

1 **Rapid learning and unlearning of predicted** 2 **sensory delays in self-generated touch**

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14 **Abstract**

15 Self-generated touch feels less intense and less ticklish than identical externally
16 generated touch. This somatosensory attenuation occurs because the brain predicts the
17 tactile consequences of our self-generated movements. To produce attenuation, the
18 tactile predictions need to be time-locked to the movement, but how the brain maintains
19 this temporal tuning remains unknown. Using a bimanual self-touch paradigm, we
20 demonstrate that people can rapidly unlearn to attenuate touch immediately after their
21 movement and learn to attenuate delayed touch instead, after repeated exposure to a
22 systematic delay between the movement and the resulting touch. The magnitudes of the
23 unlearning and learning effects are correlated and dependent on the number of trials
24 that participants have been exposed to. We further show that delayed touches feel less
25 ticklish and non-delayed touches more ticklish after exposure to the systematic delay.
26 These findings demonstrate that the attenuation of self-generated touch is adaptive.

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29 **Keywords**

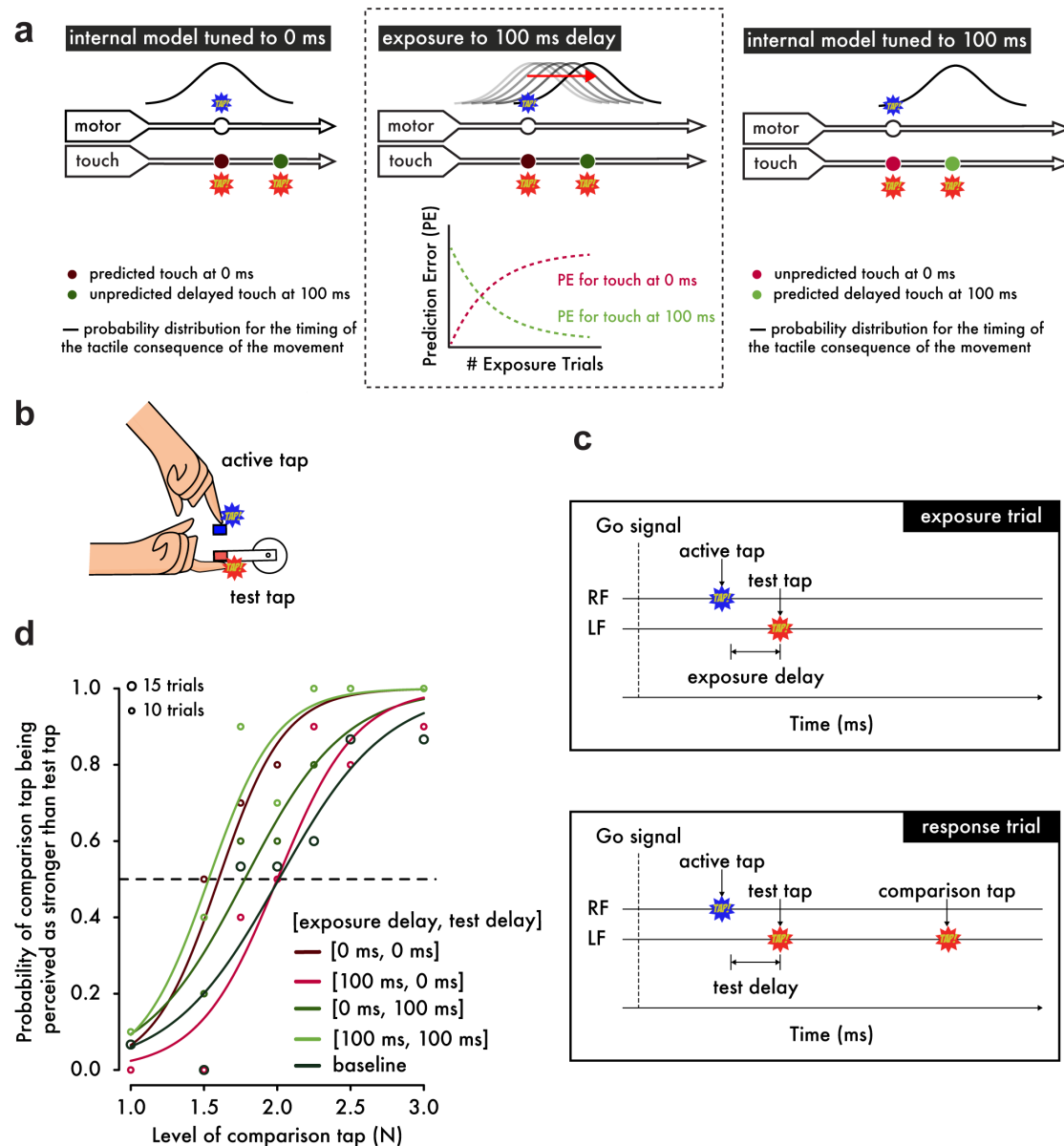
30 somatosensory attenuation, sensorimotor delays, prediction errors, forward models,
31 tickling; motor learning

32 Introduction

33 It is theorized that the brain uses internal models to anticipate the sensory consequences
34 of voluntary movements on the basis of a copy of the motor command (efference copy)
35 [1–4]. These sensory predictions are used to achieve efficient online motor control, to
36 ensure movement stability and to reduce uncertainty, as the actual sensory feedback is
37 delayed due to sensory transduction times [5–7]. In addition, the predictions of the
38 internal models are also used for attenuating the perception of self-produced input,
39 thereby increasing the salience of unpredicted external signals and facilitating the
40 perceptual distinction between the self and the environment [8,9]. For example, when
41 one actively touches one’s left hand with one’s right (self-touch), the touch feels less
42 intense than identical touches applied to the left hand by another person or a machine
43 [8,10,11]. This is because the self-induced touch has been predicted by the internal
44 model.

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46 Importantly, the predictions of the internal models are useful only if the models
47 constitute accurate representations of the body and the current environmental dynamics
48 [1,7,12–15]. Biased predictions would not only be detrimental to motor performance
49 but also prevent one from distinguishing the sensory feedback of one’s own movements
50 from that produced by external causes. A good illustration of this sharp tuning of the
51 internal models is that their predictions are temporally locked to the given movement
52 (**Fig. 1a**, left): for example, during self-touch, tactile feedback is expected at the time
53 of contact between the hands, and touch that is artificially delayed (even by only 100
54 ms) shows reduced attenuation and is attributed to external causes rather than the self
55 [11,16].

56
57 Here, we demonstrate that the brain can rapidly (a) unlearn to expect touch at the
58 moment of contact between the hands and (b) learn to predict delayed touch instead.
59 Using a device that simulates bimanual self-touch (**Fig. 1b**), thirty subjects were
60 initially exposed to 500 trials in which a systematic delay of 0 ms or 100 ms (*exposure*
61 *delay*) was inserted between the voluntary tap of the right index finger and the resulting
62 touch on the pulp of the relaxed left index finger [17] (**Fig. 1c**). We reasoned that when
63 repeatedly presented with the 100 ms discrepancy between the predicted and actual
64 somatosensory feedback, the brain would be forced to retune the internal model in order
65 to account for this delay and thus keep the predictions accurate (**Fig. 1a**, middle). This
66 hypothesis led to two specific predictions (**Fig. 1a**, right). First, when the 100 ms delay
67 is removed after the exposure period, participants should have stopped predicting and
68 therefore attenuating the sensation of the tap. Second, when the delay is maintained
69 after the exposure period, the participants should have started predicting and thus
70 attenuating the delayed tap. We tested both of these predictions in a psychophysical
71 task [16] performed immediately after the initial exposure (**Fig. 1d**) (see also *Materials*
72 *and Methods*).



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Figure 1 | Experimental Hypotheses, Procedures and Psychophysical Analysis. (a) (Left)

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When the internal model is tuned to 0 ms as in natural situations, the probability distribution

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for the occurrence of touch on the left index finger (approximated as a normal distribution [16])

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peaks at 0 ms after the movement of the right index finger. Touch presented at 0 ms shows the

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strongest attenuation, while touch at 100 ms is less attenuated because it is less likely to have

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been self-generated. (Middle) When exposed to systematic delays of 100 ms between the finger

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movement and the touch, the model parameter is gradually updated to 100 ms, which can be

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viewed as a simple incremental shift in the probability distribution by 100 ms. Before the

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exposure, there is an error associated with the touch predicted at 0 ms and presented at 100 ms

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but no error related to the naturally presented touch at 0 ms. During the learning period, this

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pattern gradually reverses: a prediction error for the touch presented at 0 ms appears and grows

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over exposure time, while the prediction error for the touch at 100 ms decays and reaches a

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minimum. (Right) After prolonged exposure, the touch at 0 ms has low probability, produces a

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large prediction error and will not be attenuated, whereas the touch at 100 ms has high

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probability, produces no prediction error and will be attenuated. (b) Participants were instructed

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to use their right index finger to tap a sensor (active tap) that delivered a tap on their left index

90 finger (test tap). (c) In the *exposure trials*, participants simply tapped the sensor with their right
91 index finger (RF) and received the tap on the left index finger (LF) with a 0 ms or a 100 ms
92 *exposure delay*. In the *response trials*, participants received a second tap on their left index
93 finger (comparison tap) and were required to indicate which tap was stronger: the test or the
94 comparison tap. The test tap could be presented with a *test delay* of either 0 ms or 100 ms. (d)
95 Psychophysical data from a representative participant demonstrate how the somatosensory
96 attenuation phenomenon is quantified. The horizontal dashed line indicates the 50% point of
97 psychometric functions, and the circle size represents the number of trials.

98

99 Results and Discussion

100 In the response trials of the task, participants were presented with two taps on the left
101 index finger – one test tap of 2 N presented at 0 ms or 100 ms after the right finger’s
102 active tap (*test delay*) and one comparison tap of variable magnitude – and their task
103 was to indicate which one felt stronger (**Fig. 1c**). The points of subjective equality
104 (PSEs) extracted from the psychophysical curves represent the attenuation of the test
105 tap and are displayed in **Fig. 2a** for each pair of exposure and test delay. A no-
106 movement condition where the participants simply relaxed their right hand served as a
107 baseline for basic somatosensory perception.

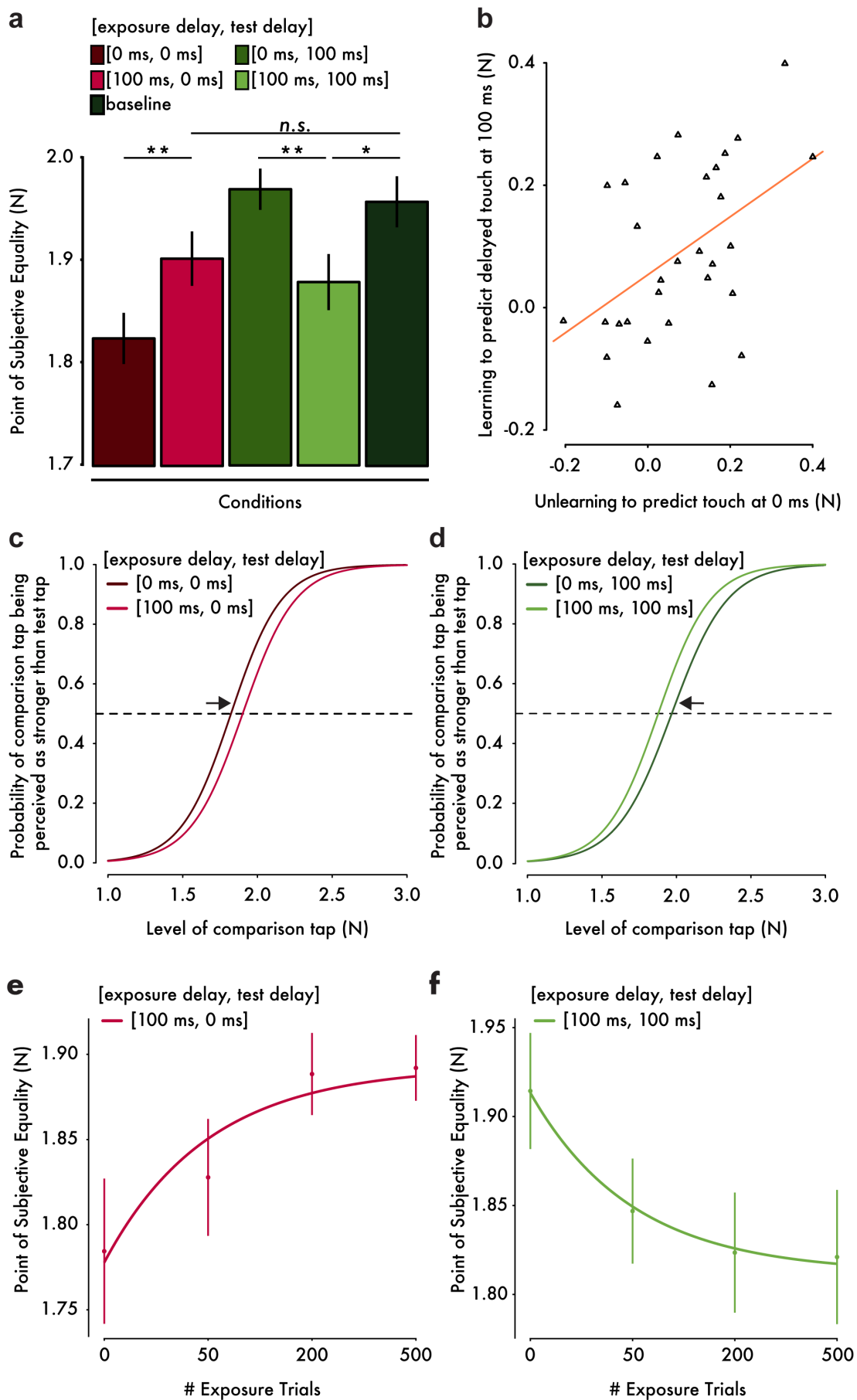
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109 As expected from previous studies [11,16], when participants were exposed to a 0 ms
110 delay, attenuation was observed only for the immediate test tap (paired t-test between
111 [exposure delay = 0 ms, test delay = 0 ms] and baseline, $t(29) = -4.84$, $p < 0.001$, CI^{95}
112 = [-0.190, -0.077]) and not for the delayed touch (paired Wilcoxon test between [0 ms,
113 100 ms] and baseline, $n = 30$, $V = 217$, $p = 0.761$, $CI^{95} = [-0.065, 0.058]$). In line with
114 this pattern, the immediate tap felt significantly less intense than the delayed one (paired
115 Wilcoxon test between [0 ms, 0 ms] and [0 ms, 100 ms], $n = 30$, $V = 15$, $p < 0.001$, CI^{95}
116 = [-0.180, -0.086]). Importantly however, the pattern of results reversed after exposure
117 to a 100 ms delay: the attenuation of the immediate tap significantly decreased (paired
118 t-test between [100 ms, 0 ms] and [0 ms, 0 ms], $t(29) = 3.03$, $p = 0.005$, $CI^{95} = [0.025,$
119 $0.131]$) and tended no longer to be significantly different from the baseline (paired t-
120 test between [100 ms, 0 ms] and baseline, $t(29) = -1.74$, $p = 0.092$, $CI^{95} = [-0.121, 0.01]$).
121 This decrease in attenuation of immediate touch (**Fig. 2c**) indicates that participants
122 *unlearned* to predict touch at the time of contact. In contrast, the attenuation of the
123 delayed tap significantly increased (paired t-test between [100 ms, 100 ms] and [0 ms,
124 100 ms], $t(29) = -3.52$, $p = 0.001$, $CI^{95} = [-0.143, -0.038]$) and it now significantly
125 differed from the baseline (paired t-test between [100 ms, 100 ms] and baseline, $t(29)$
126 $= -2.24$, $p = 0.033$, $CI^{95} = [-0.15, -0.007]$). This shift in attenuation of the delayed touch
127 (**Fig. 2d**) indicates that participants *learned* to predict the touch at the delay to which
128 they were exposed. Importantly, the extent to which participants unlearned to predict
129 the immediate touch was significantly positively correlated with the extent to which
130 participants learned to predict the delayed one (Pearson’s $r = 0.473$, $t(28) = 2.84$, $p =$
131 0.008 , $CI^{95} = [0.136, 0.712]$); **Fig. 2b**), implying a temporal shift in the probability
132 distribution of the tactile consequences in line with our hypothesized model (**Fig. 1a**,
133 middle and right). Finally, we noted that there were no significant differences in the

134 participants' discrimination ability, i.e., just noticeable difference, between conditions
135 (paired t-test between [0 ms, 0 ms] and [100 ms, 0 ms], $t(29) = -0.64$, $p = 0.528$, $CI^{95} =$
136 $[-0.030, 0.016]$); paired t-test between [0 ms, 100 ms] and [100 ms, 100 ms], $t(29) =$
137 0.73 , $p = 0.473$, $CI^{95} = [-0.020, 0.043]$). This finding excludes the presence of response
138 sensitivity differences between conditions as an alternative explanation of the present
139 results. Taken together, these findings suggest that the internal model generating the
140 tactile predictions that produce the somatosensory attenuation can be temporally
141 retuned.

142

143 To quantitatively strengthen our conclusion that the abovementioned findings are due
144 to the retuning of the internal model, we performed an additional experiment in which
145 we explicitly tested our theoretical prediction that the longer the participants are
146 exposed to the systematic delays between movement and touch, the larger the temporal
147 shift in the probability distribution of the internal model will be, and therefore the larger
148 the perceptual effects on somatosensory attenuation will be (**Fig. 1a**, middle). Two new
149 groups of fifteen participants each were continuously presented with 100 ms exposure
150 trials while being tested for the attenuation of immediate (**Fig. 2e**) or delayed touch
151 (**Fig. 2f**) after 0, 50, 200 and 500 exposure trials. The results revealed a significant
152 effect of number of exposure trials in the learning and unlearning of the tested delays:
153 the attenuation of immediate touch [100 ms, 0 ms] decreased significantly as the
154 number of exposure trials increased ($F(3,42) = 4.92$, $p = 0.005$), while the attenuation
155 of delayed touch [100 ms, 100 ms] increased significantly as the number of exposure
156 trials increased ($F(3,42) = 5.27$, $p = 0.004$). Replicating our previous results, the
157 pairwise comparisons indicated a significant decrease in the attenuation of immediate
158 touch after 200 exposure trials ($t(14) = -2.94$, $p = 0.011$, $CI^{95} = [-0.180, -0.028]$) and
159 500 exposure trials ($t(14) = -2.62$, $p = 0.020$, $CI^{95} = [-0.196, -0.019]$) compared to the
160 initial performance after 0 exposure trials, as well as a significant increase in the
161 attenuation of the delayed touch after 50 exposure trials ($t(14) = 3.44$, $p = 0.004$, $CI^{95} =$
162 $[0.025, 0.110]$), 200 exposure trials ($t(14) = 2.76$, $p = 0.015$, $CI^{95} = [0.020, 0.161]$) and
163 500 exposure trials ($t(14) = 3.40$, $p = 0.004$, $CI^{95} = [0.035, 0.152]$) compared to the
164 initial test. Collectively, these results demonstrate that the retuning of the internal model
165 underlying somatosensory attenuation occurs through error-driven processes that
166 evolve over time in response to repeated exposure to unexpected delays in the
167 sensorimotor system.



169 **Figure 2 | Results from the somatosensory attenuation experiments. (a)** Mean PSE (\pm
170 s.e.m.) for each condition. Only the important planned comparisons are displayed ($*p < 0.05$,
171 $**p < 0.01$, *n.s.* not significant). **(b)** Scatterplot of the attenuation shifts in immediate touch
172 (unlearning) and delayed touch (learning). The more participants unlearned to predict the
173 immediate touch, the more they learned to predict the delayed one. The orange line indicates
174 the fitted regression line. **(c, d)** Group psychometric functions indicating significant attenuation
175 shifts for immediate **(c)** and delayed touch **(d)**. **(e, f)** Mean PSE (\pm s.e.m.) as a function of the
176 number of exposure trials. Unlearning and learning curves were fitted with an exponential
177 model.

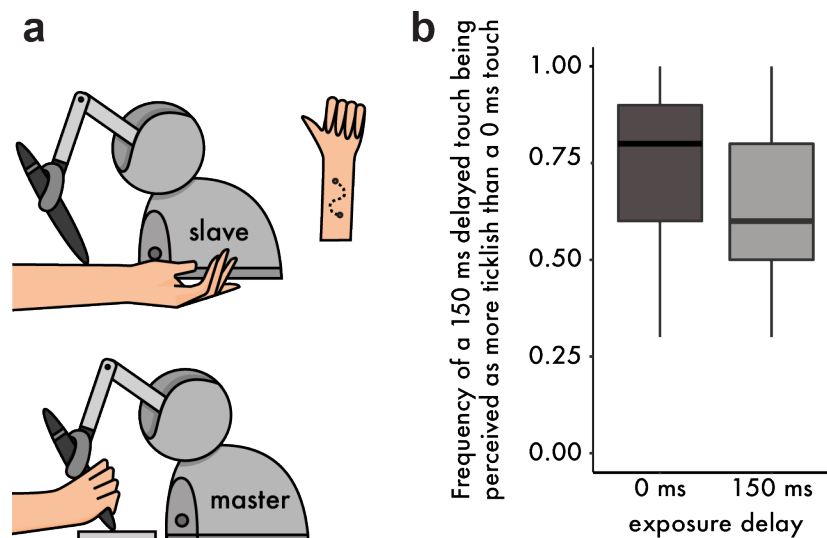
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179 Somatosensory attenuation is considered one of the reasons for which we cannot tickle
180 ourselves [18]. Accordingly, self-tickling sensations are cancelled because the
181 somatosensory feedback of our movement matches the tactile prediction of the internal
182 model and thus gets attenuated. In contrast, ticklish sensations arise from discrepancies
183 (prediction errors) between the predicted feedback of the internal model and the actual
184 somatosensory input [8]. An earlier study showed that participants rated their self-
185 generated touch as more ticklish when a delay greater than 100 ms was introduced
186 between the movement of one hand and the resulting touch on the other, compared to
187 when a 0 ms delay was introduced. We hypothesized that after exposure to systematic
188 delays the delayed self-generated touch would feel less ticklish because the retuning of
189 the internal model of somatosensory attenuation would reduce this delay-induced
190 prediction error (**Fig. 1a**, middle). Reversely, natural (non-delayed) self-generated
191 touch would feel more ticklish since the prediction error between the delayed prediction
192 and the immediate tactile feedback would increase after the exposure.

193

194 To this end, we performed an additional experiment in which a new group of thirty
195 participants moved the arm of a robot with their right hand to apply touch on their left
196 forearm through a second robot. The second robot (slave) copied the movement of the
197 first robot (master) either with a 0 ms or a 150 ms delay (**Fig. 3a**). As expected from
198 the literature, after exposure to the 0 ms delay participants judged more frequently the
199 delayed touch as being more ticklish than the immediate touch (median frequency =
200 0.8, mean frequency = 0.73). Critically, after exposure to the 150 ms delay, this
201 frequency significantly dropped (median frequency 0.6, mean frequency 0.65): $t(29) =$
202 2.28 , $p = 0.030$, $CI^{95} = [0.009, 0.158]$ (**Fig. 3b**). That is, the delayed touch was rated
203 significantly less frequently as the more ticklish one, or, reversely, the immediate touch
204 was rated significantly more frequently as the more ticklish one. This result suggests
205 that ticklishness sensations depend on the same learning mechanism that supports the
206 attenuation of self-touch, thereby generalizing our findings beyond force intensity
207 perception and suggesting a universal role of the sensory predictions –generated by a
208 continuously retuned internal model– in the perceptual discrimination of self and non-
209 self.

210



211

212 **Figure 3 | Methods and Results from the tickling experiment. (a)** Participants were
213 instructed to move the stylus of a robot with their right hand (master robot). The stylus was free
214 to move along a sinusoidal path within a 3D-printed mold, thus constraining the movement
215 trajectory. A second robot (slave) copied the master robot and delivered the touch on the volar
216 (anterior) part of their left forearm. Participants were asked to perform two sinusoidal
217 movements (twice back and forth) with their right hand and received two stimulations on the
218 left forearm (one with a 0 ms and one with a 150 ms delay). Afterwards they had to indicate
219 which touch felt more ticklish. **(b)** Boxplot of the frequencies at which participants rated the
220 delayed touch (150 ms) as more ticklish than the immediate touch. After exposure to the 150
221 ms delay, participants chose the delayed touch less frequently (or reversely, they chose the
222 immediate touch with higher frequency). The horizontal black bars represent the medians, and
223 the boxes denote the interquartile ranges.

224

225 The present study investigated the temporal retuning of the internal model underlying
226 the perceptual attenuation of self-generated touch, the latter being a well-established
227 index of the efference-copy-based sensory predictions [1,8,9,16]. Our findings are
228 strongly consistent with a gradual updating of the internal model during exposure to
229 systematic delays between the movement and the tactile feedback from the resulting
230 self-touch (**Fig. 1a**). After exposure to such delays, the delayed touch was predicted
231 and thus attenuated, while the immediate (non-delayed) touch was not predicted and
232 thus not attenuated. Moreover, the magnitudes of these effects were correlated and
233 dependent on the number of exposure trials, in line with our proposal that the retuning
234 of the internal model was driven by a prediction-error-based learning process. Finally,
235 we demonstrated that this dynamic retuning of the internal model influences the
236 perceived ticklishness of tactile stimulation, so that delayed touches feel less ticklish
237 and non-delayed touches more ticklish after exposure to systematic delays. This
238 demonstrates that the predictive learning process under discussion affects the
239 perceptual quality of touch as being self- or externally generated beyond the mere
240 intensity of the somatosensory feedback. Taken together, the present study brings
241 compelling evidence that somatosensory attenuation is an adaptive phenomenon.

242

243 We propose that the internal model underlying somatosensory attenuation during
244 normal temporal conditions is dynamically retuned in presence of systematic delays, to
245 encode the new temporal relationship between the motor command and the tactile
246 consequence. Rather than the adaptation of an existing internal model, it could be
247 argued that the exposure to the delays leads to the acquisition of a new internal model
248 instead. In a bimanual object manipulation task, Witney et al. [19] demonstrated a
249 significant grip force modulation after repeated exposure to a systematic delay between
250 the movement of one hand and the resulting effects on the other hand, in a direction
251 that is consistent with the acquisition of new internal model rather than the update of
252 an existing one. According to this proposal, the brain would learn different internal
253 models for the different delays and would switch between them [20]. Our data cannot
254 differentiate between these two hypotheses since in both scenarios we would expect a
255 decrease in the attenuation of the immediate touch and an increase in the attenuation of
256 delayed touch. Moreover, it is not known whether the same internal model underlies
257 the anticipatory grip force modulation during object manipulation and the sensory
258 attenuation during self-touch. Nevertheless, based on the correlation between the shifts
259 in the attenuation of immediate touch and the attenuation of delayed touch (**Fig. 2e-f**),
260 we consider that a shift in the predicted temporal distribution towards the newly
261 predicted timing (update of an existing internal model) is more likely than the
262 acquisition of a new one.

263
264 Our study goes beyond earlier studies on crossmodal lag adaptation and sensorimotor
265 temporal recalibration (see [21,22] for reviews). By employing the self-touch paradigm,
266 we kept the relationship between the movement and its feedback from the body natural,
267 in contrast to previous studies that provided participants with artificial feedback, e.g.
268 visual flashes on the screen [17,23] or white noise bursts [24] in response to keypresses.
269 Most importantly, rather than measuring changes in the perceived order of the
270 participants' movements and those associated external events – effects present in mere
271 crossmodal asynchronies [25–27] in the absence of movement– we measured the
272 attenuation of self-generated touch that requires active movement [16] and thus,
273 efference-copy-based predictions.

274
275 What could be the neural mechanism of the temporal retuning of the internal model
276 underlying somatosensory attenuation? A candidate brain area is the cerebellum, given
277 its involvement in the implementation of the internal models [13], its well-established
278 relationship with motor learning [28] and somatosensory attenuation [18,29] and its
279 relevance to time perception and temporal coordination of movement according to
280 evidence from nonhuman primates [30], cerebellar patients [31] and healthy subjects
281 [32]. A mechanism through which the cerebellum could acquire prior distributions of
282 time intervals has recently been suggested [33]. Given that maintaining unbiased
283 sensorimotor predictions is the root of motor learning [12,28,34], we propose that the
284 observed effects are a new form of learning that represents the updating of the internal
285 model's parameter specifying the temporal relationship between the motor command
286 and its sensory feedback from the body. In contrast to the classically studied motor

287 (force-field and visuomotor) adaptation paradigms [12,34], the present learning occurs
288 in the temporal rather than the spatial domain, and it serves to keep the sensorimotor
289 predictions regarding one's own body [35] temporally tuned. This space-time analogy
290 becomes more apparent when we consider that our observed temporal aftereffects – i.e.
291 the reduced attenuation observed during 0 ms delay after exposure to the 100 ms –
292 mirror the classic spatial aftereffects (e.g. reaching errors) observed in force-field and
293 visuomotor adaptation after removing the spatial perturbation participants have been
294 exposed to [12]).

295
296 The adaptive nature of sensory attenuation has broad implications for cognitive
297 neuroscience beyond motor control. Accurate comparisons of predicted and actual
298 sensory feedback underpin the distinction of self and environment [36–39], the
299 perception of ticklishness [11] and the sense of agency, i.e., the sense of being the
300 author of voluntary action [40]. The present results reveal how such fundamental
301 cognitive distinctions between the self and external causes are supported by a dynamic
302 and flexible error-driven learning process. Indeed, the data from our tickling experiment
303 submit that it is possible to learn to tickle oneself: after the retuning of the internal
304 model to the delay, natural (non-delayed) self-touch feels more intense and more
305 ticklish, as an external touch does.

306
307 Our findings on learning and unlearning mechanisms could have important clinical
308 relevance for schizophrenia research. In healthy subjects, reduced sensory attenuation
309 was associated with a high tendency towards delusional ideation [41], and the frequency
310 of passivity experiences in non-pathological subjects with high schizotypal traits was
311 related to increased ticklishness ratings for self-produced touch [42]. Similarly,
312 schizophrenic patients [43,44] and patients with auditory hallucinations and/or
313 passivity experiences [45] were shown to exhibit reduced attenuation of their self-
314 generated touches with respect to matched controls, with the severity of the
315 schizophrenic patients' hallucinations being a predictor of their reduced somatosensory
316 attenuation [44]. This relationship between somatosensory attenuation and
317 schizophrenia was proposed to reflect deficits in the patients' internal models
318 mechanisms [46]. Specifically, Whitford et al. [47] proposed that schizophrenia is
319 related to an abnormal myelination of frontal white matter that produces delays in the
320 generation of the predicted consequences based on the efference copy (internal model).
321 That is, the predicted timing of the sensory feedback lags the movement and feedback
322 time and therefore, non-delayed feedback (0 ms) comes before its predicted time and it
323 is not attenuated, thereby producing uncertainty about the origin of the signal (the self
324 or the others). In agreement with this view, a study using encephalography showed that
325 schizophrenic patients exhibited reduced cortical suppression of self-generated sounds
326 when these were presented without delay but normal attenuation when presented with
327 a delay, compared to healthy controls [48]. Accordingly, we theorize that schizophrenic
328 patients would perceive their delayed touch as less intense and less ticklish, reflecting
329 an internal model erroneously tuned at that delay; a prediction that should be tested in
330 future experiments.

331

332 More fundamentally, since our study suggests that sensory attenuation relies on online
333 updating prediction estimations it opens up for the possibility that it could be this
334 learning process that is impaired in schizophrenia. We therefore speculate that
335 schizophrenic patients might have no problem in generating motor commands or
336 generating sensory predictions as such, but it is the continuous updating of these
337 predictions that is impaired. In other words, rather than a structural change *per se*
338 causing the changes in sensory attenuation, it might be that it is the inability to retune
339 the internal model to compensate for these changes in the brain that is causing the
340 cognitive deficits and psychiatric symptoms. We therefore propose that future
341 computational psychiatry research should specifically investigate the capacity of these
342 individuals to learn and unlearn new temporal relationships between their movements
343 and their sensory feedback.

344

345 **Materials and Methods**

346 **Materials**

347 In all conditions, participants rested their left hand, palm up, with the left index finger
348 placed inside a molded support. Participants received forces on the pulp of their left
349 index finger from a cylindrical probe (20 mm diameter) that was attached to a lever
350 controlled by a DC electric motor (Maxon EC Motor EC 90 flat; manufactured in
351 Switzerland). The right hand and forearm were comfortably placed on top of boxes
352 made of sponge, with the right index finger resting on top of a force sensor
353 (FSG15N1A, Honeywell Inc.; diameter, 5 mm; minimum resolution, 0.01 N; response
354 time, 1 ms; measurement range, 0–15 N). The force sensor was placed on top of (but
355 not in contact with) the cylindrical probe that was contacting their relaxed left index.

356

357 A screen blocked the participants' view of their hands and forearms during all
358 conditions, and the participants were further asked to fixate their gaze on a fixation
359 cross marked at 2 meters across from them. In addition, participants were wearing
360 headphones through which white noise was administered so that no sound created either
361 by the motor or by the right hand's tap could be used as a cue for the psychophysics
362 task. An auditory cue (tone) served to indicate to participants when to press the force
363 sensor with their right index finger during the task.

364

365 **Participants**

366 After providing written informed consent, thirty naïve participants (15 women and 15
367 men, 27 right-handed and 3 ambidextrous [49]) aged 18-32 years participated in the
368 experiment. The sample size was decided based on previous studies [17,23].

369

370 **Conditions and Procedures**

371 The experiment included five conditions: four movement conditions and one baseline
372 (no movement) condition. Each movement condition included both *exposure* and
373 *response* trials. The baseline condition assessed the participants' somatosensory

374 perception of two successive taps on the left index finger without any movement of the
375 right index finger and thus included only response trials.

376

377 Exposure trials

378 On each exposure trial (**Fig. 1c**), participants tapped the force sensor with their right
379 index finger (active tap) after an auditory cue. This tap triggered the test tap on their
380 left index finger. The test tap could be presented either with a 0 ms delay – therefore
381 simulating self-touch – or with a 100 ms delay (*exposure delay*).

382

383 Response trials

384 In each response trial (**Fig. 1c**), as in the exposure trials, participants tapped the force
385 sensor after the auditory cue and received the test tap on their left index finger with a
386 delay of either 0 ms or 100 ms (*test delay*). After a random delay of 800-1500 ms from
387 the test tap, a second tap (comparison tap) was delivered to the left index finger, and
388 participants were required to indicate using a foot pedal which tap (the test tap or the
389 comparison tap) was stronger. The test tap was always 2 N, while the intensity of the
390 comparison tap was systematically varied among seven different force levels (1, 1.5,
391 1.75, 2, 2.25, 2.5 or 3 N). Both test and comparison taps had a fixed duration of 100 ms
392 each. In a short session just before the experiment, we taught participants how to tap
393 the sensor with their right index finger to prevent them from pressing too forcefully or
394 too gently during the experiment. This psychophysical task has been previously
395 validated to assess the magnitude of somatosensory attenuation [16].

396

397 The four movement conditions corresponded to the four combinations of exposure and
398 test delay levels: [0 ms, 0 ms], [0 ms, 100 ms], [100 ms, 0 ms], and [100 ms, 100 ms].
399 Each movement condition consisted of 500 initial exposure trials (to 0 ms or 100 ms)
400 and 70 response trials (each of the 7 intensities of the comparison tap was repeated 10
401 times). Each response trial followed 5 re-exposure trials, resulting in 850 exposure trials
402 in total, per condition. The baseline condition consisted of 105 response trials (each of
403 the 7 intensities of the comparison tap was repeated 15 times).

404

405 No feedback was ever provided to subjects with respect to their performance on the
406 psychophysical task. The order in which the volunteers participated in the conditions
407 was randomized. As a technical side note, the intrinsic delay of our system was 35 ms;
408 therefore, the experimental conditions labeled ‘0 ms’ and ‘100 ms’ actually correspond
409 to effective delays of 35 ms and 135 ms.

410

411 **Data and Statistical Analysis**

412 For each condition, we used a logistic regression model to fit the proportion of the
413 participants’ responses that the comparison tap was stronger than the test tap (**Eq. 1**,
414 **Fig. 1d**):

415

$$416 \quad f(x) = \frac{1}{1 + \exp(-(a + \beta x))} \quad (1)$$

417

418 where α represents the intercept and β represents the slope. We used the function *glm*
419 with a *logit* link function in the software R version 3.3.2. We extracted the point of
420 subjective equality (PSE), which corresponds to the intensity of the comparison tap at
421 which the participant perceives the test tap (2 N) and the comparison tap as equal ($p =$
422 0.5). Furthermore, we extracted the just noticeable difference (JND), an index of the
423 participant's response sensitivity.

424

425 We checked the normality of the distributions of PSEs and JNDs with Shapiro-Wilk
426 tests. Accordingly, we performed planned comparisons with either a paired t-test or a
427 Wilcoxon signed-rank test. To test for perceptual shifts due to the 100 ms exposure
428 delays, we contrasted the conditions featuring a 100 ms exposure delay with those
429 featuring a 0 ms exposure delay for the same test delay. We also compared all the
430 movement conditions with the baseline condition. To calculate the correlation
431 coefficient between the attenuation shift of immediate touch (unlearning, i.e., PSE at
432 [100 ms, 0 ms] - PSS at [0 ms, 0 ms]) and the attenuation shift of delayed touch
433 (learning, i.e., PSE at [0 ms, 100 ms] - PSS at [100 ms, 100 ms]), we used the Pearson
434 correlation coefficient, since the data were normally distributed. All statistical tests
435 were two-tailed. As mentioned above, for the group psychometric functions (**Fig. 2c-**
436 **d**), we generated the plots using the mean PSE and the mean JND across the thirty
437 participants.

438

439 **Participants, Procedure and Analysis in the Effect of Exposure Experiment**

440 We performed an additional experiment in which a new set of 30 naïve volunteers (12
441 women and 18 men, all 30 right-handed [49]) aged 18-35 years participated after
442 providing written informed consent. Each participant was exposed to 500 trials with a
443 systematic delay of 100 ms. Half of the participants were tested for the attenuation of
444 the immediate touch [100 ms, 0 ms], and the other half were tested for the attenuation
445 of the delayed touch [100 ms, 100 ms]. The psychophysical tests were performed at the
446 beginning of the experiment (no initial exposure) and then at three time points spaced
447 at intervals of 50, 150, and 300 exposure trials. That is, participants performed the
448 psychophysical task after 0, 50, 200 and 500 cumulative initial exposure trials. One
449 response (out of seventy) was missing for one participant in one psychophysical test.
450 For each experiment, we performed a repeated-measures analysis of variance
451 (ANOVA) on the PSEs with time as the within-participants factor. We then performed
452 planned comparisons using paired t-tests, since all distributions satisfied the assumption
453 of normality.

454

455 **Participants, Procedure and Analysis in the Tickling Experiment**

456 A new set of 30 naïve volunteers (16 women and 14 men, 28 right-handed, 1
457 ambidextrous and 1 left-handed [49]) aged 20-38 years participated in the Tickling
458 experiment after providing written informed consent. Two robots (Touch™ Haptic
459 Devices, 3D systems, <https://www.3dsystems.com/haptics-devices/touch>) were placed

460 in front of the participants with a distance of 10 cm between them. Participants rested
461 their left arm palm up within a forearm support made of sponge, just beneath the stylus
462 of a robot (*slave* robot). The tip of the stylus was covered with sponge to reduce its
463 sharpness. Participants rested their right elbow on an arm support and grabbed with
464 their right hand the stylus of another robot (*master* robot). The lower part of the stylus
465 of the master robot could freely move within a sinusoidal 3D printed path. The distal
466 point of the path (the one closest to the hand) served as a starting point. Each trial lasted
467 three seconds and upon an auditory cue, participants were asked to move the stylus
468 from the distal point (**Fig. 3a**) to the proximal point along the path, and back to the
469 distal point. In two different conditions, participants performed 50 exposure trials with
470 a systematic delay of 0 or 150 ms between the movement of the master robot and the
471 movement (and stimulation) of the slave robot (*exposure delay*). In the response trials,
472 as in the exposure trials, participants performed two consecutive trials (the first with a
473 0 ms and the second with a 150 ms delay). Immediately afterwards, they were asked to
474 report which of the two stimulations on their left forearm (the first or the second) felt
475 more ticklish to them. As in the previous experiments, each response trial followed 5
476 re-exposure trials. There were 10 response trials per condition. The order in which the
477 volunteers participated in the conditions was counterbalanced. We calculated the
478 frequency at which participants judged the second (150 ms) touch as more ticklish in
479 the two conditions. The data could be approximated by a normal distribution (Shapiro
480 -Wilk test) and thus we performed the planned comparison using a paired t-test.

481

482 In the tickling experiment, we chose a delay of 150 ms and not a delay of 100 ms as in
483 the sensory attenuation experiments. This was because our pilot tickling experiments
484 indicated that a 100 ms delay was not sufficient to differentiate the perception of a
485 delayed stroke on the arm from that of an immediate stroke. We consider that this
486 asymmetry of the delay sensitivity between attenuation and tickling should not be
487 surprising: a 100 ms delay would be more salient for a self-induced tap of 100 ms
488 duration than a continuous stroke of 3 seconds duration.

489

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494

495 **Author Contributions**

496 Konstantina Kilteni and H. Henrik Ehrsson conceived the experiment. Konstantina
497 Kilteni, H. Henrik Ehrsson and Christian Houborg designed the experiment. Christian
498 Houborg collected the data of the two experiments on somatosensory attenuation.
499 Konstantina Kilteni collected the data of the tickling experiment. Konstantina Kilteni
500 conducted the statistical analysis. Konstantina Kilteni and H. Henrik Ehrsson wrote the
501 manuscript, and Christian Houborg read and approved the final version.

502

503 **Competing interests**

504 The authors declare no competing interests.

505

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