional magnetic resonance
752 imaging of impaired sensory prediction in schizophrenia. *JAMA Psychiatry* 71: 28–35, 2014.
- 753 **Skedung L, El Rawadi C, Arvidsson M, Farcet C, Luengo GS, Breton L, Rutland MW.** Mechanisms of
754 tactile sensory deterioration amongst the elderly. *Sci Rep* 8, 2018.
- 755 **Solesio-Jofre E, Serbruyns L, Woolley DG, Mantini D, Beets IAM, Swinnen SP.** Aging effects on the
756 resting state motor network and interlimb coordination. *Hum Brain Mapp* 35: 3945–3961, 2014.
- 757 **Stevens JC, Cruz LA.** Spatial acuity of touch: Ubiquitous decline with aging revealed by repeated
758 threshold testing. *Somatosens Mot Res* 13: 1–10, 1996.
- 759 **Tremblay F, Mireault AC, Dessureault L, Manning H, Sveistrup H.** Postural stabilization from
760 fingertip contact: II. Relationships between age, tactile sensibility and magnitude of contact forces.
761 *Exp Brain Res* 164: 155–164, 2005.
- 762 **Vandevoorde K, Orban de Xivry JJ.** Internal model recalibration does not deteriorate with age while
763 motor adaptation does. *Neurobiol Aging* 80: 138–153, 2019.
- 764 **Wang L, Zhang Y, Zhang J, Sang L, Li P, Yan R, Qiu M, Liu C.** Aging Changes Effective Connectivity of
765 Motor Networks During Motor Execution and Motor Imagery. *Front Aging Neurosci* 11: 1–10, 2019.
- 766 **Weiskrantz L, Elliott J, Darlington C.** Preliminary observations on tickling oneself. *Nature* 230: 598–
767 599, 1971.
- 768 **Wickremaratchi MM, Llewelyn JG.** Effects of ageing on touch. *Postgrad Med J* 82: 301–304, 2006.
- 769 **Wolpe N, Ingram JN, Tsvetanov KA, Geerligs L, Kievit RA, Henson RN, Wolpert DM, Rowe JB, Tyler
770 LK, Brayne C, Bullmore E, Calder A, Cusack R, Dalgleish T, Duncan J, Matthews FE, Marslen-Wilson
771 W, Shafto MA, Campbell K, Cheung T, Davis S, McCarrey A, Mustafa A, Price D, Samu D, Taylor JR,
772 Treder M, van Belle J, Williams N, Bates L, Emery T, Erzinclioglu S, Gadie A, Gerbase S, Georgieva S,
773 Hanley C, Parkin B, Troy D, Auer T, Correia M, Gao L, Green E, Henriques R, Allen J, Amery G,
774 Amunts L, Barcroft A, Castle A, Dias C, Dowrick J, Fair M, Fisher H, Goulding A, Grewal A, Hale G,
775 Hilton A, Johnson F, Johnston P, Kavanagh-Williamson T, Kwasniewska M, McMinn A, Norman K,
776 Penrose J, Roby F, Rowland D, Sargeant J, Squire M, Stevens B, Stoddart A, Stone C, Thompson T,
777 Yazlik O, Barnes D, Dixon M, Hillman J, Mitchell J, Willis L.** Ageing increases reliance on sensorimotor
778 prediction through structural and functional differences in frontostriatal circuits. *Nat Commun* 7,
779 2016.
- 780 **Wolpe N, Ingram JN, Tsvetanov KA, Henson RN, Wolpert DM, Tyler LK, Brayne C, Bullmore ET,
781 Calder AC, Cusack R, Dalgleish T, Duncan J, Matthews FE, Marslen-Wilson WD, Shafto MA,
782 Campbell K, Cheung T, Davis S, Geerligs L, Kievit R, McCarrey A, Mustafa A, Price D, Samu D, Taylor
783 JR, Treder M, van Belle J, Williams N, Bates L, Emery T, Erzinclioglu S, Gadie A, Gerbase S,
784 Georgieva S, Hanley C, Parkin B, Troy D, Auer T, Correia M, Gao L, Green E, Henriques R, Allen J,
785 Amery G, Amunts L, Barcroft A, Castle A, Dias C, Dowrick J, Fair M, Fisher H, Goulding A, Grewal A,**

- 786 **Hale G, Hilton A, Johnson F, Johnston P, Kavanagh-Williamson T, Kwasniewska M, McMinn A,**
787 **Norman K, Penrose J, Roby F, Rowland D, Sargeant J, Squire M, Stevens B, Stoddart A, Stone C,**
788 **Thompson T, Yazlik O, Barnes D, Dixon M, Hillman J, Mitchell J, Willis L, Rowe JB.** Age-related
789 reduction in motor adaptation: brain structural correlates and the role of explicit memory. *Neurobiol*
790 *Aging* 90: 13–23, 2020.
- 791 **Wolpe N, Zhang J, Nombela C, Ingram JN, Wolpert DM, Rowe JB.** Sensory attenuation in Parkinson's
792 disease is related to disease severity and dopamine dose. *Sci Rep* 8, 2018.
- 793 **Wolpert DM, Flanagan JR.** Motor prediction. *Current Biology* 11: R729–R732, 2001.
- 794 **Zapparoli L, Mariano M, Paulesu E.** How the motor system copes with aging: a quantitative meta-
795 analysis of the effect of aging on motor function control. *Commun Biol* 5: 1–15, 2022.
- 796 **Zhao L, Matloff W, Ning K, Kim H, Dinov ID, Toga AW.** Age-Related Differences in Brain Morphology
797 and the Modifiers in Middle-Aged and Older Adults. *Cerebral Cortex* 29: 4169–4193, 2019.
- 798 **Ziegler G, Dahnke R, Jäncke L, Yotter RA, May A, Gaser C.** Brain structural trajectories over the adult
799 lifespan. *Hum Brain Mapp* 33: 2377–2389, 2012.
- 800