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

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Abstract

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

Keywords

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

New and Noteworthy

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

Introduction

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

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

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

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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.

Materials and Methods

Preregistration

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

Participants

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

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

Screening methods and exclusion criteria

Cognitive function

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

Tactile working memory

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

Exclusion of participants

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

Psychophysical task

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

Participants rested their left hands palm up with their index fingers on a molded support and their right hands palm down on top of a set of sponges. A vacuum pillow (Germa protec, AB Germa) was provided to support the participants' left arm and increase their comfort. Every trial started with an auditory tone. Next, a DC electric motor (Maxon EC Motor EC 90 flat; manufactured in Switzerland) delivered two brief (100-ms) forces to the pulp of participants' 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
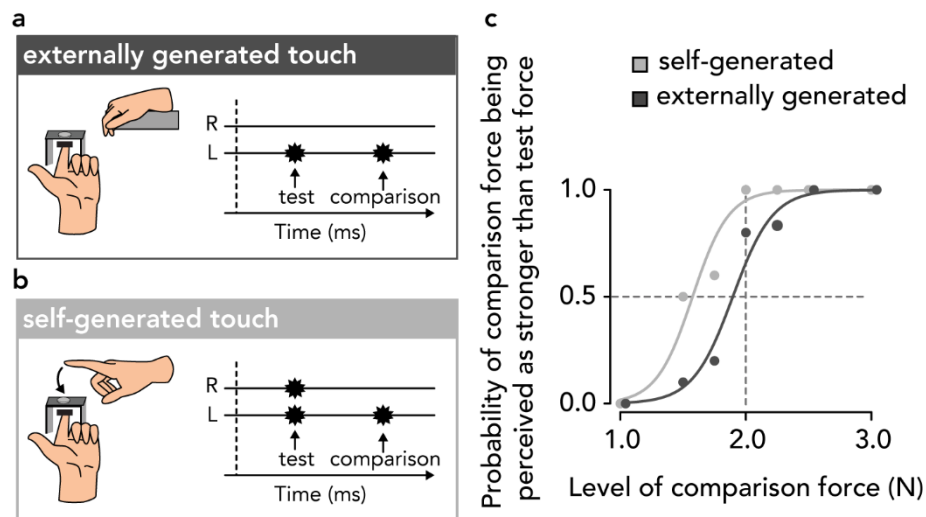250 them.

251

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.

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
$$p = \frac{e^{\beta 0 + \beta 1 x}}{1 + e^{\beta 0 + \beta 1 x}} \text{ (Equation 1)}$$

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 $p = 0.75$.

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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.

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-
289 trackers/liberty). If somatosensory attenuation is increased in *elderly* participants compared to
290 *younger* participants, as we expected, these additional measures could be used to explore the
291 relationships of age with forces, timing, and kinematics together with attenuation. Due to
292 technical reasons, the movements of the right index finger were not correctly registered; thus,
293 supplementary analyses were performed with only the active peak forces and their times.

Hypotheses

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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).

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.

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.

Results

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

Somatosensory attenuation – preregistered analysis

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

Somatosensory attenuation – supplementary analysis

Additional supplementary analyses showed that the attenuation effect was observed in every age group: PSEs in the *self-generated touch* condition were significantly lower than those in the *externally generated touch* condition within the *young* ($W = 0$, $p < .001$, $CI^{95} = [-\infty, -0.2]$, $r_{rb} = -1.0$, one-tailed) (**Figure 2b**), *middle-aged* ($W = 10$, $p < .001$, $CI^{95} = [-\infty, -0.205]$, $r_{rb} = -0.97$, one-tailed) (**Figure 2c**) and *elderly* groups ($W = 26$, $p < .001$, $CI^{95} = [-\infty, -0.225]$, $r_{rb} = -0.922$, one-tailed) (**Figure 2d**).
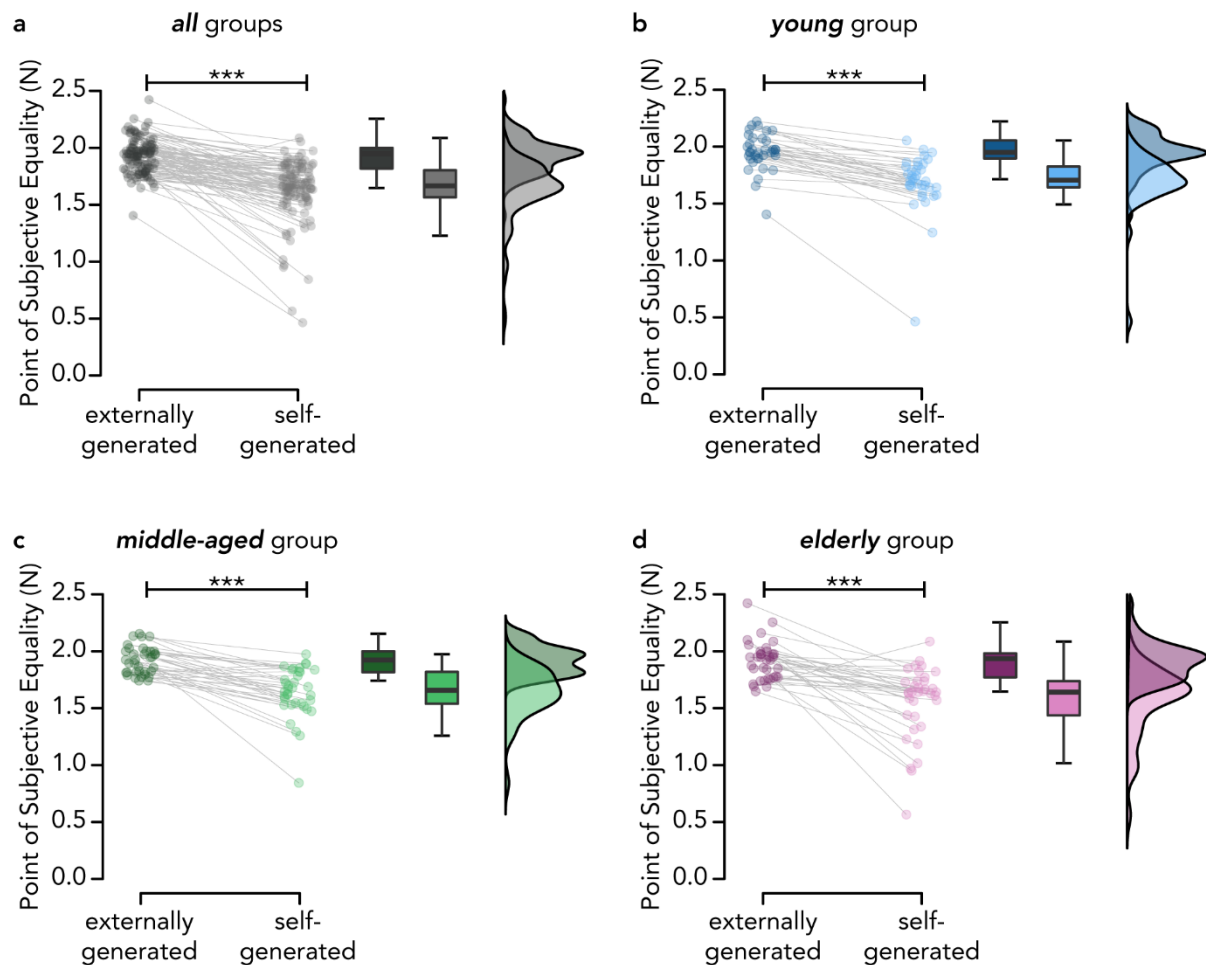
Figure 2. Somatosensory attenuation across age groups. (a) Across all age groups (pooled data; n = 108), self-generated touches were perceived as significantly weaker than externally generated touches of identical intensity. The same effect was found separately for the *young* **(b)**, *middle-aged* **(c)**, and *elderly* groups **(d)** (n = 36 for each group). The boxplots display the median and interquartile ranges of the PSEs in the *externally generated* and *self-generated touch* conditions per age group. Markers denote the PSE values for each participant, and raincloud plots show the distribution of the data. Line plots illustrate the PSE differences between the *externally generated* and *self-generated touch* conditions for each participant (*** p <.001).

Aging and somatosensory precision – preregistered analysis

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

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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**).
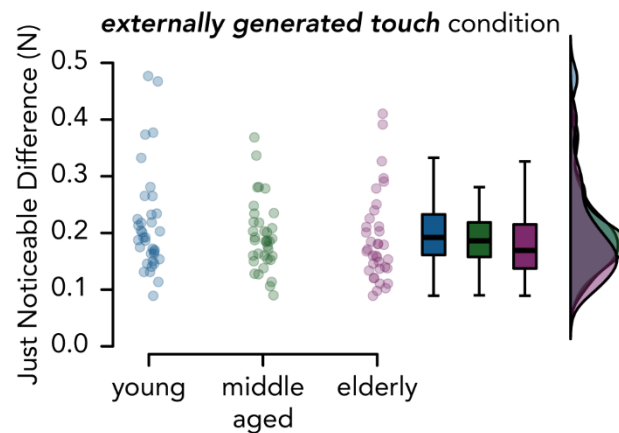

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Figure 3. Somatosensory precision across age groups. JND values in the *externally generated touch* condition across the three age groups. There were no significant differences among the three groups, and the Bayesian analyses supported the absence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

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.

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, $CI^{95} = [-0.057, \infty]$, $r_{rb} = 0.099$, one-tailed), nor between the *middle-aged* and *young* groups ($W = 673$,
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*: $BF_{0+} = 3.896$).
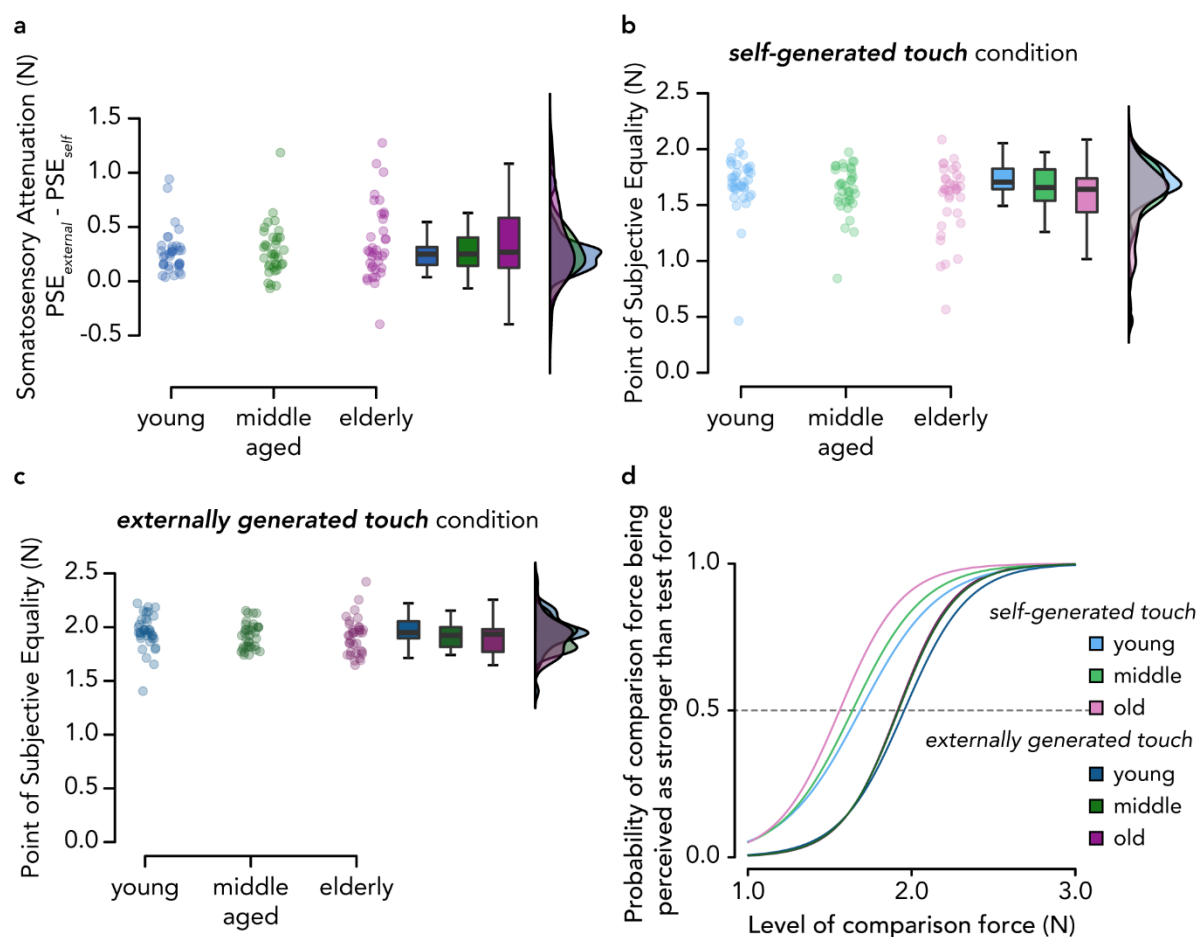
13

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

Aging and somatosensory attenuation – supplementary analyses

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

14

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

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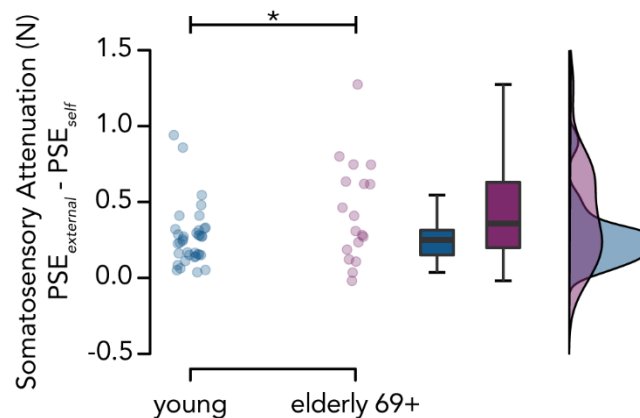

Figure 5. Somatosensory attenuation in *young* and *elderly 69+* participants. We observed greater somatosensory attenuation in the *elderly* 69+ group ($n = 18$) than in the *young* group ($n = 36$).

Somatosensory attenuation, aging, and somatosensory precision – preregistered analysis

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

15

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)**.

Discussion

469

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 $\geq$ 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; Vandevoorde 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).

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.

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.

Acknowledgments

Disclosures

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

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