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Predictive attenuation of touch and tactile gating are distinct perceptual phenomena

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In recent decades, research on somatosensory perception has led to two important observations. First, self-generated touches that are predicted by voluntary movements become attenuated compared to externally generated touches of the same intensity (attenuation). Second, externally generated touches feel weaker and are more difficult to detect during movement compared to rest (gating). Researchers today often consider gating and attenuation to be the same suppression process; however, this assumption is unwarranted because, despite more than forty years of research, no study has combined them in a single paradigm. We quantified how people perceive self-generated and externally generated touches during movement and rest. We demonstrate that whereas voluntary movement gates the precision of both self-generated and externally generated touch, the amplitude of self-generated touch is selectively attenuated compared to externally generated touch. We further show that attenuation and gating neither interact nor correlate, and we conclude that they represent distinct perceptual phenomena.

Let's imagine you are at your doctor for a medical examination. Upon her request, you apply pressure with your index finger on your leg to indicate where exactly you feel the pain. The pressure you feel on your leg and the tip of your finger is the feedback from your voluntary finger movement, and it is called *somatosensory reafference*. To reproduce and confirm your sensations, imagine that the doctor now applies pressure with her index finger at the same spot on your leg. This pressure is generated by the doctor and not from you, and it is called *somatosensory exafference*. Now imagine that the doctor asks you to first keep your leg relaxed and then flex and extend it while you or her continuously apply pressure on your leg. You can therefore experience your reafferent or her exafferent touches on your leg, while it is moving or resting. Distinguishing between these four conditions is fundamental for your sensorimotor control; your nervous system must know both the source of the touch and the state of your limb to make appropriate use of the sensory feedback. A cutaneous mechanoreceptor in your peripheral nervous system though, cannot distinguish whether a touch is reafferent or exafferent, and thus this distinction must be made centrally, where tactile signals from the skin, sensory information from muscles and joints, and information from motor commands are available. How, then, does the central nervous system classify somatosensory signals during movement?

Several experimental studies in humans have shown that the brain *attenuates* somatosensory reafference compared to exafference. In behavioral research, this refers to participants perceiving self-generated strokes, forces, or taps as weaker than external equivalents of the same intensity¹⁻¹⁰. This somatosensory attenuation has been related to reduced activity in the secondary somatosensory cortex¹¹⁻¹³ and the cerebellum^{11,13,14} and an increased connectivity between the two areas^{13,15} during self-generated compared to externally generated touches. Somatosensory attenuation was found in 98% or 315 out of 322 people across a wide age range¹⁶, and it is considered one of the reasons why we cannot tickle ourselves¹⁷⁻¹⁹.

50 Sensory attenuation is not exclusive to humans; similar strategies are used in other species
51 across the animal kingdom (for reviews, see ^{20–24}). For example, during self-chirping, the
52 cricket’s central auditory processing is inhibited (both presynaptically and postsynaptically) in
53 phase with the insect’s chirps to prevent desensitization of its auditory system while
54 maintaining sensitivity to external sounds ^{25,26}. In mice, auditory cortical responses in response
55 to self-generated sounds are attenuated, and this attenuation is present only for the tone
56 frequencies the animal has associated with its locomotion and absent when the same sounds are
57 externally produced ²⁷. A weakly electric fish ²⁸ is able to respond exclusively to externally
58 generated electrical discharges by attenuating its predicted electrosensory reafference ^{21,29}. In
59 primates, activity in the vestibular nucleus in response to vestibular reafference is attenuated
60 during active head movements compared to passive head movements, allowing the animal to
61 maintain its head and body posture and activate the vestibular-related reflexes when appropriate
62 ^{20,21,30–32}.

63
64 At the same time, another branch of experimental research has shown that somatosensory
65 sensitivity in response to externally generated stimuli is *gated* during and before a voluntary
66 movement. In human psychophysical research, this phenomenon of *movement-related tactile*
67 *gating* or *tactile suppression* manifests as an elevation in the detection threshold ^{33–42} and a
68 decrease in the subjective intensity of externally generated stimuli ^{35,37,43} when the stimulated
69 body part moves compared to when it is at rest. Several electrophysiological studies have shown
70 this gating as an inhibition of somatosensory evoked potentials during active movement
71 compared to rest, at subcortical and cortical sites along the somatosensory pathway ^{43–48}.
72 Similar to somatosensory attenuation, tactile gating is a biologically preserved mechanism that
73 is seen across different species ⁴⁹. For example, responses recorded at the cat’s medial
74 lemniscus evoked by nerve stimulation are suppressed prior to and during limb movements ⁵⁰.
75 Similarly, the transmission of cutaneous afferent signals to the primary somatosensory cortex
76 is suppressed in rats during movement compared to rest ⁵¹. In monkeys, the gating of cutaneous
77 afferent input during active movement has been observed both in the primary somatosensory
78 cortex ^{52–54} and the spinal cord ^{54,55}.

79
80 Somatosensory attenuation and tactile gating share two important conceptual similarities. First,
81 they both refer to a modulation—either in terms of magnitude or precision—in the perception
82 of cutaneous stimuli during movement. Second, they have been assigned the same functional
83 role ³⁹: to reduce the flow of afferent information that can be predicted from the motor
84 command, so that detection of external input that can be biologically important, such as touches
85 caused by predators ^{17,24,56}, or input that is task-relevant for the upcoming or ongoing movement
86 ^{45,47,57} is facilitated.

87
88 Importantly, however, the two phenomena present one striking difference. Somatosensory
89 attenuation relates to somatosensory reafference, that is, touches caused *by* our voluntary
90 movement. In contrast, gating relates to somatosensory exafference, that is, external touches
91 occurring *during* our voluntary movement. Nevertheless, somatosensory research, including
92 very recent studies and review articles, e.g., ^{41,42,58–64}, often treats the two phenomena as a single
93 generalized suppression strategy of the brain and uses the terms attenuation and gating
94 interchangeably. If the two phenomena are indeed different, this false equivalence is
95 detrimental for understanding human sensorimotor control. First, it cannot advance our
96 understanding at the computational level because researchers try to explain gating (e.g., ⁴¹) and
97 attenuation (e.g., ⁶⁵) using the computational processes proposed for attenuation and gating,
98 respectively. Similarly, at the neurobiological level, researchers intermix neural correlates of
99 gating and attenuation (e.g., ^{62,63}) because they assume that these measure the same single

100 phenomenon. Second, this confusion becomes particularly disadvantageous in clinical studies
101 using gating and attenuation when interpreting findings of sensorimotor deficits in patients with
102 schizophrenia^{66–68}, functional movement disorders⁶⁹ or Parkinson’s disease^{45,70,71}.

103
104 Are these phenomena the same, or do they represent two fundamentally distinct processes?
105 Does the brain treat all sensory stimuli similarly during movement, independent of whether
106 they are reafferent or exafferent? To the best of our knowledge, there has been no previous
107 attempt to simultaneously test attenuation and gating with the same stimulus and psychophysics
108 task. Here, in a single experimental design, we investigated the perception of touches applied
109 on the left hand while manipulating whether the left arm was in movement or resting (left limb
110 state). We additionally manipulated whether the touches were reafferent, generated by the right
111 hand, or exafferent, generated by an external source (origin of touch). We reasoned that if the
112 two phenomena are the same, then they should influence somatosensory perception in similar
113 ways. Our results demonstrate that this is not the case: voluntary movement reduces the
114 somatosensory precision of both sensory reafference and exafference (gating), while the
115 perceived amplitude of sensory reafference is selectively attenuated compared to exafference
116 (attenuation). Notably, the two phenomena do not correlate with each other or interact when
117 present simultaneously. Thus, collectively, our results show that gating and attenuation are two
118 separate processes that can be experimentally dissociated.

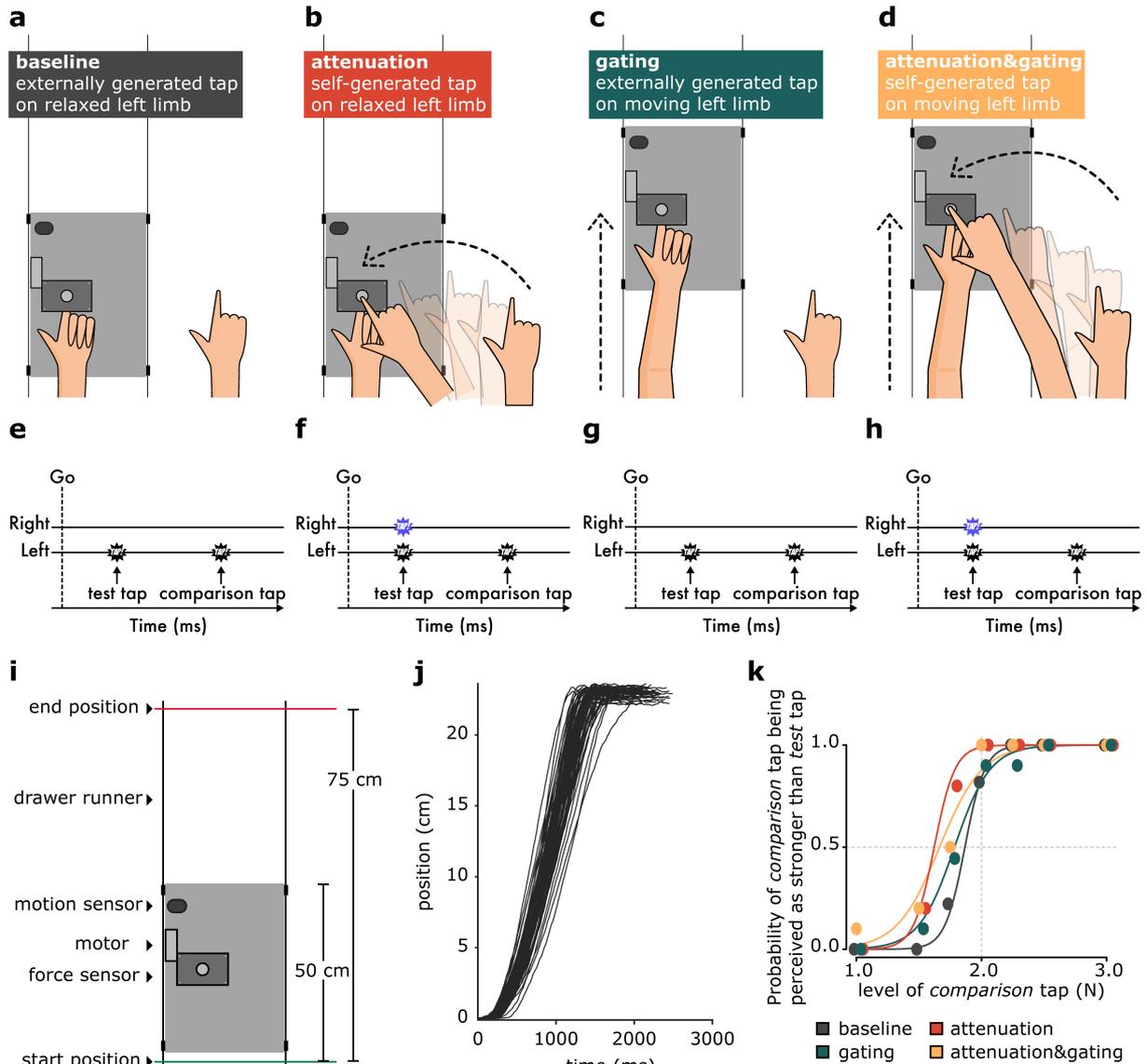
119 120 121 **Results**

122 Participants rested their left hands palm up with their index fingers placed on a molded support,
123 and their right hands were palm down on top of a set of sponges (**Fig. 1a-d**). In all conditions,
124 they performed a force-discrimination task^{3,4,10,67}: in each trial, a motor delivered two taps (the
125 *test* tap and the *comparison* tap) on the pulp of their left index finger, and they were asked to
126 verbally indicate which tap felt stronger (**Fig. 1e-h**). While the *test* tap had a fixed intensity (2
127 N), the *comparison* tap randomly changed its intensity on every trial (1, 1.5, 1.75, 2, 2.25, 2.5,
128 or 3 N). An auditory ‘go’ signal indicated the trial’s onset and the onset of the response period.

129
130 In all conditions, our experimental manipulation exclusively concerned the *test tap*; the
131 *comparison* tap was always externally triggered and delivered on the relaxed left arm, serving,
132 therefore, as a reference stimulus. In a factorial design, we controlled for whether the left arm
133 moved (**Fig. 1c, d**) or remained relaxed (**Fig. 1a, b**) during the *test* tap, and whether the *test* tap
134 was produced by the right hand (self-generated) (**Fig. 1b, d**) or not (externally generated) (**Fig.**
135 **1a, c**). This design resulted in four experimental conditions, the order of which was fully
136 counterbalanced (**Fig. 1a-d**).

137
138 In the *baseline* condition (**Fig. 1a**), participants did not move their limbs but passively received
139 the *test* and the *comparison* taps on the left index. This control condition assesses the
140 participants’ somatosensory perception in the absence of any movement^{2,4,10}. In the *attenuation*
141 condition (**Fig. 1b**), participants actively tapped with their right index finger a force sensor
142 placed on top of their left index finger. The tap of their right index finger on the force sensor
143 triggered the *test* tap on their left index finger. This classic condition assesses the perception of
144 a self-generated tap on a passive limb^{2,4,10}. In the *gating* condition (**Fig. 1c**), participants were
145 asked to continuously move their left arm forward, sliding the experimental setup with the
146 motor and the force sensors between a start and an end position (distance 25 cm) at a
147 comfortable velocity of approximately 20 cm/sec (**Fig. 1i-j, Supplementary Fig. S1, S2**).
148 During this movement, participants received the *test* tap on their left index finger. This is a
149 gating condition because it assesses the perception of an externally generated tap on a moving

150 limb^{36–38,40}. Finally, in the *attenuation&gating* condition (**Fig. 1d**), the participants performed
 151 the same movement with their left arm, but they were additionally asked to actively tap with
 152 their right index finger on the force sensor that triggered the *test* tap on their left index finger
 153 during the movement. The force sensor was attached to the experimental setup and moved
 154 together with the left hand. This condition combines the gating and attenuation phenomena
 155 since it assesses the perception of a self-generated tap on a moving limb.
 156



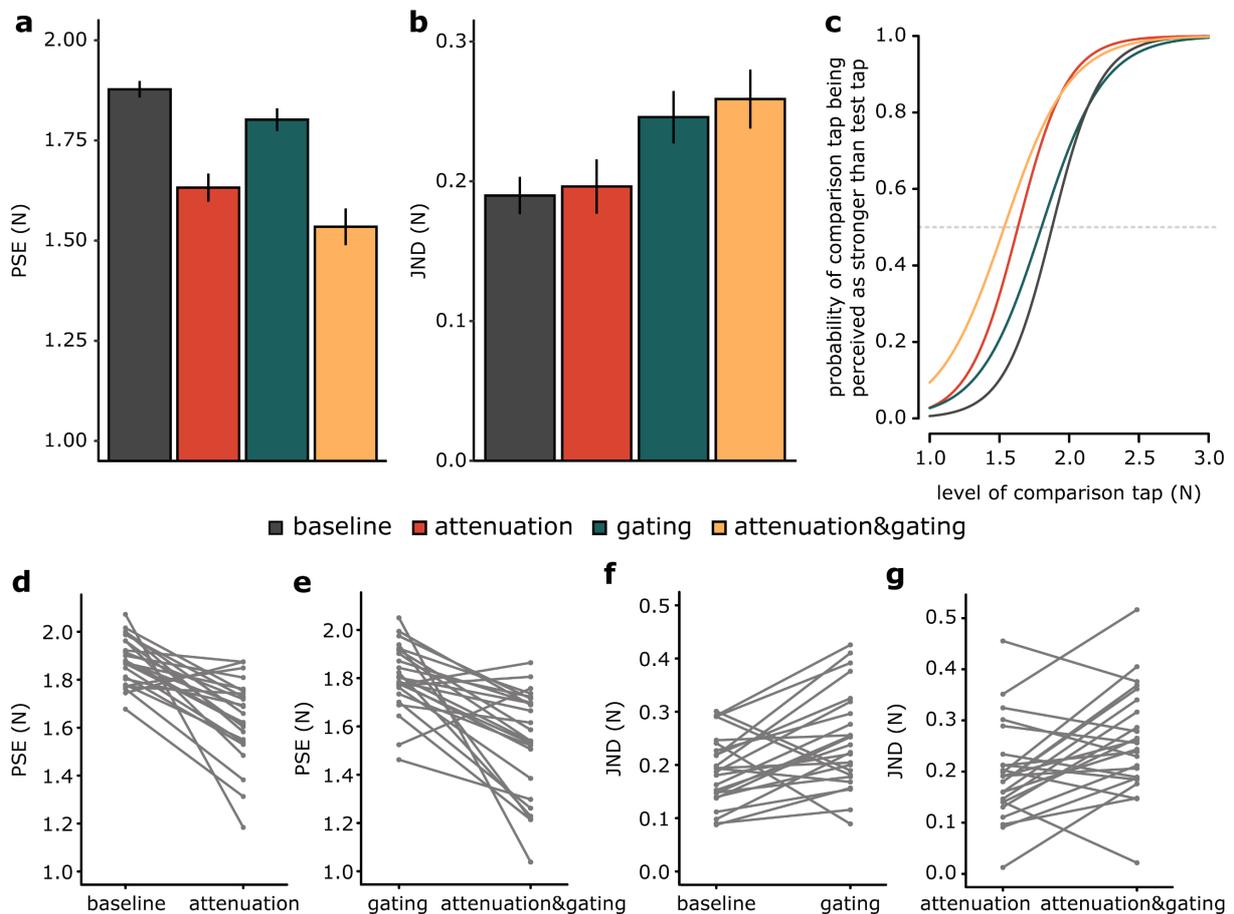
157
 158 **Fig. 1. Experimental conditions.** Two factors were manipulated in the experiment, resulting in four
 159 experimental conditions: whether the left arm was in rest (**a, b**) or in movement while receiving the *test*
 160 tap (**c, d**) (state of the left limb) and whether the *test* tap was externally triggered by the motor (**a, c**) or
 161 self-triggered by the participants' right hand (**b, d**) (origin of touch). In all four conditions (**e-h**), the
 162 participants received the two taps (*test* and *comparison* tap) on the pulp of their left index fingers from
 163 the motor (black stars), and they had to verbally indicate which was stronger: the first or the second tap.
 164 In the *attenuation* and *attenuation&gating* conditions, the participants self-triggered the test tap on their
 165 left index finger by moving their right arm to tap a sensor with their right index finger (blue stars). **(i)**
 166 In the *gating* and *attenuation&gating* conditions (**c** and **d**), the participants extended their left arm from
 167 a start position to an end position, sliding the experimental setup along two drawer runners. During this
 168 movement, participants experienced the *test* tap. A motion sensor recorded the position of the platform
 169 in time. **(f)** Example position traces recorded by the motion sensor for the movements of one participant
 170 during the *attenuation&gating* condition. **(g)** Responses of a representative participant and fitted logistic

171 models for the four experimental conditions. Data points have been horizontally jittered to avoid
 172 overlapping.

173

174 The participant's responses in each condition were fitted with a generalized linear model (**Fig.**
 175 **1k, Supplementary Fig. S3**), and two parameters of interest were extracted: the point of
 176 subjective equality (PSE), which represents the intensity at which the test tap felt as strong as
 177 the comparison tap ($p = 0.5$), and the just noticeable difference (JND), which reflects the
 178 participants' sensitivity in force discrimination. We hypothesized that the two phenomena are
 179 different and, thus, that they would affect the PSE and JND differently. Specifically, we
 180 expected a decrease in the perceived magnitude (lower PSE) for the conditions with sensory
 181 refference (*attenuation* and *attenuation&gating* conditions), with no effects on the sensory
 182 precision of the participants (JND) when they received the refference on a still limb
 183 (*attenuation* condition). In contrast, we predicted a decrease in the sensory precision (higher
 184 JND) of both sensory refference and exafference for the conditions where the limb that
 185 receives the touches moves (*gating*, *attenuation&gating*) and small, if any, effects in the PSE.
 186 In other words, we expected that the attenuation phenomenon affects the PSE and not the JND,
 187 and the gating phenomenon mainly affects the JND. Our hypotheses were supported by the data
 188 (**Fig. 2a-g**).

189



190

191 **Fig. 2. Experimental results.** (a, b) Bar graphs show the PSEs and JNDs (mean \pm SEM) for each
 192 condition. A lower PSE value indicates a lower perceived magnitude, while a higher JND value indicates
 193 a lower somatosensory sensory precision. Refferent touches produced by the movement of the right
 194 arm (*attenuation* and *attenuation&gating* conditions) were associated with a significant drop in the
 195 PSEs, while the movement of the left arm that receives the touches (*gating* and *attenuation&gating*)
 196 produces a significant increase in the JNDs. (c) Group psychometric functions for each condition
 197 generated using the mean PSE and the mean JND across participants. The leftward shift of the curves

198 for the *attenuation* and *attenuation&gating* conditions illustrates that somatosensory refference is
199 perceived as weaker than exafference. The flattening of the curves for the *gating* and *attenuation&gating*
200 conditions illustrates the worsening in somatosensory precision of both refference and exafference on
201 a moving limb. **(d, e)** Line plots illustrate the decreases in PSEs when experiencing refferent touches
202 compared to exafferent touches, when the left arm is still **(d)** and when the left arm moves **(e)**. **(f, g)**
203 Line plots illustrate the increases in JNDs when receiving the touches on a moving limb compared to
204 rest, when the touches are exafferent **(f)** and when the touches are refferent **(g)**.
205

206 We performed a repeated-measures ANOVA on the PSEs with the origin of the touch
207 (refference vs exafference) and the state of the left limb (movement vs rest) as factors. This
208 revealed a significant main effect of the origin of the touch ($F(1, 23) = 36.10, p < 0.001, \eta_p^2 =$
209 0.611), a significant main effect of the left limb state ($F(1, 23) = 13.91, p = 0.001, \eta_p^2 = 0.377$)
210 and a nonsignificant interaction ($F(1, 23) = 0.26, p = 0.615, \eta_p^2 = 0.011$) **(Fig. 2a)**. A Bayesian
211 repeated-measures ANOVA further concluded against the interaction term, by supporting the
212 model without the interaction term compared to the full factorial ($BF_{M1} / BF_{M2} = 3.631$). The
213 *attenuation* condition produced a significant drop in the PSE compared to the *baseline* condition
214 ($n = 24, t(23) = -5.908, p < 0.001, Cohen's d = -1.206, CI^{95} = [-0.332, -0.160], BF_{01} < 0.0003$)
215 **(Fig. 2d)**. This replicates previous attenuation findings indicating that a self-generated tap on a
216 passive limb feels weaker than a tap of the same intensity but of an external origin ^{2,4-7,10,13,16}.
217 Similarly, the PSE in the *attenuation&gating* condition was significantly lower than that in the
218 *gating* condition ($n = 24, t(23) = -5.032, p < 0.001, Cohen's d = -1.027, CI^{95} = [-0.377, -0.157],$
219 $BF_{01} = 0.002$) **(Fig. 2e)**, extending the previous conclusion to when the receiving limb is
220 moving. Together, these two contrasts show that refferent (self-generated) touches feel weaker
221 than exafferent touches, both when the receiving hand is in movement or rest.
222

223 The *gating* and *attenuation&gating* conditions also produced a significant drop in the PSE
224 compared to the *baseline* condition ($n = 24, t(23) = -2.409, p = 0.024, Cohen's d = -0.492, CI^{95}$
225 $= [-0.141, -0.011]$) and the *attenuation* condition ($n = 24, V = 55, p = 0.005, rrb = -0.633, CI^{95}$
226 $= [-0.161, -0.022]$), respectively. However, these decreases were quite modest ($\cong 30\%$ of the
227 weakening produced by the *attenuation* condition) and supported only by anecdotal evidence
228 from Bayesian statistics ($BF_{01} = 0.433$ and $BF_{01} = 0.738$, respectively). Together, these
229 contrasts suggest that exafferent touches can feel slightly weaker on a moving limb than on a
230 passive limb, in agreement with previous findings for tactile gating ^{35,37,43}. Nevertheless, when
231 compared with tactile refference, the perceived magnitude of tactile exafference is not strongly
232 decreased.
233

234 When testing for the effects of the conditions on the somatosensory precision of the participants
235 (JND), there was a significant main effect of the state of the left limb ($F(1, 23) = 17.1, p <$
236 $0.001, \eta_p^2 = 0.426$), but there was neither a significant main effect of the origin of touch ($F(1,$
237 $23) = 0.52, p = 0.478, \eta_p^2 = 0.022$) nor a significant interaction ($F(1, 23) = 0.06, p = 0.809, \eta_p^2$
238 $= 0.003$) **(Fig. 2b)**. As with PSEs, the absence of interaction for the JNDs was further supported
239 with a Bayesian repeated-measures ANOVA that provided evidence against the interaction term
240 ($BF_{M1} / BF_{M2} = 3.522$). The *attenuation* condition did not produce any change in the JND with
241 respect to the *baseline* condition ($n = 24, t(23) = 0.331, p = 0.744, Cohen's d = 0.068, CI^{95} = [-$
242 $0.034, 0.047]$), and this was substantially confirmed with a Bayesian analysis ($BF_{01} = 4.432$).
243 In alignment, no significant differences in the JND were detected between the *gating* and the
244 *attenuation&gating* conditions ($n = 24, t(23) = 0.72, p = 0.481, Cohen's d = 0.146, CI^{95} = [-$
245 $0.024, 0.05]$), and this was again confirmed with a Bayesian analysis ($BF_{01} = 3.691$). Together,
246 these two contrasts demonstrate that receiving sensory refference *per se* is not accompanied
247 by a worsening of sensory precision on the receiving limb.
248

249 In contrast, moving the limb while receiving an external touch (*gating* condition) produces a
250 significant increase in the JND compared to the *baseline* condition ($n = 24$, $t(23) = 3.134$, $p =$
251 0.005 , *Cohen's d* = 0.640, $CI^{95} = [0.019, 0.093]$, $BF_{01} = 0.108$) (**Fig. 2f**). This was further
252 confirmed by a significant increase in JND between the *attenuation* and the *attenuation&gating*
253 conditions ($n = 24$, $t(23) = 2.984$, $p = 0.007$, *Cohen's d* = 0.609, $CI^{95} = [0.019, 0.106]$, $BF_{01} =$
254 0.146) (**Fig. 2g**). Together, these two contrasts indicate that voluntary movement *per se*
255 deteriorates the precision with which reafferent and exafferent stimuli are perceived on the
256 moving limb.

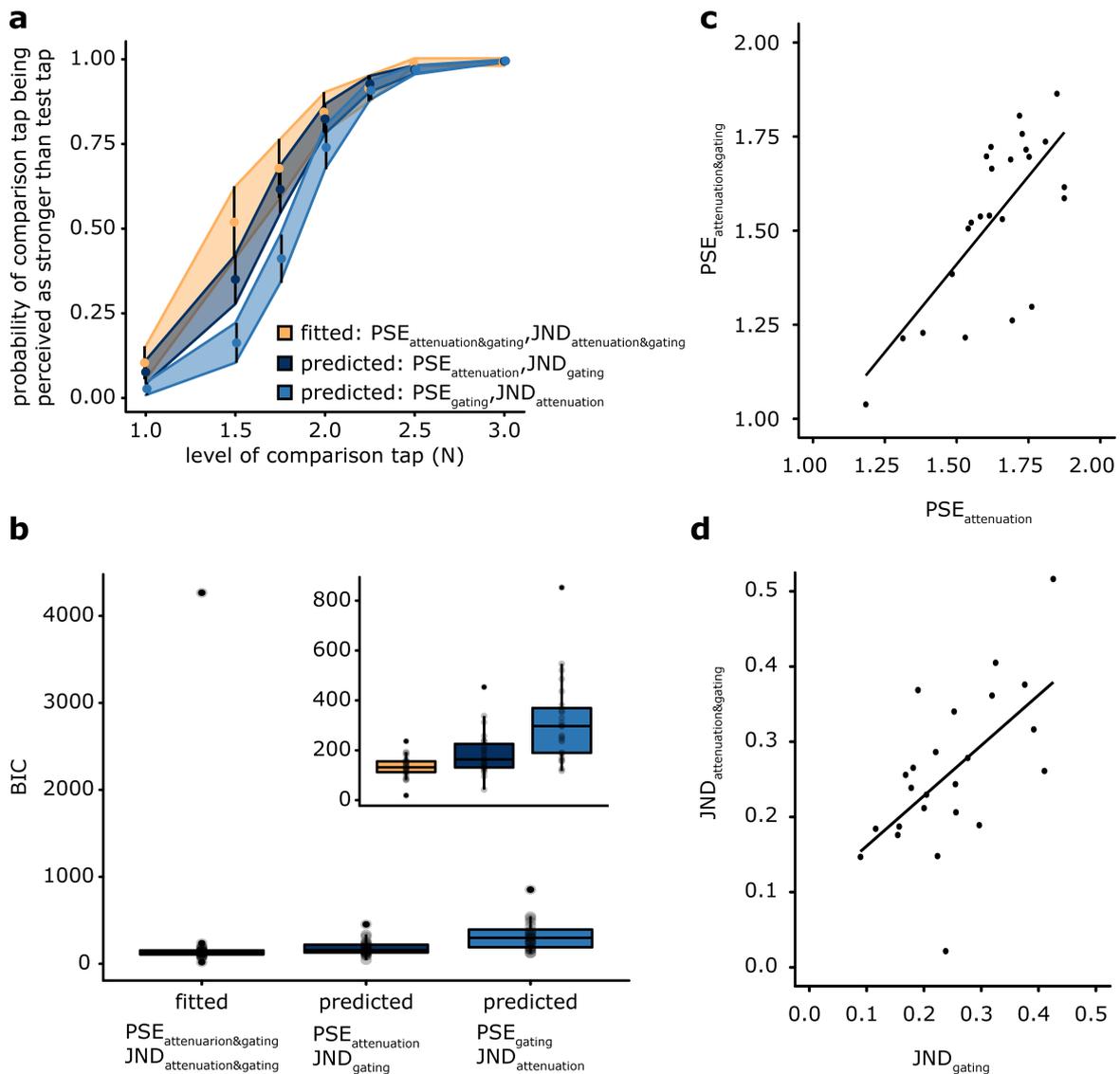
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258 Together, our results indicate that predicting the sensory consequences of a voluntary
259 movement produces a decrease in the perceived magnitude of sensory reafference (PSE)
260 without a concomitant worsening in somatosensory precision (JND). In contrast, a voluntary
261 movement leads to a decrease in somatosensory precision (JND) for both sensory reafference
262 and exafference. These effects are observed in the group psychometric fits (**Fig. 2c**). To further
263 illustrate that somatosensory attenuation affects the amplitude (PSE), while tactile gating
264 affects the precision (JND) and not *vice versa*, we tested whether we could predict better the
265 participants' performance in the *attenuation&gating* condition when using the PSE from the
266 *attenuation* condition and the JND from the *gating* condition than the PSE from the *gating*
267 condition and the JND from the *attenuation* condition. Indeed, the first model was significantly
268 better: $n = 24$, $V = 39$, $p < 0.001$, $rrb = -0.74$, $CI^{95} = [-68.980, -12.736]$, $BF_{01} = 0.443$
269 (**Supplementary Fig. S4, Fig. 3a-b**).

270

271 In the abovementioned ANOVAs, there were no significant interactions between the two factors
272 (the origin of touch and the state of the limb), neither for the PSEs nor for the JNDs, according
273 to both frequentist and Bayesian analyses. This indicates that the effect of the left limb state
274 was not influenced by the effect of the origin of touch, neither for the PSE nor for the JND.
275 Instead, the two effects just added up when simultaneously present. To further test whether the
276 effects produced by each phenomenon relate to each other at all, we performed a correlation
277 analysis across the PSEs and JNDs. No significant correlations were detected between any of
278 the PSEs and any of the JNDs (all p -values > 0.225 , $BF_{01} = [1.971, 3.950]$). The only significant
279 correlation found within PSEs was between the PSE in the *attenuation* condition and the PSE
280 in the *attenuation&gating* condition ($t(22) = 4.89$, $r = 0.722$, $p < 0.001$, $CI^{95} = [0.449, 0.871]$,
281 $BF_{01} = 0.002$) (**Fig. 3c**). That is, the weaker the participants perceived the magnitude of their
282 self-generated touch during rest, the weaker the magnitude of their self-generated touch during
283 movement felt. Given that the PSEs significantly dropped in these two conditions and that these
284 decreases correlated with each other, this result provides further support that their common
285 experimental denominator, i.e., the reafferent nature of the touch, was responsible for the drop
286 in the PSE and thus for the attenuation phenomenon. In contrast, the JND in the *gating* condition
287 was significantly correlated only with the *attenuation&gating* condition ($t(22) = 3.47$, $r = 0.595$,
288 $p = 0.008$, $CI^{95} = [0.252, 0.805]$, $BF_{01} = 0.047$) (**Fig. 3d**). This specific correlation means that
289 the worse the somatosensory precision of an external touch when participants moved their
290 receiving hand, the worse the sensory precision for a self-generated touch during the same
291 movement of the receiving hand. Given that the JNDs significantly increased only in these two
292 conditions and that these increases correlated with each other, this result provides evidence that
293 their common experimental denominator, i.e., the left limb's movement that receives the
294 touches, was responsible for the increase in the JND.

295



296
297

Fig. 3. Model predictions and scatterplots for PSEs and JNDs. (a) Average participants' responses in the *attenuation&gating* condition (yellow) and average predicted responses using the parameters from the *attenuation* and *gating* conditions (blue). The responses depicted in dark blue used the PSE of the *attenuation* condition and the JND from the *gating* condition, while the responses depicted in light blue used the PSE of the *gating* condition and the JND of the *attenuation* condition. Error bars and ribbons represent 95% confidence intervals. (b) For each participant, we estimated the Bayesian Information Criterion (BIC) of the fitted logistic model in the *attenuation&gating* condition and the two models with fixed parameters from the *attenuation* and *gating* conditions. The model using the PSE of the *attenuation* condition and the JND of the *gating* condition was a significantly better model than the one using the PSE of the *gating* condition and the JND from the *attenuation* condition. The upper right panel represents the same data after excluding one participant corresponding to the outlier observation, for illustration purposes. The exclusion of the outlier did not change the statistical results. (c) The participants' PSEs in the *attenuation* condition were significantly correlated with those in the *attenuation&gating* condition. (d) The participants' JNDs in the *gating* condition were significantly correlated with those in the *attenuation&gating* condition. There were no significant correlations between PSEs and JNDs.

314

315 A common finding in tactile gating studies is that the gating effects are stronger with higher
316 movement velocities^{33,36,40,41}; that is, the faster the limb movements are, the worst the

317 perception of the moving limb. Therefore, one could hypothesize that any differences observed
318 between the *gating* and the *attenuation&gating* conditions might be due to differences in the
319 velocity of the participants' movements. Since there were no significant JND differences in
320 these two conditions (**Fig. 2**), which was further supported by a Bayesian analysis, this concern
321 can be ruled out. However, one can argue that the PSE in the *attenuation&gating* condition was
322 lower than the PSE in the *attenuation* condition because the participants moved faster in the
323 *attenuation&gating* condition and not because of the refferent nature of the touch. This
324 concern can also be ruled out since, rather than faster, we observed that the participants moved
325 slightly slower in the *attenuation&gating* condition (20.3 ± 0.003 cm/s) than in the *gating*
326 condition (23.3 ± 0.003 cm/s): (peak trial velocity; $t(23) = -4.062$, $p < 0.001$, *Cohen's d* = -
327 0.829, $CI^{95} = [-0.001, -0.004]$, $BF_{01} = 0.015$). Although the total distances the participants ran
328 with their left arm were comparable, participants in the *attenuation&gating* condition moved
329 slower because they had to coordinate both their arms to tap the sensor that the left arm moves
330 with the right hand (**Fig. 1d**). This difference was further confirmed when looking at the peak
331 velocities during the *test* tap between the two conditions (*gating*: 22.2 ± 0.003 cm/s;
332 *attenuation&gating*: 19 ± 0.003 cm/s) (**Supplementary Fig. S5**). Therefore, these kinematic
333 differences cannot explain the significant decrease in the PSEs in the *attenuation&gating*
334 condition compared to the *gating* condition, but they actually underscore the importance of
335 refference in somatosensory attenuation.
336
337

338 Discussion

339
340 The present study contrasted the conditions of attenuation and gating in a single experimental
341 paradigm to investigate the relationship between the two phenomena. To this end, we
342 independently manipulated the origin of the touch (refference *vs* exafference) and the state of
343 the receiving limb (movement *vs* rest), taking on all four possible combinations of these levels.
344 We replicated the classic phenomenon of predictive attenuation of touch^{1,2,16,3-10} by showing
345 that somatosensory refference feels weaker than somatosensory exafference. Importantly,
346 however, this decrease in the perceived amplitude (PSE) was not accompanied by a
347 concomitant worsening in somatosensory precision (JND). Participants had the same
348 discrimination capacity for both refferent and exafferent touches applied on their passive limb,
349 a conclusion supported by Bayesian statistics. Nevertheless, when the limb that receives the
350 touches moved, this voluntary movement *per se* led to a decrease in somatosensory precision
351 (JND) for both refferent and exafferent touches, replicating the classic tactile gating
352 phenomenon^{33-36,39-42}. The two effects did not correlate and did not interact but summed up
353 when present together.
354

355 The main conclusion of the present study is that the predictive attenuation of touch and tactile
356 gating are two distinct perceptual phenomena. Our findings can help conciliate several previous
357 observations on gating and attenuation that have been studied in isolation during recent decades.
358 First, attenuation is observed not only on the active limb⁸ but also on a passive limb (the
359 contralateral hand in the present study), as long as the contact between the body parts is
360 predicted by the voluntary movement^{2-7,9,10,13,16}. In contrast, there is abundant evidence that
361 external touches applied to the limb contralateral to the one that moves are not gated^{34,43,45,72,73}.
362 Second, a touch that results from a passive movement¹⁰ or touches that are simultaneously
363 presented in both hands (double touch)⁶⁷ are not attenuated. In contrast, gating effects have
364 been repeatedly demonstrated for passive movements, both electrophysiologically⁴⁵ and
365 behaviorally^{34,38,39}. Third, self-generated tactile signals are attenuated as long as they are
366 presented at the timing predicted by the action^{1,2,4}; even a 100 ms delay between the movement

367 and its tactile feedback greatly reduces the attenuation of the latter. In contrast, externally
368 generated stimuli are gated when presented at any (unpredicted) timing during the movement
369 ⁴⁵, and importantly, even at hundreds of milliseconds before the movement onset ³⁶. Fourth,
370 whereas gating shows no specificity for the type of motor activity and manifests both during
371 isotonic ^{33–35,43} and isometric ^{35,73} contractions, attenuation is motor command-specific; a
372 consistent but arbitrary and unnatural mapping between the motor command and the touch, for
373 example, moving a joystick with one hand to produce touch on the other, does not produce
374 attenuation ^{5,6,69}. Together, when seen in light of our findings, these results are not
375 contradictory; instead, they refer to different perceptual phenomena.

376
377 Motor control relies on integrating afferent sensory information with efferent motor signals ⁷⁴.
378 Distinguishing between gating and attenuation is fundamentally important for motor control
379 theories because this can indicate a different integration or weighting mechanism of the motor
380 and sensory information depending on the context. One well-established computational
381 framework inspired by engineering approaches poses that the brain produces the motor
382 command through an inverse model ⁷⁵ or controller ⁷⁶. A copy of the motor command — termed
383 ‘efference copy’ — is used by a forward model to predict the expected sensory feedback of the
384 movement, which is then combined with the actual sensory input to estimate the state of the
385 body ^{56,75–77}. With respect to the attenuation of sensory reafference, it has been proposed that
386 the prediction signal of the forward model is used to ‘cancel’ the sensory reafference ^{17,56,78–80}.
387 In other words, central motor processes play a major role in somatosensory attenuation
388 compared to the actual sensory feedback. Support for this comes from studies showing that
389 conditions that present highly predictable touches but in the absence of movement do not yield
390 attenuation ^{2,10} (see also ^{81–83} for similar conclusions). The dependence of attenuation on action
391 prediction was further shown when participants attenuated touches applied on one hand that
392 were predicted by their other hand’s movement, even when the two hands unexpectedly failed
393 to make contact ³. In further agreement, neuroimaging studies on somatosensory attenuation
394 consistently report activation of the cerebellum ^{11–14,84}, a structure that is associated with motor
395 prediction ^{74,85–88}.

396
397 In contrast, this computational account that relies on action prediction, efference copy, and
398 internal forward models is inapplicable for tactile gating, since gated touches can be of
399 exafferent nature and occur at any (unpredictable) time during movement, even before
400 movement onset ^{36–38,47}. In other words, there is no information that the brain can use to predict
401 the exafferent touches with the forward model because there is no causal relationship between
402 the motor command and sensory input. This observation agrees with the proposal that
403 peripheral afferent signals from muscle spindles and joint afferents play the major role in gating
404 ^{36,45}, and the fact that gating effects have also been observed during passive movement, without
405 significant differences from active movements ^{34,38}. Then, if efference copy is not the basis for
406 gating, how can the gating effects be computationally explained?

407
408 The alternative computational framework of active inference has been proposed to explain
409 somatosensory attenuation⁵⁹; however, based on an assumed equivalence between attenuation
410 and gating. The active inference approach refutes the necessity of an efference copy, and
411 emphasizes the importance of a generative model and reflex arcs in the place of forward and
412 inverse models, and controllers ^{89,90}. According to the active inference account, the brain
413 predicts the sensory input that would be expected from a specific action, and the body moves
414 in order to fulfill these sensory predictions. Motor commands are thus conceptually replaced by
415 proprioceptive predictions, and action occurs as a way to minimize the proprioceptive
416 prediction errors when the movement has not been yet executed ⁹¹. A major role is assigned to

417 the precision (i.e., reliability) that weights these sensory prediction errors depending on the
418 context, and can be manipulated through attention allocation. Within this computational
419 architecture, attenuation of somatosensory reafference is seen as a reduction in the precision of
420 somatosensory evidence during movement in order to allow the expression of proprioceptive
421 predictions that trigger the movement ⁵⁹. In other words, the agent attends away from
422 somatosensory input in order to execute the movement. However, this proposal does not address
423 the attenuation of sensory reafference with respect to exafference, since the agent should
424 theoretically attend away from *all* somatosensory input, independently of their source.
425 Moreover, the proposal cannot explain why increasing the precision of the proprioceptive
426 prediction errors on the hand that is to move would reduce the precision of somatosensory
427 prediction errors on the contralateral limb that is not meant to move and thus, there should not
428 exist any proprioceptive predictions about it. In contrast, the active inference account can
429 sufficiently explain the tactile gating effect; i.e., the reduction in the precision of somatosensory
430 input on the moving limb during the movement.

431
432 A recent study ⁶⁴ suggested that action prediction does not produce somatosensory attenuation
433 but enhancement and argued that the attenuation observed in all earlier experiments is actually
434 due to nonpredictive gating processes. This claim cannot be supported based on several
435 observations and arguments. First, the present results showed that the predictive attenuation of
436 touch and gating are different phenomena; if sensory attenuation was the same as tactile gating,
437 then *all* stimuli applied on the moving limb would be attenuated. In contrast, we show that
438 sensory reafference is selectively attenuated compared to sensory exafference, both in a passive
439 and a moving limb. Similar results were shown in ⁷⁹, where participants attenuated only their
440 reafferent touches and not exafferent touches presented at the same limb simultaneously.
441 Second, Thomas and colleagues ⁶⁴ provided participants with an arbitrary mapping between the
442 movement of one hand and sensory feedback on the other hand. Using a very similar setup, a
443 study from 2006 ³ found neither attenuation, which is consistent with the predictive account of
444 attenuation, nor enhancement effects, which is inconsistent with those from Thomas and
445 colleagues ⁶⁴. Third, it is essential to keep in mind that attenuation has also been shown on an
446 anesthetized limb ⁸ and for imagined movements ⁹, further emphasizing the contribution of
447 motor prediction in relation to peripheral feedback for somatosensory attenuation. Finally, it
448 has been shown that when reaching with one arm towards the other, the perceived intensity of
449 an external tactile stimulus applied to the passive target limb is enhanced ⁹². Although we
450 believe that future experimentation is needed to understand and replicate the reported
451 enhancement effects ⁶⁴, we speculate that, as in ⁹², increased spatial attention or other kinematic
452 differences play a significant role in the somatosensory enhancement reported by Thomas and
453 colleagues ⁶⁴.

454
455 We conclude that the human brain uses two different basic processes to suppress reafferent and
456 exafferent information during movement and rest. This separation of attenuation and gating can
457 explain why although we cannot tickle ourselves because we attenuate our self-tickles, we do
458 tense our muscles when being tickled by others to decrease our sensitivity to the external tickles.

459

460 **Materials and Methods**

461

462 *Participants*

463 After providing written informed consent, twenty-four participants (12 women and 12 men, 22
464 right-handed, 1 ambidextrous, 1 left-handed) aged 21–40 years participated. Handedness was
465 assessed using the Edinburgh Handedness Inventory ⁹³. The sample size was set to twenty-four
466 (24) before data collection commenced based on our previous studies using the same methods

467 ^{4,10} while ensuring a counterbalanced order of conditions. The Swedish Ethical Review
468 Authority (<https://etikprovningssmyndigheten.se/>) approved the study (no. 2016/445- 31/2,
469 amendment 2019-04536). All participants provided their written informed consent.

470

471 *General Procedure*

472 Participants sat comfortably on a chair with their arms placed on a table. Their left hands rested
473 palm up, with their index fingers placed on a molded support. The right arms rested palm down
474 on top of a set of sponges. In each trial, a motor (Maxon EC Motor EC 90 flat; Switzerland)
475 delivered two taps (the *test* tap and the *comparison* tap) on the pulp of their left index finger
476 through a cylindrical probe (25 mm height) with a flat aluminum surface (20 mm diameter)
477 attached to the motor's lever. A force sensor (FSG15N1A, Honeywell Inc.; diameter, 5 mm;
478 minimum resolution, 0.01 N; response time, 1 ms; measurement range, 0–15 N) within the
479 probe recorded the forces applied on the left index finger. Following the presentation of the two
480 taps, participants had to verbally indicate which tap felt stronger: the first or the second.

481

482 A wooden surface was placed under the motor and the sensors. This surface was placed on top
483 of two commercially available drawer runners (IKEA, [https://www.ikea.com/us/en/p/besta-
484 drawer-runner-soft-closing-40348715/](https://www.ikea.com/us/en/p/besta-drawer-runner-soft-closing-40348715/)). One side of the runners was attached to the table with
485 Velcro material, and the other side was attached to the bottom side of the surface. With this
486 configuration, the surface – with the motor, the sensors and the participants' hands – could be
487 moved forward and backward.

488

489 In all conditions, the *comparison* tap was delivered on the left index finger with a random delay
490 of 800-1500 ms from the *test* tap. In the *attenuation* and *attenuation&gating* conditions (**Fig.**
491 **1b, d**), the tap of the participants' right index fingers on the force sensor triggered the *test* tap
492 on their left index finger with an intrinsic delay of ≈ 36 ms.

493

494 In the *gating* and *attenuation&gating* conditions (**Fig. 1c, d**), participants were asked to extend
495 their elbow upon the auditory 'go' cue. The extension of the elbow moved the platform forward
496 on the table (**Fig. 1f**). A green tape on the table (**Fig. 1i**) indicated the start position of the
497 platform, while a red tape indicated its end position. The participants were asked to move the
498 platform from the start position to the end position (distance = 25 cm). During the movement
499 of the left arm, the participants received the *test* tap on their left index finger. Before the
500 condition started, we emphasized to the subjects that their task was to pay attention to the force
501 that they would receive during the movement, rather than covering exactly the distance between
502 the lines. Moreover, the participants were trained to perform the movement in approximately
503 1000-1500 ms after the 'go' cue and then stop. In the *gating* condition, the *test* tap was applied
504 800 ms after the 'go' cue so that its delivery was during the movement. Similarly, in the
505 *attenuation&gating* condition, the participants triggered the *test* tap during the movement. The
506 *comparison* tap was applied 800-1500 ms after the test tap to ensure that the participants had
507 stopped moving. Once the participants gave a response, they returned the platform to the start
508 position.

509

510 A motion tracking sensor (6DOF Polhemus Fastrak, USA, weight = 9.1 g, dimensions = 2.29
511 cm x 2.82 cm x 1.52 cm) was placed on top of the platform to record the motion of the platform
512 due to the movement of the participants' left arm. The sensor recorded the x, y and z positions
513 at a sampling rate of approximately 120 Hz.

514

515 Each condition included 70 trials. The test tap was set to 2 N, while the intensity of the
516 comparison tap was systematically varied among seven different force levels (1, 1.5, 1.75, 2,

517 2.25, 2.5 or 3 N). Each tap lasted for 100 ms. On every trial, participants verbally indicated
518 which tap on their left index finger felt stronger: the first (*test*) or the second (*comparison*).
519 Participants were told not to try to balance their responses (50% first and 50% second), and
520 they were further instructed to make their best guess if the intensity of the two taps felt similar.
521

522 In addition, participants were administered white noise through a pair of headphones to
523 preclude any sounds created by the motor to serve as a cue for the task. The loudness of the
524 white noise was adjusted so that participants could clearly hear the auditory cues of the trial. In
525 all conditions, the view of the pulp of the left index finger was occluded. Participants were
526 asked to fixate on a cross placed on a wall 2 m opposite them, but they were allowed to look at
527 the force sensor to guide the movement of the right index finger when needed (**Fig. 1b, d**). No
528 feedback was provided to the participants about their responses.
529

530 *Force discrimination analysis*

531 In each condition, the participants' responses were fitted with a generalized linear model using
532 a *logit* link function (Equation 1):

$$533 \quad p = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}} \text{ (Equation 1)}$$

534
535 We extracted two parameters of interest: the PSE, which represents the intensity at which the
536 test tap felt as strong as the comparison tap ($p = 0.5$) and which quantifies the perceived
537 intensity, and the JND, which reflects the participants' discrimination capacity. Before fitting
538 the responses, the values of the applied comparison taps were binned to the closest value with
539 respect to their theoretical values (1, 1.5, 1.75, 2, 2.25, 2.5 or 3 N).
540

541 *Kinematic analysis.*

542 Both position and velocity data were smoothed with a moving average filter in MATLAB
543 2018a. Velocity was calculated as the first derivative of position. To calculate the distance
544 participants ran in every trial of each condition, we calculated the minimum and the maximum
545 position of the platform during the entire trial duration. The peak trial velocity was defined as
546 the peak velocity of the entire trial. The peak tap velocity was defined as the peak velocity
547 during the period that the *test* tap was applied.
548

549 *Rejection of trials*

550 After data collection, one hundred seventy-three (173) trials out of 6720 (2.57%) were rejected.
551 First, in thirty-four trials (34), the intensity of the *test* tap (2 N) was not applied accurately (*test*
552 tap < 1.85 N or *test* tap > 2.15 N), and in sixteen (16) trials, the responses were missing. Second,
553 we rejected one hundred seventeen (117) trials in total from the *gating* and *attenuation&gating*
554 conditions because participants either did not move their left arm (or moved it too slowly)
555 during the *test* tap (mean velocity < 10 cm/s) or they moved it during the *comparison* tap (mean
556 velocity > 5 cm/s). The thresholds were based on a previous study⁴⁰ showing no gating effects
557 for velocities smaller than 5 cm/s. The analysis was therefore performed with 6547 trials in
558 total.
559

560 *Statistical analysis*

561 We used R⁹⁴ and JASP⁹⁵ to analyze our data. The data normality was assessed using the
562 Shapiro-Wilk test. Depending on the data normality, we then performed planned comparisons
563 using either a paired t-test or a Wilcoxon signed-rank test. We report 95% confidence intervals
564 (CI^{95}) for each statistical test. Effect sizes are given by the partial eta-squared (η_p^2) for the
565 ANOVAs, by the Cohen's *d* for t-tests or by the matched rank biserial correlation *rrb* for the
566 Wilcoxon signed-rank tests. In addition, a Bayesian factor analysis using default Cauchy priors

567 with a scale of 0.707 was carried out for all statistical tests to provide information about the
568 level of support for the null hypothesis compared to the alternative hypothesis (BF_{01}) given the
569 data. Finally, correlations were performed using Pearson's coefficient r given that the data were
570 normally distributed. All tests were two-tailed.

571
572 *Corrections for multiple comparisons*

573 Since our PSE and JND comparisons were planned, we did not apply corrections for multiple
574 comparisons. However, all results remained exactly the same when applying corrections for
575 false discovery rate (FDR) ⁹⁶. In the correlation analyses, we did apply corrections for multiple
576 comparisons (FDR) since, although we expected correlations between the PSEs and between
577 the JNDs, we had no *a priori* hypotheses for correlations between PSEs and JNDs.

578
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585
586 **Conflicts of interest/Competing interests**

587 The authors declare no competing financial interests.

588
589 **Authors' contributions**

590 K.K. and H.H.E. conceived and designed the experiment. K.K. collected the data and conducted
591 the statistical analysis. K.K. and H.H.E. wrote the manuscript.

592
593 **References**

- 594 1. Blakemore, S. J., Frith, C. D. & Wolpert, D. M. Spatio-temporal prediction modulates
595 the perception of self-produced stimuli. *J. Cogn. Neurosci.* **11**, 551–559 (1999).
- 596 2. Bays, P. M., Wolpert, D. M. & Flanagan, J. R. Perception of the consequences of self-
597 action is temporally tuned and event driven. *Curr. Biol.* **15**, 1125–1128 (2005).
- 598 3. Bays, P. M., Flanagan, J. R. & Wolpert, D. M. Attenuation of self-generated tactile
599 sensations is predictive, not postdictive. *PLoS Biol.* **4**, 281–284 (2006).
- 600 4. Kilteni, K., Houborg, C. & Ehrsson, H. H. Rapid learning and unlearning of sensory
601 delays in self-touch. *Elife* 1–17 (2019). doi:10.7554/eLife.42888.001
- 602 5. Shergill, S. S., Bays, P. M., Frith, C. D. & Wolpert, D. M. Two eyes for an eye: the
603 neuroscience of force escalation. *Science* **301**, 187 (2003).
- 604 6. Kilteni, K. & Ehrsson, H. H. Sensorimotor predictions and tool use: Hand-held tools
605 attenuate self-touch. *Cognition* **165**, 1–9 (2017).
- 606 7. Kilteni, K. & Ehrsson, H. H. Body ownership determines the attenuation of self-
607 generated tactile sensations. *Proc. Natl. Acad. Sci.* 201703347 (2017).
608 doi:10.1073/PNAS.1703347114
- 609 8. Walsh, L. D., Taylor, J. L. & Gandevia, S. C. Overestimation of force during matching
610 of externally generated forces. *J. Physiol.* **589**, 547–557 (2011).
- 611 9. Kilteni, K., Andersson, B. J., Houborg, C. & Ehrsson, H. H. Motor imagery involves
612 predicting the sensory consequences of the imagined movement. *Nat. Commun.* **9**,
613 1617 (2018).
- 614 10. Kilteni, K., Engeler, P. & Ehrsson, H. H. Efference Copy Is Necessary for the
615 Attenuation of Self-Generated Touch. *iScience* (2020). doi:10.1016/j.isci.2020.100843
- 616 11. Blakemore, S. J., Wolpert, D. M. & Frith, C. D. Central cancellation of self-produced

- 617 tickle sensation. *Nat. Neurosci.* **1**, 635–640 (1998).
- 618 12. Shergill, S. S. *et al.* Modulation of somatosensory processing by action. *Neuroimage*
619 **70**, 356–362 (2013).
- 620 13. Kilteni, K. & Ehrsson, H. H. Functional Connectivity between the Cerebellum and
621 Somatosensory Areas Implements the Attenuation of Self-Generated Touch. *J.*
622 *Neurosci.* **40**, 894 LP – 906 (2020).
- 623 14. Blakemore, S. J., Frith, C. D. & Wolpert, D. M. The cerebellum is involved in
624 predicting the sensory consequences of action. *Neuroreport* **12**, 1879–1884 (2001).
- 625 15. Blakemore, S. J., Wolpert, D. M. & Frith, C. D. The cerebellum contributes to
626 somatosensory cortical activity during self-produced tactile stimulation. *Neuroimage*
627 **10**, 448–459 (1999).
- 628 16. Wolpe, N. *et al.* Ageing increases reliance on sensorimotor prediction through
629 structural and functional differences in frontostriatal circuits. *Nat. Commun.* **7**, (2016).
- 630 17. Blakemore, S. J., Wolpert, D. M. & Frith, C. Why can't you tickle yourself?
631 *Neuroreport* **11**, R11–R16 (2000).
- 632 18. Leavens, D. A. & Bard, K. A. Tickling. *Current Biology* (2016).
633 doi:10.1016/j.cub.2015.06.014
- 634 19. Weiskrantz, L., Elliott, J. & Darlington, C. Preliminary observations on tickling
635 oneself. *Nature* **230**, 598–599 (1971).
- 636 20. Crapse, T. B. & Sommer, M. A. Corollary discharge across the animal kingdom.
637 *Nature Reviews Neuroscience* **9**, 587–600 (2008).
- 638 21. Cullen, K. E. Sensory signals during active versus passive movement. *Curr. Opin.*
639 *Neurobiol.* **14**, 698–706 (2004).
- 640 22. Straka, H., Simmers, J. & Chagnaud, B. P. A New Perspective on Predictive Motor
641 Signaling. *Curr. Biol.* **28**, R232–R243 (2018).
- 642 23. Schneider, D. M. & Mooney, R. How movement modulates hearing. *Annual Review of*
643 *Neuroscience* (2018). doi:10.1146/annurev-neuro-072116-031215
- 644 24. Brooks, J. X. & Cullen, K. E. Predictive Sensing: The Role of Motor Signals in
645 Sensory Processing. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*
646 (2019). doi:10.1016/j.bpsc.2019.06.003
- 647 25. Poulet, J. F. A. & Hedwig, B. The cellular basis of a corollary discharge. *Science (80-*
648 *).* (2006). doi:10.1126/science.1120847
- 649 26. Poulet, J. F. A. & Hedwig, B. Corollary discharge inhibition of ascending auditory
650 neurons in the stridulating cricket. *J. Neurosci.* (2003). doi:10.1523/jneurosci.23-11-
651 04717.2003
- 652 27. Schneider, D. M., Sundararajan, J. & Mooney, R. A cortical filter that learns to
653 suppress the acoustic consequences of movement. *Nature* (2018). doi:10.1038/s41586-
654 018-0520-5
- 655 28. Fukutomi, M. & Carlson, B. A. A History of Corollary Discharge: Contributions of
656 Mormyrid Weakly Electric Fish. *Frontiers in Integrative Neuroscience* (2020).
657 doi:10.3389/fnint.2020.00042
- 658 29. Sawtell, N. B. Neural Mechanisms for Predicting the Sensory Consequences of
659 Behavior: Insights from Electrosensory Systems. *Annual Review of Physiology* (2017).
660 doi:10.1146/annurev-physiol-021115-105003
- 661 30. Cullen, K. E. The vestibular system: Multimodal integration and encoding of self-
662 motion for motor control. *Trends in Neurosciences* (2012).
663 doi:10.1016/j.tins.2011.12.001
- 664 31. Brooks, J. X., Carriot, J. & Cullen, K. E. Learning to expect the unexpected: Rapid
665 updating in primate cerebellum during voluntary self-motion. *Nat. Neurosci.* **18**, 1310–
666 1317 (2015).

- 667 32. Roy, J. E. & Cullen, K. E. Dissociating Self-Generated from Passively Applied Head
668 Motion: Neural Mechanisms in the Vestibular Nuclei. *J. Neurosci.* (2004).
669 doi:10.1523/JNEUROSCI.3988-03.2004
- 670 33. Angel, R. W. & Malenka, R. C. Velocity-dependent suppression of cutaneous
671 sensitivity during movement. *Exp. Neurol.* (1982). doi:10.1016/0014-4886(82)90244-8
- 672 34. Chapman, C. E., Bushnell, M. C., Miron, D., Duncan, G. H. & Lund, J. P. Sensory
673 perception during movement in man. *Exp. Brain Res.* **68**, 516–524 (1987).
- 674 35. Post, L. J., Zompa, I. C. & Chapman, C. E. Perception of vibrotactile stimuli during
675 motor activity in human subjects. *Exp. Brain Res.* **100**, 107–120 (1994).
- 676 36. Williams, S. R., Shenasa, J. & Chapman, C. E. Time course and magnitude of
677 movement-related gating of tactile detection in humans. I. Importance of stimulus
678 location. *J. Neurophysiol.* **79**, 947–963 (1998).
- 679 37. Williams, S. R. & Chapman, C. E. Time course and magnitude of movement-related
680 gating of tactile detection in humans. II. Effects of stimulus intensity. *J. Neurophysiol.*
681 (2000). doi:10.1152/jn.2000.84.2.863
- 682 38. Williams, S. R. & Chapman, C. E. Time course and magnitude of movement-related
683 gating of tactile detection in humans. III. Effect of motor tasks. *J. Neurophysiol.* **88**,
684 1968–1979 (2002).
- 685 39. Chapman, C. E. & Beauchamp, E. Differential controls over tactile detection in
686 humans by motor commands and peripheral reafference. *J. Neurophysiol.* **96**, 1664–
687 1675 (2006).
- 688 40. Cybulska-Klosowicz, A., Meftah, E. M., Raby, M., Lemieux, M. L. & Chapman, C. E.
689 A critical speed for gating of tactile detection during voluntary movement. *Exp. Brain*
690 *Res.* **210**, 291–301 (2011).
- 691 41. Gertz, H., Voudouris, D. & Fiehler, K. Reach-relevant somatosensory signals modulate
692 tactile suppression. *J. Neurophysiol.* **117**, 2262–2268 (2017).
- 693 42. Fraser, L. E. & Fiehler, K. Predicted reach consequences drive time course of tactile
694 suppression. *Behav. Brain Res.* **350**, 54–64 (2018).
- 695 43. Papakostopoulos, D., Cooper, R. & Crow, H. J. Inhibition of cortical evoked potentials
696 and sensation by self-initiated movement in man. *Nature* **258**, 321–324 (1975).
- 697 44. Starr, A. & Cohen, L. G. ‘Gating’ of somatosensory evoked potentials begins before
698 the onset of voluntary movement in man. *Brain Res.* **348**, 183–186 (1985).
- 699 45. Rushton, D. N., Roghwell, J. C. & Craggs, M. D. Gating of somatosensory evoked
700 potentials during different kinds of movement in man. *Brain* **104**, 465–491 (1981).
- 701 46. Giblin, D. R. SOMATOSENSORY EVOKED POTENTIALS IN HEALTHY
702 SUBJECTS AND IN PATIENTS WITH LESIONS OF THE NERVOUS SYSTEM.
703 *Ann. N. Y. Acad. Sci.* **112**, 93–142 (1964).
- 704 47. Chapman, C. E. Active versus passive touch: Factors influencing the transmission of
705 somatosensory signals to primary somatosensory cortex. *Can. J. Physiol. Pharmacol.*
706 **72**, 558–570 (1994).
- 707 48. Lei, Y., Ozdemir, R. A. & Perez, M. A. Gating of sensory input at subcortical and
708 cortical levels during grasping in humans. *J. Neurosci.* (2018).
709 doi:10.1523/JNEUROSCI.0545-18.2018
- 710 49. Azim, E. & Seki, K. Gain control in the sensorimotor system. *Curr. Opin. Physiol.* **8**,
711 177–187 (2019).
- 712 50. Ghez, C. & Lenzi, G. L. Modulation of sensory transmission in cat lemniscal system
713 during voluntary movement. *Pflügers Arch. Eur. J. Physiol.* **323**, 273–278 (1971).
- 714 51. Chapin, J. K. & Woodward, D. J. Modulation of sensory responsiveness of single
715 somatosensory cortical cells during movement and arousal behaviors. *Exp. Neurol.*
716 (1981). doi:10.1016/0014-4886(81)90135-7

- 717 52. Jiang, W., Chapman, C. E. & Lamarre, Y. Modulation of the cutaneous responsiveness
718 of neurones in the primary somatosensory cortex during conditioned arm movements in
719 the monkey. *Exp. Brain Res.* (1991). doi:10.1007/BF00231455
- 720 53. Jiang, W., Lamarre, Y. & Chapman, C. E. Modulation of cutaneous cortical evoked
721 potentials during isometric and isotonic contractions in the monkey. *Brain Res.* (1990).
722 doi:10.1016/0006-8993(90)90010-9
- 723 54. Seki, K. & Fetz, E. E. Gating of sensory input at spinal and cortical levels during
724 preparation and execution of voluntary movement. *J. Neurosci.* **32**, 890–902 (2012).
- 725 55. Seki, K., Perlmutter, S. I. & Fetz, E. E. Sensory input to primate spinal cord is
726 presynaptically inhibited during voluntary movement. *Nat. Neurosci.* **6**, 1309–1316
727 (2003).
- 728 56. McNamee, D. & Wolpert, D. M. Internal Models in Biological Control. *Annu. Rev.*
729 *Control. Robot. Auton. Syst.* **2**, 339–364 (2019).
- 730 57. Collins, D. F., Cameron, T., Gillard, D. M. & Prochazka, A. Muscular sense is
731 attenuated when humans move. *J. Physiol.* **508**, 635–643 (1998).
- 732 58. Juravle, G., Binsted, G. & Spence, C. Tactile suppression in goal-directed movement.
733 *Psychon. Bull. Rev.* (2017). doi:10.3758/s13423-016-1203-6
- 734 59. Brown, H., Adams, R. a., Parees, I., Edwards, M. & Friston, K. Active inference,
735 sensory attenuation and illusions. *Cogn. Process.* **14**, 411–427 (2013).
- 736 60. Limanowski, J. *et al.* Action-Dependent Processing of Touch in the Human Parietal
737 Operculum and Posterior Insula. *Cereb. Cortex* (2020). doi:10.1093/cercor/bhz111
- 738 61. Saradjian, A. H. Sensory modulation of movement, posture and locomotion.
739 *Neurophysiol. Clin.* **45**, 255–267 (2015).
- 740 62. Palmer, C. E., Davare, M. & Kilner, J. M. Physiological and Perceptual Sensory
741 Attenuation Have Different Underlying Neurophysiological Correlates. *J. Neurosci.* **36**,
742 10803–10812 (2016).
- 743 63. Boehme, R., Hauser, S., Gerling, G. J., Heilig, M. & Olausson, H. Distinction of self-
744 produced touch and social touch at cortical and spinal cord levels. *Proc. Natl. Acad.*
745 *Sci.* 201816278 (2019). doi:10.1073/PNAS.1816278116
- 746 64. Thomas, E. R., Yon, D., Lange, F. P. de & Press, C. Action enhances predicted touch.
747 *bioRxiv* (2020). doi:10.1101/2020.03.26.007559
- 748 65. Voss, M., Ingram, J. N., Wolpert, D. M. & Haggard, P. Mere expectation to move
749 causes attenuation of sensory signals. *PLoS One* **3**, 2–6 (2008).
- 750 66. Blakemore, S. J., Smith, J., Steel, R., Johnstone, C. E. & Frith, C. D. The perception of
751 self-produced sensory stimuli in patients with auditory hallucinations and passivity
752 experiences: evidence for a breakdown in self-monitoring. *Psychol. Med.* **30**, 1131–
753 1139 (2000).
- 754 67. Shergill, S. S., Samson, G., Bays, P. M., Frith, C. D. & Wolpert, D. M. Evidence for
755 sensory prediction deficits in schizophrenia. *Am. J. Psychiatry* **162**, 2384–2386 (2005).
- 756 68. Shergill, S. S. *et al.* Functional magnetic resonance imaging of impaired sensory
757 prediction in schizophrenia. *JAMA psychiatry* **71**, 28–35 (2014).
- 758 69. Parees, I. *et al.* Loss of sensory attenuation in patients with functional (psychogenic)
759 movement disorders. *Brain* **137**, 2916–2921 (2014).
- 760 70. Wolpe, N. *et al.* Sensory attenuation in Parkinson’s disease is related to disease
761 severity and dopamine dose. *Sci. Rep.* (2018). doi:10.1038/s41598-018-33678-3
- 762 71. Macerollo, A. *et al.* Dopaminergic Modulation of Sensory Attenuation in Parkinson’s
763 Disease: Is There an Underlying Modulation of Beta Power? *Front. Neurol.* **10**, 1–14
764 (2019).
- 765 72. Cohen, L. G. & Starr, A. Localization, timing and specificity of gating of
766 somatosensory evoked potentials during active movement in man. *Brain* (1987).

- 767 doi:10.1093/brain/110.2.451
- 768 73. Pertovaara, A., Kemppainen, P. & Leppänen, H. Lowered cutaneous sensitivity to
769 nonpainful electrical stimulation during isometric exercise in humans. *Exp. Brain Res.*
770 **89**, 447–452 (1992).
- 771 74. Shadmehr, R. & Krakauer, J. W. A computational neuroanatomy for motor control.
772 *Exp. Brain Res.* **185**, 359–381 (2008).
- 773 75. Kawato, M. Internal models for motor control and trajectory planning. *Curr Opin*
774 *Neurobiol* **9**, 718–727 (1999).
- 775 76. Todorov, E. Optimality principles in sensorimotor control. *Nat. Neurosci.* **7**, 907–15
776 (2004).
- 777 77. Wolpert, D. M. & Ghahramani, Z. Computational principles of movement
778 neuroscience. *Nat. Neurosci.* **3**, 1212–1217 (2000).
- 779 78. Bays, P. M. & Wolpert, D. M. Computational principles of sensorimotor control that
780 minimize uncertainty and variability. *J. Physiol.* **578**, 387–396 (2007).
- 781 79. Bays, P. M. & Wolpert, D. M. Predictive attenuation in the perception of touch. in
782 *Sensorimotor Foundations of Higher Cognition* (eds. Haggard, E. P., Rosetti, Y. &
783 Kawato, M.) **22**, 339–358 (Oxford University Press, 2008).
- 784 80. Wolpert, D. M. & Flanagan, J. R. Motor prediction. *Curr. Biol.* **11**, R729–R732 (2001).
- 785 81. Diedrichsen, J., Verstynen, T., Hon, A., Lehman, S. L. & Ivry, R. B. Anticipatory
786 adjustments in the unloading task: Is an efference copy necessary for learning? *Exp.*
787 *Brain Res.* **148**, 272–276 (2003).
- 788 82. Klaffehn, A. L., Baess, P., Kunde, W. & Pfister, R. Sensory attenuation prevails when
789 controlling for temporal predictability of self- and externally generated tones.
790 *Neuropsychologia* (2019). doi:10.1016/j.neuropsychologia.2019.107145
- 791 83. Bäß, P., Jacobsen, T. & Schröger, E. Suppression of the auditory N1 event-related
792 potential component with unpredictable self-initiated tones: Evidence for internal
793 forward models with dynamic stimulation. *Int. J. Psychophysiol.* (2008).
794 doi:10.1016/j.ijpsycho.2008.06.005
- 795 84. Blakemore, S. J., Wolpert, D. M. & Frith, C. D. The cerebellum contributes to
796 somatosensory cortical activity during self-produced tactile stimulation. *Neuroimage*
797 **10**, 448–459 (1999).
- 798 85. Miall, R. C. & Wolpert, D. M. Forward models for physiological motor control. *Neural*
799 *Networks* **9**, 1265–1279 (1996).
- 800 86. Wolpert, D. M., Miall, R. C. & Kawato, M. Internal models in the cerebellum. *Trends*
801 *in Cognitive Sciences* **2**, 338–347 (1998).
- 802 87. Shadmehr, R., Smith, M. a & Krakauer, J. W. Error correction, sensory prediction, and
803 adaptation in motor control. *Annu. Rev. Neurosci.* **33**, 89–108 (2010).
- 804 88. Therrien, A. S. & Bastian, A. J. The cerebellum as a movement sensor. *Neurosci. Lett.*
805 **0–1** (2018). doi:10.1016/j.neulet.2018.06.055
- 806 89. Adams, R. a., Shipp, S. & Friston, K. J. Predictions not commands: Active inference in
807 the motor system. *Brain Struct. Funct.* **218**, 611–643 (2013).
- 808 90. Friston, K. The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* **11**,
809 127–38 (2010).
- 810 91. Pickering, M. J. & Clark, A. Getting ahead: Forward models and their place in
811 cognitive architecture. *Trends Cogn. Sci.* **18**, 451–456 (2014).
- 812 92. Voudouris, D. & Fiehler, K. Enhancement and suppression of tactile signals during
813 reaching. *J. Exp. Psychol. Hum. Percept. Perform.* (2017). doi:10.1037/xhp0000373
- 814 93. Oldfield, R. C. The assessment and analysis of handedness: the Edinburgh inventory.
815 *Neuropsychologia* **9**, 97–113 (1971).
- 816 94. Core Team, R. R: A language and environment for statistical computing. *R Foundation*

817 *for Statistical Computing* (2018). doi:10.1007/978-3-540-74686-7
818 95. JASP & JASP Team. JASP. [*Computer software*] (2019).
819 96. Benjamini, Y. & Hochberg, Y. Controlling the False Discovery Rate: A Practical and
820 Powerful Approach to Multiple Testing. *J. R. Stat. Soc. Ser. B* (1995).
821 doi:10.1111/j.2517-6161.1995.tb02031.x

Figures

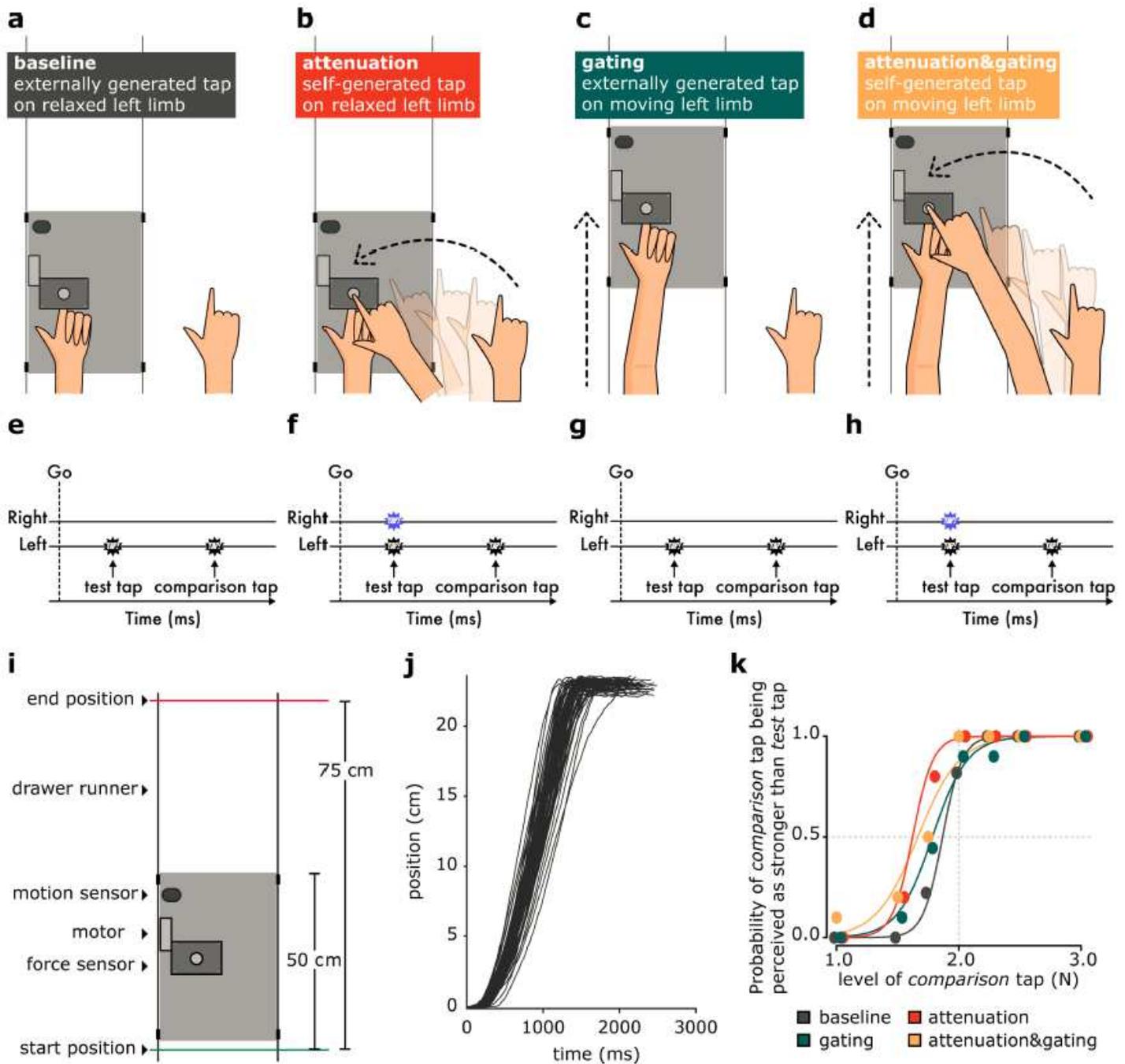


Figure 1

Experimental conditions. Two factors were manipulated in the experiment, resulting in four experimental conditions: whether the left arm was in rest (a, b) or in movement while receiving the test tap (c, d) (state of the left limb) and whether the test tap was externally triggered by the motor (a, c) or self-triggered by the participants' right hand (b, d) (origin of touch). In all four conditions (e-h), the participants received the two taps (test and comparison tap) on the pulp of their left index fingers from the motor (black stars), and they had to verbally indicate which was stronger: the first or the second tap. In the attenuation and

attenuation&gating conditions, the participants self-triggered the test tap on their left index finger by moving their right arm to tap a sensor with their right index finger (blue stars). (i) In the gating and attenuation&gating conditions (c and d), the participants extended their left arm from a start position to an end position, sliding the experimental setup along two drawer runners. During this movement, participants experienced the test tap. A motion sensor recorded the position of the platform in time. (f) Example position traces recorded by the motion sensor for the movements of one participant during the attenuation&gating condition. (g) Responses of a representative participant and fitted logistic models for the four experimental conditions. Data points have been horizontally jittered to avoid overlapping.

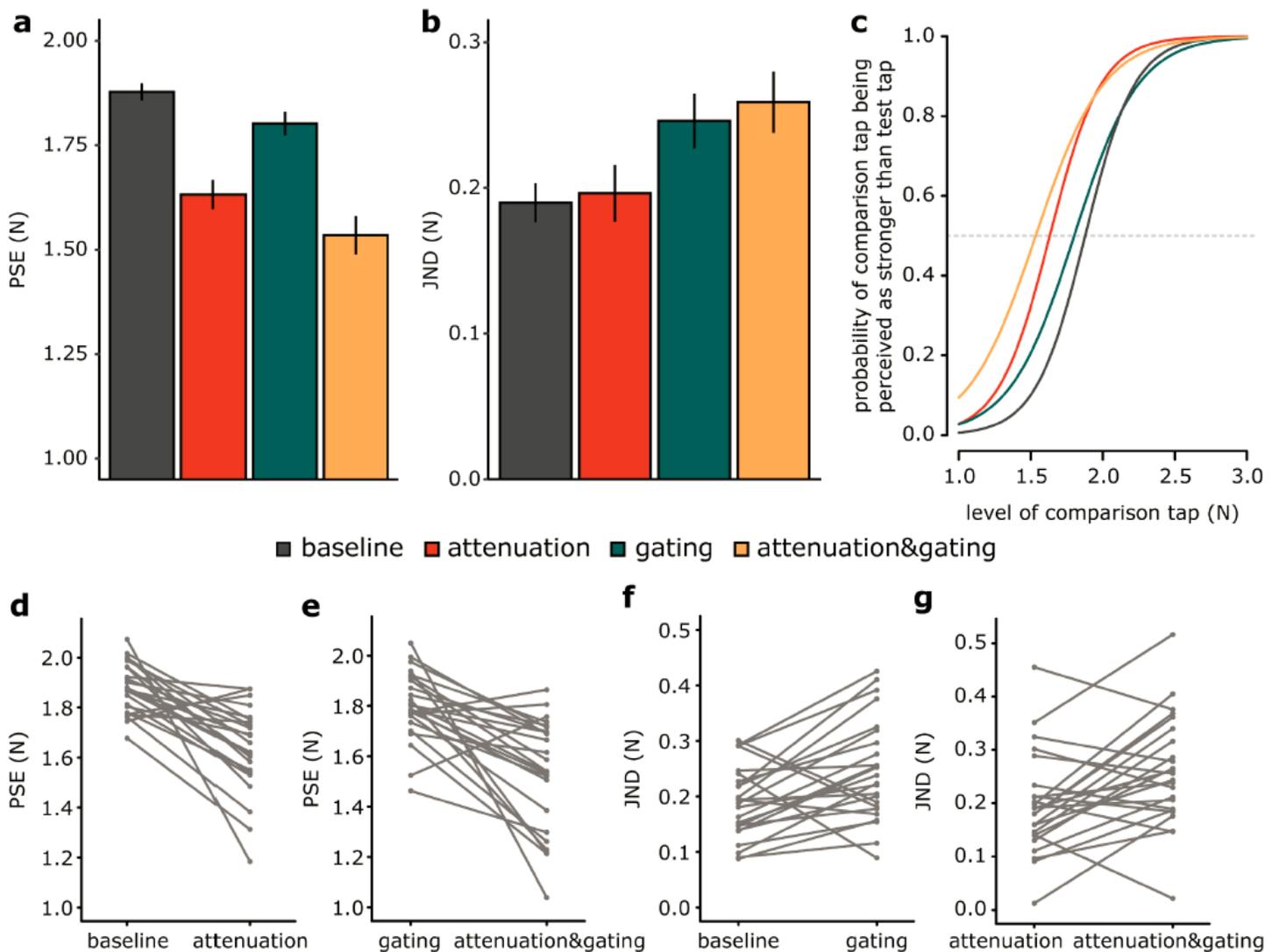


Figure 2

Experimental results. (a, b) Bar graphs show the PSEs and JNDs (mean \pm SEM) for each condition. A lower PSE value indicates a lower perceived magnitude, while a higher JND value indicates a lower somatosensory sensory precision. Reafferent touches produced by the movement of the right arm (attenuation and attenuation&gating conditions) were associated with a significant drop in the PSEs, while the movement of the left arm that receives the touches (gating and attenuation&gating) produces a significant increase in the JNDs. (c) Group psychometric functions for each condition generated using the

mean PSE and the mean JND across participants. The leftward shift of the curves for the attenuation and attenuation&gating conditions illustrates that somatosensory reafference is perceived as weaker than exafference. The flattening of the curves for the gating and attenuation&gating conditions illustrates the worsening in somatosensory precision of both reafference and exafference on a moving limb. (d, e) Line plots illustrate the decreases in PSEs when experiencing reafferent touches compared to exafferent touches, when the left arm is still (d) and when the left arm moves (e). (f, g) Line plots illustrate the increases in JNDs when receiving the touches on a moving limb compared to rest, when the touches are exafferent (f) and when the touches are reafferent (g).

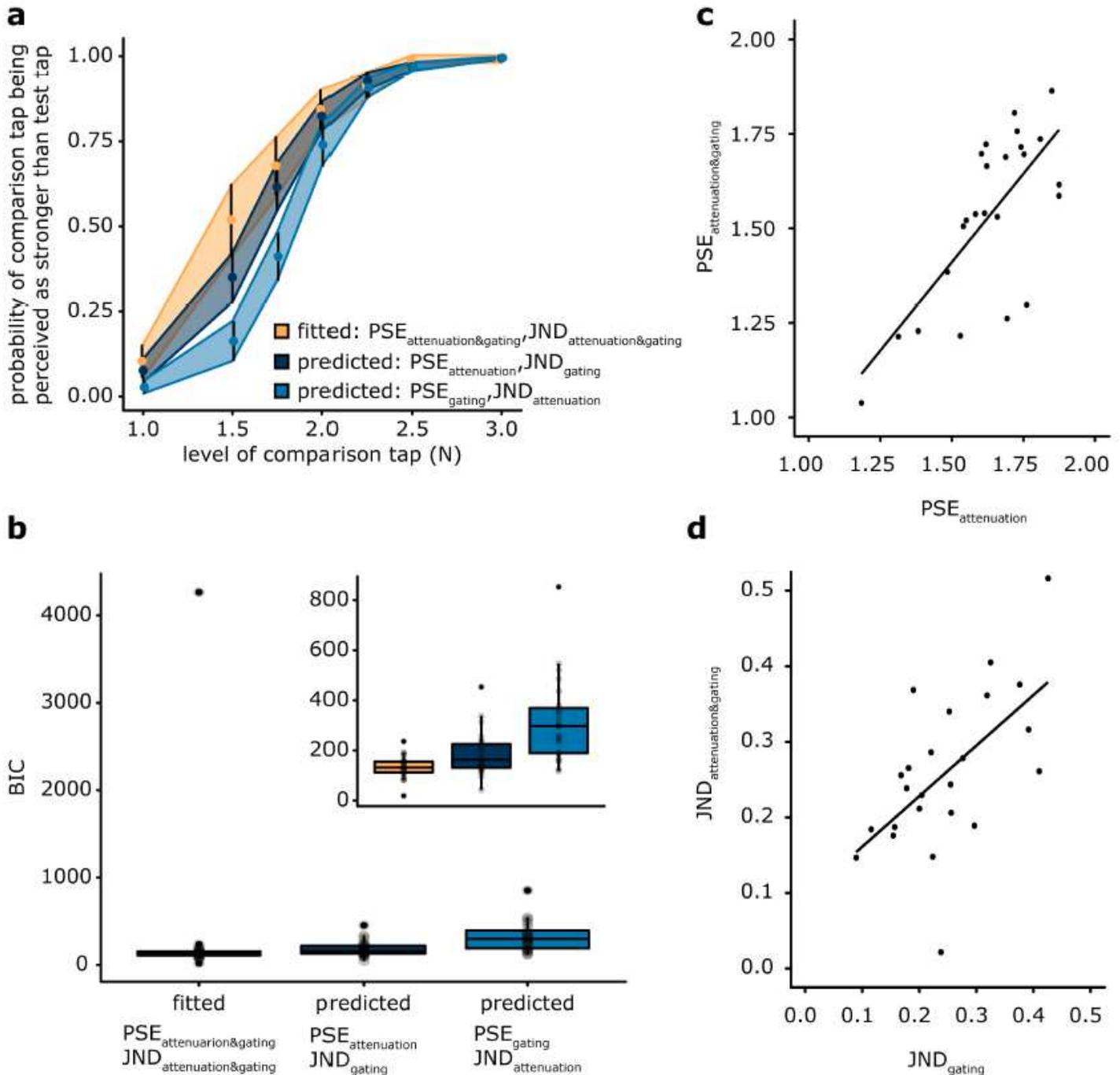


Figure 3

Model predictions and scatterplots for PSEs and JNDs. (a) Average participants' responses in the attenuation&gating condition (yellow) and average predicted responses using the parameters from the attenuation and gating conditions (blue). The responses depicted in dark blue used the PSE of the attenuation condition and the JND from the gating condition, while the responses depicted in light blue used the PSE of the gating condition and the JND of the attenuation condition. Error bars and ribbons represent 95% confidence intervals. (b) For each participant, we estimated the Bayesian Information Criterion (BIC) of the fitted logistic model in the attenuation&gating condition and the two models with fixed parameters from the attenuation and gating conditions. The model using the PSE of the attenuation condition and the JND of the gating condition was a significantly better model than the one using the PSE of the gating condition and the JND from the attenuation condition. The upper right panel represents the same data after excluding one participant corresponding to the outlier observation, for illustration purposes. The exclusion of the outlier did not change the statistical results. (c) The participants' PSEs in the attenuation condition were significantly correlated with those in the attenuation&gating condition. (d) The participants' JNDs in the gating condition were significantly correlated with those in the attenuation&gating condition. There were no significant correlations between PSEs and JNDs.

Supplementary Files

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