# **1** Action does not enhance but attenuates predicted touch

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# 4 Abstract

5 Dominant motor control theories propose that the brain uses efferent information to predict and attenuate the somatosensory consequences of actions, referred to as sensory 6 attenuation. Support for this model comes from psychophysical and neuroimaging studies 7 showing that touch applied on a passive hand elicits attenuated perceptual and neural 8 9 responses if it is generated by actively tapping with one's other hand, compared to identical touch from an external origin. However, recent experimental findings have 10 11 challenged this view by providing psychophysical evidence that the perceived intensity of 12 touch on the passive hand is enhanced if the active hand does not receive simultaneous tactile stimulation with the passive hand (somatosensory enhancement) and by further 13 attributing attenuation effects to the double tactile stimulation of the hands upon contact. 14 Here, we directly contrasted the hypotheses of the attenuation and enhancement models 15 16 regarding how action influences somatosensory perception by manipulating whether the active hand contacts the passive hand. In three preregistered experiments, we demonstrate 17 18 that action does not enhance the perceived intensity of touch (Experiment 1), that the previously reported "enhancement" effects are driven by the baseline condition used 19 20 (Experiment 2), and that self-generated touch is robustly attenuated regardless of whether 21 the two hands make contact (Experiment 3). Our results provide conclusive evidence that 22 action does not enhance but attenuates predicted touch. These findings prompt a reappraisal of recent experimental findings upon which theoretical frameworks proposing 23 24 a perceptual enhancement by action prediction are based.

# 25 Highlights

- Dominant motor control theories propose that action attenuates or cancels
   predicted touch.
- Recent theories propose that action enhances predicted touch.
- We show that action does not enhance but attenuates predicted touch.

# 30 Keywords

31 somatosensory attenuation; prediction; cancellation; sharpening; enhancement

### 32 Introduction

Dominant motor control theories propose that the brain uses an internal forward model in 33 combination with a copy of the motor command (efference copy) to predict the sensory 34 35 consequences of our movements (McNamee & Wolpert, 2019; Shadmehr et al., 2008; Daniel M Wolpert & Flanagan, 2001). For example, the brain predicts the upcoming 36 37 touch as one reaches towards an object. These predictions allow for the correction of 38 motor errors without relying on sensory feedback that suffers from intrinsic delays (Shadmehr et al., 2010), thereby improving the estimation of the current state of our body 39 by combining the predicted touch with the actual sensory input (Scott, 2004; Shadmehr et 40 al., 2008; Todorov & Jordan, 2002). These predictions attenuate the perception of the 41 self-generated input (sensory reafference) compared to that of externally generated input 42 43 (Davidson & Wolpert, 2005; Franklin & Wolpert, 2011; D. M. Wolpert & Kawato, 1998) 44 and infer whether the cause of the sensory input is the self or the environment (Brown et 45 al., 2013; P. Corlett, 2020; Idei et al., 2022). A classic example of this attenuation is that we are unable to tickle ourselves with our own touch, yet we are easily tickled by the 46 touch of others (S.-J. Blakemore, Wolpert, et al., 2000). The attenuation of sensory 47 48 reafference – also referred to as sensory cancelation – is thought to be necessary to compensate for the limited capacity of the sensory systems by optimally prioritising the 49 perception of more informative externally generated stimuli (Bays & Wolpert, 2012; 50 51 McNamee & Wolpert, 2019). Thus, the attenuation model proposes that we dampen 52 perceptual representations of expected self-generated stimuli to reduce redundancy and to highlight behaviourally relevant unexpected externally generated stimuli. 53

In contrast, an alternative theoretical framework proposes that predictions, including 54 55 those arising from our motor commands, should not attenuate but instead enhance 56 sensory signals, thereby allowing for sharper (*i.e.*, more accurate) representations of 57 predicted compared to unpredicted sensory events (Press et al., 2020; Press & Yon, 2019; 58 Yon et al., 2020a). This *enhancement* account – also referred to as the sharpening account 59 - posits that predictions based on our motor commands are equivalent to expectations formed by statistical regularities in sensory input or from prior knowledge (e.g., at the 60 61 North Pole, one expects to see a polar bear rather than an elephant) and that these 62 predictions should bias our perception towards our expectations. The proposal mainly stems from experimental research outside the domain of action and argues that weak, 63 noisy, or ambiguous sensory input that is in line with prior expectations should be 64 enhanced to achieve, on average, more accurate representations. For example, we are 65 more biased to report the presence of visual events that are statistically likely to occur 66 rather than unlikely events (Chalk et al., 2010; Wyart et al., 2012), more sensitive to low-67 level visual features that are in line with prior expectations (Stein & Peelen, 2015; Teufel 68 69 et al., 2018), and show greater biases when perceiving visual events that are congruent 70 with our expectations (Hudson, Nicholson, Ellis, et al., 2016; Hudson, Nicholson, 71 Simpson, et al., 2016). Such effects are thought to result from mechanisms that increase the "gain" of expected information by altering the weights of different sensory signals 72 73 (Summerfield & de Lange, 2014). Thus, the enhancement model proposes that we amplify the perceptual representations of expected compared to unexpected sensory 74 75 input.

In the somatosensory domain, evidence supporting the attenuation model has repeatedly 76 77 shown that touch delivered to one (passive) hand by the other (active) hand (*i.e.*, selfgenerated touch) is perceived as weaker or less ticklish (Asimakidou et al., 2022; Bays et 78 79 al., 2005, 2006; Sarah J. Blakemore et al., 1999; Kilteni et al., 2018, 2019, 2020, 2021; Kilteni & Ehrsson, 2017a, 2017b, 2022; Knoetsch & Zimmermann, 2021; McNaughton 80 81 et al., 2022; Weiskrantz et al., 1971; Wolpe et al., 2016) and evokes attenuated 82 somatosensory cortical activation (Sarah J. Blakemore et al., 1998; Hesse et al., 2010; Kilteni & Ehrsson, 2020; Shergill et al., 2013, 2014) compared to touch of identical 83 84 intensity applied on the passive hand that is externally generated. In contrast, one study 85 supporting the enhancement model has shown that the action of the active hand results in an increase in the perceived intensity of touch on the passive hand, provided that the 86 active hand never receives touch simultaneously with the passive hand (*i.e.*, hands do not 87 88 make contact) (Thomas et al., 2022). This enhancement finding has been recently used to support the sharpening model and to argue that attenuation effects are due to unspecific 89 90 gating processes caused by the simultaneous double tactile stimulation of the two hands (Press et al., 2022). 91

92 The attenuation (or cancellation) and enhancement (or sharpening) models present strikingly different hypotheses regarding how action influences the perception of sensory 93 input and are supported by contradictory experimental evidence, leading to debates 94 95 between researchers (P. Corlett, 2020; Führer et al., 2022; Kilteni & Ehrsson, 2022; Press et al., 2020, 2022). The present study aimed to contribute to this debate by revisiting the 96 97 enhancement findings (Thomas et al., 2022) and directly contrasting them with earlier attenuation findings (Bays et al., 2006) which used similar experimental manipulations 98 99 with respect to the contact between the hands. To this end, the same force discrimination task employed in earlier studies reporting attenuation (Asimakidou et al., 2022; Bays et 100 al., 2005, 2006; Kilteni et al., 2019, 2020, 2021, 2022; Kilteni & Ehrsson, 2022) and 101 enhancement (Thomas et al., 2022) was used to determine (a) whether movement of the 102 right hand enhances or attenuates the perceived magnitude of touch applied on the left 103 hand when the two hands do not make contact (Experiments 1 and 2) and (b) whether 104 105 attenuation effects are due to double tactile stimulation caused by the contact of the two hands or action prediction (Experiment 3). Capitalizing on the fact that any conclusion 106 about whether action prediction "attenuates" or "enhances" the perception of the 107 108 somatosensory input needs to be made with a comparison to one's somatosensory perception in the absence of action, we also included a condition in which participants 109 passively received externally generated touch, with which we compared the participants' 110 perception in all experimental conditions. Consequently, if participants perceive a touch 111 as less or more intense during action than in the absence of action, we can infer that the 112 received touch was attenuated or enhanced, respectively. This is a critical methodological 113 detail compared to previous studies (Bays et al., 2006; Thomas et al., 2022) because if 114 such baseline conditions are missing, the same patterns of results can be incorrectly 115 attributed to "attenuation" or "enhancement": for example, if one condition produces less 116 attenuation than another, it may be interpreted as enhancement, and vice versa. All 117 studies and analysis plans were preregistered on the Open Science Framework prior to 118 119 data collection (STAR Methods).

### 120 **Results**

#### 121 Experiment 1. Action does not enhance predicted touch.

Thirty naïve participants moved their right index finger towards their left index finger to generate the touch on their left index finger with (*contact* condition) or without (*nocontact* condition) simultaneous stimulation on their active finger. A *baseline* condition in which the participants did not move their right index finger and received touch on the left index finger passively (externally generated touch) was included in order to distinguish between effects of attenuation or enhancement (**Figure 1A**).

During the force-discrimination task, participants judged the intensity of a 'test' force and 128 129 a '*comparison*' force (100 ms duration each) separated by a random interval ranging from 800 ms to 1200 ms. The forces were delivered to the pulp of the left index finger by a 130 cylindrical probe attached to a lever driven by a DC electric motor. In each trial, 131 participants reported which force they felt was stronger (the *test* or the *comparison*). The 132 133 intensity of the *test* force was fixed at  $2\Box N$ , while the intensity of the *comparison* force was systematically varied among seven force levels  $(1, 1.5, 1.75, 2, 2.25, 2.5 \text{ or } 3 \Box \text{N})$ . In 134 135 the *contact* condition, participants moved their right index finger towards their left index 136 finger after an auditory cue and actively tapped on a force sensor placed on top of, but not 137 in direct contact with, the probe. The participant's active tap on the force sensor triggered the *test* force on their left index finger, thereby producing simultaneous stimulation of 138 139 both fingers in the *contact* condition and the sensation of pressing with the right index finger against the left index finger through a rigid object. Participants were told that they 140 would always make contact between their fingers (through the probe) in this condition. In 141 142 the *no-contact* condition, following the same auditory cue, participants moved their right 143 index finger towards their left index finger. At the beginning of the condition, the force sensor was removed and replaced with a distance sensor that detected the relative 144 145 distance of their active finger as it approached their left index finger to trigger the test force, similar to (Bays et al., 2006; Thomas et al., 2022). The distance threshold was set 146 such that the position of the right index finger when triggering the *test* force was 147 equivalent to that in the *contact* condition. Participants were told that they would never 148 make contact between their fingers. Before the experiment, participants were trained to 149 150 make similar movements with their right index finger in the *contact* and *no-contact* conditions. Finally, in the *baseline* condition (externally generated touch), participants 151 were told to relax their right hand, and each trial began with the same auditory cue 152 followed by the *test* force delivered to the participants' left index finger 800 ms after the 153 cue. In all trials, the *comparison* force was delivered after the *test* force, and participants 154 verbally reported their judgement (STAR Methods). 155

Participants' responses were fitted with logistic psychophysics curves, and we extracted the point of subjective equality (PSE), which represents the intensity of the comparison force at which the test force feels equally as strong. Consequently, a PSE in a movement condition (*contact* or *no-contact*) that is lower than the PSE of the *baseline* condition indicates attenuation, while a PSE that is higher than the PSE of the *baseline* condition indicates enhancement (**STAR Methods**). According to the attenuation model (**Figure** 

**1B**), attenuation of the somatosensory input on the left hand in the *contact* condition 162 compared to the *baseline* condition should be observed (*i.e.*, lower PSEs) due to the *test* 163 force being predicted from the action of the right hand. Moreover, earlier studies have 164 shown that the mere movement of one hand is not sufficient to produce predictions of 165 somatosensory input simultaneously applied on the other hand (Bays et al., 2005; Kilteni 166 167 et al., 2018; Kilteni & Ehrsson, 2017a, 2017b, 2020; Shergill et al., 2003; Wolpe et al., 2018). Instead, a bimanual sensorimotor context is needed such as during bimanual object 168 manipulation and bimanual contact of the hands (Blakemore et al., 1998). Based on this, 169 170 neither attenuation nor enhancement should be observed in the *no-contact* condition (*i.e.*, 171 no change in PSEs from *baseline*). In contrast, according to the enhancement model, if action enhances the received sensation (Thomas et al., 2022), then higher PSEs in the no-172 contact condition compared to the baseline condition should be observed (Figure 1C). 173 Finally, since the enhancement model proposes that attenuation effects are attributed to 174 unspecific (nonpredictive) gating effects caused by the simultaneous tactile stimulation of 175 176 the two hands, touch in the *contact* condition should also be perceived as weaker, albeit not due to action prediction. In summary, Experiment 1 explicitly assessed whether 177 action enhances the received touch when the index fingers of the two hands do not make 178 179 contact.

The results showed a robust attenuation of the perceived touch when the two fingers 180 made contact (*contact* condition) (**Figure 1D, E, F**): the PSEs were significantly lower in 181 the *contact* condition than in the *baseline* condition (W = 422.00, p < 0.001, rrb = 0.82, 182  $CI^{95} = [0.08 \ 0.25], BF_{01} < 0.005)$ . Similarly, the PSEs were significantly lower in the 183 contact condition than in the no-contact condition (W = 441.00, p < 0.001, rrb = 0.90, 184  $CI^{95} = [0.13\ 0.26], BF_{01} < .001)$  (Figure 1D, E, G). Critically, however, in the comparison 185 that contrasts the hypotheses of the two models, the *no-contact* condition did not produce 186 any significant change in the perceived magnitude of the touch compared to the *baseline* 187 condition (W = 187.00, p = 0.360, rrb = -0.20,  $CI^{95} = [-0.08\ 0.030]$ ) (Figure 1D, E, H). A 188 Bayesian factor analysis provided strong support for the absence of any difference 189  $(BF_{01}=3.58)$ . (See also Supplementary Material for individual fits and additional 190 191 analyses).

In summary, we used both frequentist and Bayesian statistics and found no evidence that action of the right index finger produces an enhancement of the touch received on the left index finger when the fingers did not make contact. Thus, Experiment 1 does not support the hypothesis of the enhancement model that action enhances predicted touch but supports the hypothesis of the attenuation model.



198 Figure 1. Experimental methods, hypotheses, and results of Experiment 1. A. In the contact condition (magenta), participants tapped with their right index finger (R) on a force sensor placed 199 200 above the probe that delivered a *test* force of 2 N to their left index finger (L), followed by a 201 comparison force randomly varying between 1 and 3 N. In the no-contact condition (green), 202 participants approached a distance sensor with their right index finger, which triggered the test 203 force on their left index finger, thus receiving no touch on their active finger. In the baseline 204 condition (blue), participants relaxed both hands and passively received the forces on their left 205 index finger. B. Hypotheses based on the attenuation model. Touch in the *contact* condition 206 (magenta) should be perceived as weaker than in the *baseline* (blue), but touch in the *no-contact* 207 condition (green) should be perceived similarly to that in the *baseline* (blue). C. Hypotheses 208 based on the enhancement model. Touch in the *no-contact* condition (green) should be perceived 209 as stronger than in the *baseline* (*i.e.*, enhanced) (blue), but touch in the *contact* condition 210 (magenta) should be perceived weaker than the *baseline* (blue). Note that attenuation effects in the *contact* condition are predicted both by the attenuation and the enhancement model with the 211 212 difference that the attenuation model attributes these effects to action prediction, while the 213 enhancement model attributes these effects to the simultaneous touch on the active hand. D-H. 214 Data are colour-coded per condition. **D.** Box plots show the median and interquartile ranges for 215 the PSE values per condition, black circles and error bars show the mean PSE  $\pm$  s.e.m, and the 216 raincloud plots show the individual PSE values and their distributions. No enhancement effects 217 were observed in the *no-contact* condition. **E.** Group psychometric functions for each condition. 218 The leftward shift of the curves in the contact condition indicates attenuated PSE values 219 compared to the other two conditions. F-H. Line plots for individual participant PSE values 220 illustrating significantly lower PSEs for the *contact* versus *baseline* (F) and *no-contact* (G) 221 conditions, but no significant differences in the PSE values between no-contact and baseline (H). 222 (\*\*\**p* <.001)

#### 223 Experiment 2. Previous 'enhancement' effects are driven by the baseline used.

224 Having found no evidence for somatosensory enhancement in Experiment 1, Experiment 2 aimed to understand the potential source of the previously reported enhancement effects 225 (Thomas et al., 2022). One critical methodological difference between Experiment 1 and 226 the experiment of Thomas et al. (Thomas et al., 2022) concerns the baseline condition, as 227 Thomas et al. (Thomas et al., 2022) compared the participants' perception in the no-228 229 *contact* condition to a condition where the participants prepared their right index 230 movement but received a NOGO cue to inhibit the movement, and it was that comparison 231 that revealed enhancement effects. However, motor inhibition (i.e. planning the hand 232 movement but not executing it) can lead to suppression of somatosensory input both on the hand that is planned to move (Hoshiyama & Sheean, 1998; Voss et al., 2008; Walsh 233 & Haggard, 2007) and the hand that would receive touch if the movement was executed 234 (Kilteni et al., 2018); moreover, such conditions result in a competition for attentional 235 resources to inhibit the motor response with processes that encode sensory stimuli into 236 237 memory (Chiu & Egner, 2015b, 2015a; Yebra et al., 2019) (e.g., the test force in this 238 paradigm). Therefore, if the motor inhibition condition used by Thomas et al. (Thomas et al., 2022) results in a suppression of the perceived touch, a comparison of the *no-contact* 239 240 condition with such a baseline would produce an apparent enhancement effect.

Thirty new naïve participants participated in Experiment 2, which included a block of *contact* trials and a block of *no-contact* trials in which participants moved their right

index finger, but each block also contained randomly intermixed NOGO trials where 243 participants were cued to withhold their movement, identical to the design of Thomas et 244 al. (Thomas et al., 2022) (Figure 2A). Participants were trained to make similar 245 movements with their right index finger in the *contact* and *no-contact* trials. An 246 externally generated touch condition was also included as an action-free baseline 247 248 condition (*i.e.*, no action execution or inhibition). If the previously reported enhancement effects are due to the baseline used, attenuated perception of touch during the motor 249 250 inhibition condition (*i.e.*, NOGO trials) should be found compared to the *baseline*, which 251 would then lead to apparent enhancement effects upon comparison with the *no-contact* 252 trials (Figure 2B, C) (STAR Methods).

253 This hypothesis (Figure 2B) was confirmed. First, all the effects of Experiment 1 were replicated in the new sample (Figure 2D, E, F & H). The contact trials yielded 254 significant attenuation (*i.e.*, lower PSEs) compared to the *baseline* condition (t(29) =255 6.79, p < 0.001, d = 1.24,  $CI^{95} = [0.18 \ 0.33]$ ,  $BF_{0l} < 0.001$ ) (Figure 2E & H). Once 256 again, there was no enhancement in the no-contact trials compared to the baseline 257 condition (t(29) = 0.45, p = 0.658, d = 0.08,  $CI^{95} = [-0.05 \ 0.07]$ ) (Figure 2D & F), and 258 259 the Bayesian analysis again yielded strong evidence for the absence of any effects ( $BF_{0l}$  = 4.69). Importantly, the PSEs in the *NOGO* (motor inhibition) trials were significantly 260 lower than the *baseline* condition both for the *contact NOGO* (t(29) = 2.99, p = 0.006, d 261  $=0.55, CI^{95} = [0.02 \ 0.09], BF_{01} = 0.136)$  and the no-contact NOGO trials (t(29) = 4.44, p) 262 < 0.001, d = 0.81,  $CI^{95} = [0.05 \ 0.13]$ ,  $BF_{01} = 0.005$ ) (Figure 2D, E & G). This 263 demonstrates that NOGO trials resulted in a suppression of perceived touch on the left 264 hand. Critically, this led to an apparent increase in the PSE from the *no-contact* trials to 265 the NOGO trials in the no-contact block (t(29) = -2.98, p = 0.006, d = -0.54,  $CI^{95} = [-0.12]$ 266 -0.02],  $BF_{01} = 0.139$ ), mimicking an 'enhancement' effect. Finally, PSEs were 267 significantly lower in the *contact* trials than in the NOGO trials (t(29) = 5.91, p < 0.001, d)268  $=1.08, CI^{95} = [0.13 \ 0.27], BF_{01} < 0.001)$ , while the NOGO trials in the *contact* and *no*-269 *contact* blocks did not significantly differ  $(t(29) = 1.58, p = 0.126, d = 0.29, CI^{95} = [-0.01, -0.01]$ 270 0.08],  $BF_{01} = 1.697$ ). (See also Supplementary Material for individual fits and 271 272 additional analyses).

In summary, identical to Experiment 1, we used both frequentist and Bayesian statistics and did not find any evidence that action of the right index finger produces an enhancement of the touch received on the left index finger when the fingers do not make contact. Moreover, we showed that the purported "enhancement" effect (Thomas et al., 2022) is driven by a suppression of the perceived intensity of touch following a cue to inhibit the planned movement. Thus, Experiment 2 does not support the hypothesis that action enhances predicted touch.



281 Figure 2. Experimental methods, hypotheses, and results of Experiment 2. A. The contact 282 (magenta) and *no-contact* (green) trials were identical to those of Experiment 1, with the only 283 difference that in 50% of the trials, the participants had to inhibit their movement (NOGO trials -284 yellow), and the test force was delivered automatically. The baseline condition (blue) was 285 identical to that of Experiment 1. B. Hypotheses based on the attenuation model. Touch in the contact condition (magenta) should be perceived as weaker than in the baseline (blue), but touch 286 287 in the *no-contact* condition (green) should be perceived similarly to that in the *baseline* (blue). 288 Critically, touch may also be perceived as weaker than *baseline* in the NOGO trials, resulting in a 289 'false enhancement' of the *no-contact* trials. C. Hypotheses based on the enhancement model. 290 Touch in the *no-contact* condition (green) should be perceived as stronger than in the *baseline* 291 (i.e., enhanced) (blue), but touch in the contact condition (magenta) should be perceived weaker 292 than the *baseline* (blue). **D-H.** Data are colour-coded per condition. **D-E.** Box plots show the 293 median and interguartile ranges for the PSE values in the *baseline* and *no-contact* blocks (**D**) and 294 in the *baseline* and *contact* blocks (E). Black circles and error bars show the mean  $PSE \pm s.e.m$ , and the raincloud plots show the individual PSE values and their distributions. F-H. Line plots for 295 296 individual participant PSE values illustrating no significant differences in the PSE values between 297 no-contact and baseline (F), significantly higher PSEs for the no-contact versus NOGO trials in 298 the same block (G) and significantly lower PSEs in the *contact* versus *baseline* trials (H). (\*\*p < 1299 0.01, \*\*\*p < 0.001)

# Experiment 3. Action attenuates predicted touch, even without simultaneous stimulation of the active hand.

Within the framework of internal forward models, the absence of attenuation in the *nocontact* conditions of Experiments 1 and 2 is expected, given the lack of a sensorimotor context conducive to perceiving the touch as self-generated: when contact is never made, the forces applied on the passive left hand are only arbitrarily, and not causally, associated with the movement of the active right hand. Alternatively, it could be argued that the absence of attenuation in the *no-contact* conditions is caused by the lack of simultaneous tactile stimulation of the active hand rather than by predictive mechanisms.

309 In Experiment 3, this hypothesis was explicitly tested with thirty new naïve participants. The same *contact* and *no-contact* conditions were included as in Experiment 1, but their 310 relative frequency was manipulated within the same block (contact trials: 80%, no-311 *contact* trials: 20%) (Figure 3A). The force sensor the participants tapped in the *contact* 312 trials was now attached to a platform that could be automatically retracted. In the *contact* 313 trials, participants tapped the force sensor to trigger the *test* force identically to 314 315 Experiments 1 and 2, but in the *no-contact* trials, the platform automatically retracted before trial onset, unbeknownst to the participants, leading them to unexpectedly miss the 316 contact with the sensor but still trigger the *test* force only by the position of their right 317 index finger. Participants' vision was occluded so that they could not know whether the 318 319 next trial would be a *contact* or a *no-contact* trial. According to the attenuation model, providing a bimanual sensorimotor context in 80% of the trials should lead participants to 320 321 form predictions about the somatosensory consequences of their movement in most of the 322 trials and thus attenuate the received touch on their passive left hand compared to the baseline, even if the touch of their active hand was unexpectedly missed (Figure 3B). In 323 contrast, if attenuation is a nonpredictive process caused by the mere simultaneous tactile 324

stimulation of the active finger, no attenuation effects in the *no-contact* trials should be observed with respect to the *baseline* (Figure 3C).

The results showed a robust attenuation in both *contact* and *no-contact* trials with respect 327 to the *baseline* condition, regardless of whether contact was made (Figure 3D, E, F & 328 H): the PSEs were significantly lower in the contact condition than in the baseline 329 condition  $(t(29) = 8.06, p < 0.001, d = 1.47, CI^{95} = [0.16, 0.27], BF_{01} < 0.001)$  and lower in 330 the *no-contact* condition than in the *baseline* condition (t(29) = 4.45, p < 0.001, d = 0.81, d = 0.81)331  $CI^{95} = [0.07 \ 0.20], BF_{01} = 0.004)$ . The magnitude of attenuation was larger in the *contact* 332 condition than in the no-contact condition, with significantly lower PSEs in the contact 333 condition than in the *no-contact* condition (t(29) = 3.94, p < 0.001, d = 0.72,  $CI^{95} = [0.04]$ 334 0.12],  $BF_{01} = 0.016$ ) (Figure 3G) (see also Supplementary Material for individual fits 335 and additional analyses). It should be mentioned however that the difference in the 336 337 attenuation magnitudes was modest ( $\cong$  35%). These findings indicate that the perceived 338 intensity of touch on the passive left hand was significantly attenuated both when the 339 active hand received touch or not, thereby ruling out the possibility that attenuation is merely due to simultaneous tactile stimulation (Thomas et al., 2022). 340

341 The results of Experiment 3 emphasise the predictive nature of somatosensory attenuation, which is observed only when the sensorimotor context allows the formation 342 of such predictions. To further strength our interpretation we performed an ANOVA on 343 the difference in the PSEs between the contact and no-contact conditions across all three 344 experiments. The ANOVA revealed a significant main effect of Experiment (F(2, 87) =345 346 8.05, p < 0.001,  $\eta p = 0.156$ ), with Bonferroni corrected post hoc comparisons indicating 347 significant differences between Experiments 1 and 3 (t(2, 87) = 3.10, p = 0.008, d = 0.80, CI [0.03 0.23],  $BF_{01} = 0.085$ ) as well as Experiments 2 and 3 (t(2, 87) = 3.76, p < 0.001, d 348 = 0.97, CI [0.06 0.26],  $BF_{01}$  = 0.002), but no significant differences between Experiments 349 1 and 2 (t(2, 87) = -0.66, p = 1.000, d = -0.17, CI [-0.13 0.07],  $BF_{01} = 3.308$ ). Thus, no-350 *contact* trials elicited attenuated perception only when the sensorimotor context allowed 351 for a prediction of self-touch (Experiment 3) and not when the action was only arbitrarily 352 353 associated with the touch (Experiments 1 and 2).



355 Figure 3. Experimental methods, hypotheses, and results of Experiment 3. A. The contact 356 (magenta) and *no-contact* (green) conditions were identical to those of Experiment 1, with the 357 only difference being their relative proportion (*contact* trials 80%, *no-contact* trials 20%). In the 358 no-contact trials, the force sensor was automatically retracted, unbeknownst to the participant, 359 revealing the distance sensor placed below. The *baseline* condition (blue) was identical to that of 360 Experiments 1 and 2. B. Hypotheses based on the attenuation model. If attenuation is due to 361 action prediction, then the perceived magnitude of touch should be reduced in both the *contact* 362 (magenta) and *no-contact* conditions (green) compared to the baseline (blue). C. Hypotheses based on the enhancement model. If attenuation effects are driven by simultaneous touch on the 363 364 active hand, then the perceived magnitude of touch should be reduced only in the *contact* 365 condition (magenta) compared to the *baseline* (blue) and not in the *no-contact* condition (green) which should be similar to the *baseline* (blue). **D-H.** Data are colour-coded per condition. **D.** Box 366 plots show the median and interquartile ranges for the PSE values per condition, black circles and 367 368 error bars show the mean PSE  $\pm$  s.e.m, and the raincloud plots show the individual PSE values and their distributions. E. Group psychometric functions for each condition. The leftward shift of 369 370 the curves in the *contact* and *no-contact* conditions indicates attenuated PSE values compared to 371 the baseline. F. Line plots for individual participant PSE values illustrating significantly lower 372 PSEs for the *contact* versus *baseline* condition. G. significantly lower PSEs in the *contact* versus no-contact condition and H. significantly lower PSEs in the no-contact versus baseline. (\*\*\*p < 373 374 0.001)

# 375 **Discussion**

Clarifying how predictions about the sensory consequences of our movements affect our 376 perception is fundamental to understanding the interaction between perception and action 377 (McNamee & Wolpert, 2019; Shadmehr et al., 2008; Daniel M Wolpert & Flanagan, 378 2001) but also for clinical and neurobiological theories of psychosis spectrum disorders, 379 such as schizophrenia (S.-J. Blakemore, Smith, et al., 2000; P. R. Corlett et al., 2019; C. 380 Frith, 2005a, 2005b; Chris D. Frith et al., 2000; Christopher D. Frith, 2019; Shergill et al., 381 2005, 2014) and schizotypy (Asimakidou et al., 2022), as well as functional movement 382 disorders (Parees et al., 2014), Parkinson's disease (Wolpe et al., 2018) and ageing 383 (Wolpe et al., 2016). In the present study, two opposing hypotheses regarding how action 384 influences somatosensory perception were contrasted: the attenuation model and the 385 enhancement model. Our findings demonstrate that action does not enhance (Experiments 386 387 1 and 2) but attenuates the predicted touch (Experiment 3).

Before discussing the findings, it is important to emphasise that to draw conclusions 388 389 about whether perception is attenuated or enhanced in an experimental condition including action, it is necessary to include a baseline condition without action. Only 390 comparing conditions that include action prevents differentiating a genuine effect of 391 392 enhancement (or attenuation) from an effect of reduced attenuation (or enhancement) in one of the two conditions. This also applies to experimental manipulations that contrast 393 predicted with unpredicted somatosensory stimuli during action (see (Thomas et al., 394 395 2022) for such comparisons). To this end, a *baseline* condition of pure somatosensory exafference (*i.e.*, externally generated touch) was included in all of the present 396 experiments that allowed us to distinguish the direction of the effects. 397

The results of Experiment 1 showed a robust attenuation of the touch applied on the 398 399 passive left hand when the two hands made contact (contact condition), but neither attenuation nor enhancement was caused by the mere movement of the right hand (no-400 contact condition). In contrast, the perceived intensity of touch in the no-contact 401 condition was similar to that of the baseline (i.e., externally generated touch). These 402 403 findings are in line with the results of Bays et al. (Bays et al., 2006), who found no change in the participants' somatosensory perception when the two hands did not make 404 contact, but do not replicate those of Thomas et al. (Thomas et al., 2022), who observed 405 406 enhancement of touch in a *no-contact* condition. Experiment 2 further investigated the 407 source of the previously reported enhancement effects and showed that they are in fact driven by the baseline condition used: enhancement was observed only relative to a 408 condition in which the touch was applied rapidly following a cue to inhibit the movement 409 410 (*i.e.*, a "do not move" cue), as in previous research (Thomas et al., 2022), but not relative to an externally generated touch condition (our baseline). In support of this claim, 411 412 Experiment 2 showed that a cue to inhibit the movement results in a significant reduction in the perceived intensity of the imperative stimulus (*i.e.*, touch on the passive hand) 413 compared to baseline perception. This is in line with previous evidence showing reduced 414 amplitude of somatosensory evoked potentials for tactile stimuli presented shortly 415 following a cue to inhibit a movement (Hoshiyama & Sheean, 1998), reduced perceived 416 amplitude for tactile stimuli under the mere expectation to move (Voss et al., 2006, 417 2008), and reduced encoding of sensory stimuli following motor inhibition (Chiu & 418 419 Egner, 2015b, 2015a; Yebra et al., 2019). Therefore, rather than participants' perception being enhanced in the *no-contact* condition, it is a reduction of the perceived intensity 420 following the cue to inhibit the movement that leads to an apparent enhancement. In 421 contrast, by including a novel externally generated touch condition as a baseline that 422 involved neither motor planning nor response inhibition, it became clear that there were 423 no enhancement effects. 424

Experiment 3 demonstrated that action attenuates the predicted touch even if the active 425 hand does not receive simultaneous tactile stimulation with the passive hand. When 426 427 participants simply moved their right hand to trigger the touch on their left hand (nocontact trials in Experiments 1 & 2), no change in their somatosensory perception was 428 found. This suggests that an arbitrary mapping between the movement of the right hand 429 430 and the delivery of touch on the left hand is insufficient to elicit attenuation. In contrast, when participants expected to touch their own hand (Experiment 3), significant 431 432 attenuation was observed, even when the active hand unexpectedly missed the contact 433 (*no-contact* trials, 20%). Thus, a sensorimotor context that closely resembles tapping directly on the left index finger with the right (self-touch) was critical (Bays et al., 2006). 434 This finding contradicts the suggestion that attenuation on a passive hand reflects a 435 436 nonpredictive gating of tactile input during movement of the active hand (Thomas et al., 2022). Indeed, several earlier studies showed gating effects only on the moving limb 437 (movement effector) and not on the passive limb (Chapman et al., 1987; Cohen & Starr, 438 1987; Colino et al., 2014; Papakostopoulos et al., 1975; Pertovaara et al., 1992; Rushton 439 et al., 1981), and we also recently showed that experimental paradigms identical to the 440

one used in the present study produce attenuation effects but not gating effects on thepassive hand (Kilteni & Ehrsson, 2022).

It is interesting to note that the magnitude of attenuation was greater in the *contact* 443 compared to the *no-contact* condition by approximately 35% in Experiment 3. We 444 445 speculate that the decrease of attenuation in the *no-contact* trials is due to the unexpected omission of contact influencing the perceived magnitude of touch in a postdictive 446 manner. Specifically, the unexpected omission of contact on the minority of trials (20%) 447 448 could be seen as a form of stimulus omission akin to so called 'silent oddballs' that are 449 known to generate prediction errors (Busse & Woldorff, 2003; Karamürsel, 2000; 450 SanMiguel, Saupe, et al., 2013; SanMiguel, Widmann, et al., 2013). Although 451 participants clearly attenuated the touch predicted by their movement in the *no-contact* 452 trials, their expectation of contact was necessarily violated. This violation could be considered a novel event, given its infrequency. Novel events can have several 453 454 consequences for cognition, including transient enhancements of perception (Schomaker & Meeter, 2012), facilitated encoding of information into working memory (Mayer et al., 455 2011) as well as changes in the allocation of attentional resources in a postdictive manner 456 457 (for a review of effects of novelty on cognition see (Schomaker & Meeter, 2015).

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459 Some authors have criticised the comparison of perceived intensity of sensory stimuli in self-generated and externally generated conditions (Press et al., 2020; Yon et al., 2018, 460 461 2020b), as tactile input may be "predicted" in self-generated conditions through action and "unpredicted" in externally generated (passive) conditions that do not involve action. 462 This concern can be ruled out since in all three experiments, the stimulus in the *baseline* 463 (*i.e.*, externally generated touch) condition was delivered at a fixed timepoint (800 ms 464 after the cue); therefore, participants could predict it in the absence of motor-based 465 466 predictions. Moreover, it has been argued that somatosensory attenuation findings may be driven by dual-task requirements (Press et al., 2020) present only in self-generated 467 conditions that could increase the working memory load or result in a shift of attention 468 469 towards the active hand. This explanation can also be ruled out, given that dual-task requirements were present in the contact and no-contact conditions of all three 470 471 experiments without concomitant attenuation effects. Finally, alternative explanations based on differences in other psychophysical parameters, movement kinematics or 472 timings between experiments can also be ruled out (see Supplementary Material for 473 474 additional analyses).

475 Overall, the results suggest that attenuation effects are driven by action prediction and not 476 the double tactile stimulation of the two hands. Somatosensory attenuation has been 477 previously observed in the absence of double tactile stimulation, for example, when imagining but not executing the right hand movement (Kilteni et al., 2018) or just before 478 479 the hands make contact (Bays et al., 2005). Similarly, no somatosensory attenuation is 480 observed in the absence of action prediction, even if the two hands received double tactile 481 stimulation; for example, the passive displacement of the right hand towards the left hand that is accompanied by double touch (Kilteni et al., 2020) or the mere delivery of double 482 483 tactile stimulation on both hands (Bays et al., 2005) does not produce attenuation. From an ecological point of view, in every self-touch behaviour, we necessarily receive 484

somatosensory input on the active hand and the body part that passively receives touch
("touchant-touché" (Schütz-Bosbach et al., 2009)), and it is within these sensorimotor
contexts that the brain forms predictions about the somatosensory consequences on
multiple body parts (S J Blakemore et al., 1998).

489 How can the findings that action prediction attenuates touch be reconciled with those showing that expectations outside the domain of action improve sensory perception 490 (Press et al., 2020)? While it is difficult to directly compare these lines of research 491 492 because of differences in the sensory modality investigated, the task designs used and the perceptual measures employed, we speculate that there are numerous possible reasons 493 494 why action prediction may not have the same effect on perception as prediction 495 mechanisms outside the domain of action. First, research on action-based predictions concerns ubiquitous associations between actions and their sensory consequences that we 496 are continually exposed to throughout the lifespan. For example, we are constantly 497 498 exposed to associations between our motor behaviours and their tactile consequences 499 during self-touch, even as early as 13 weeks in utero (Kurjak et al., 2003). In contrast, research on sensory expectations outside the domain of action primarily concerns 500 501 arbitrary associations between stimuli that are typically learned only during the time 502 course of a given task. It is therefore conceivable that separable mechanisms may operate to predict action effects versus stimulus-stimulus associations (see (Dogge, Custers, & 503 Aarts, 2019; Dogge, Custers, Gayet, et al., 2019) for discussion). Second, higher-level 504 expectations, such as explicit prior knowledge that a specific sensory event is likely, 505 might not operate in the same way as lower-level action predictions; for example, it has 506 been proposed that action-based predictions inhibit expected stimuli, while sensory 507 508 expectations potentiate the expected sensory inputs (de Lange et al., 2018). Most 509 importantly, from a theoretical perspective, attenuating the predicted sensory consequences of actions does not necessarily mean that the brain forms inaccurate 510 511 representations of the world but instead indicates a flexible strategy that prioritises more informative externally generated events. 512

Debates between researchers supporting attenuation or enhancement are useful and 513 fruitful for scientific dialogue and advancement. The present study revisited recent 514 findings on somatosensory enhancement during action and showed that when the 515 516 requirement to inhibit the action is removed from the baseline, action predictions do not enhance but attenuate the received somatosensory input. Our results are in strong 517 518 alignment with animal studies showing that action attenuates the predicted sensory 519 consequences (for reviews, see (Brooks & Cullen, 2019; Crapse & Sommer, 2008; 520 Cullen, 2004; Schneider & Mooney, 2018; Straka et al., 2018)). For example, crickets 521 and mice suppress auditory reafferent signals but maintain their sensitivity to external sounds (Audette et al., 2021; J. F. A. A. Poulet & Hedwig, 2006; J. F. A. Poulet & 522 Hedwig, 2003; Schneider et al., 2018), the weakly electric fish attenuates its 523 electrosensory reafference to respond to externally generated electrical signals (Cullen, 524 525 2004; Sawtell, 2017), and primates attenuate their vestibular reafference and activate vestibular-related reflexes only when the vestibular input is exafferent (Brooks et al., 526 2015; Cullen, 2012; Roy, 2004). To this end, the results of the present study prompt a 527

reappraisal of recent experimental findings upon which theoretical frameworks proposinga perceptual enhancement by action prediction are based.

# 530 Acknowledgments

We thank Evridiki Asimakidou and Lili Timar for their assistance during data collection.
We also thank Henrik Ehrsson for his helpful comments on an earlier version of the
manuscript. X.J. and K.K. were supported by the Swedish Research Council (VR Starting

Grant 2019-01909 granted to K.K.). Experimental costs were covered by the same grant.

# 535 Author Contributions

536 K.K. and X.J. designed the experiments; X.J. collected the data; X.J. analysed the data;

537 X.J. and K.K. wrote the manuscript.

# 538 **Declaration of interests**

539 The authors declare no competing interests.

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# 853 STAR Methods

### 854 **KEY RESOURCES TABLE**

#### 855 Key resources table

RESOURCE	SOURCE	IDENTIFIER
Preregistered studies		
Pre-registered experimental designs, methods and analyses	Open Science Framework (OSF)	Experiment 1: <u>https://osf.io/9jkqt</u> Experiment 2: <u>https://osf.io/hs8au</u> Experiment 3: <u>https://osf.io/gkwu7</u>
Deposited Data		
Extracted PSEs and JNDs for analysis	This paper	Supplementary material
Software and algorithms		
R Studio Version 1.4.1717	R Studio Team (2021)	https://www.rstudio.com/
JASP Version 0.13.1	JASP Team (2020)	https://jasp-stats.org/
MATLAB 2020b	MATLAB	https://www.mathworks.com/products/ new_products/release2021b.html
Other		
Motor	Maxon Group	https://www.maxongroup.com/
Servo	Hitec	https://hitecrcd.com/products/servos/an alog/micromini/hs-81/product
Force sensor	Honeywell Inc	https://buildings.honeywell.com/us/en
Motion tracking device	Polhemus Liberty	https://polhemus.com/motion- tracking/all-trackers/liberty
Distance sensor	Distance sensor	Ultrasonic Distance Sensor HC-SR04 5V Version
Arduino	Arduino DUE	https://store.arduino.cc/products/arduin o-due

856

### 857 **RESOURCE AVAILABILITY**

#### 858 Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Konstantina Kilteni (konstantina.kilteni@ki.se).

- 861 Materials availability
- This study did not generate new unique material.

#### 863 Data and code availability

All data (PSEs and JNDs) have been deposited at Open Science Framework and are publicly available as of the date of publication. DOIs are listed in the key resources table.

- 866 This paper does not report original code.
- 867 Any additional information is available from the lead contact upon request.

#### 868 EXPERIMENTAL MODEL AND SUBJECT DETAILS

#### 869 **Participants**

870 Thirty naive adults participated in Experiment 1 (18 female, aged 18-36, 28 right-handed and 2 ambidextrous), thirty naive adults participated in Experiment 2 (17 female, aged 871 20-37, 29 right-handed and 1 left-handed) and thirty naive adults participated in 872 Experiment 3 (12 female, aged 21-40, 29 right-handed, 1 ambidextrous, 1 left-handed). 873 874 Current or history of psychological or neurological conditions, as well as the use of any psychoactive drugs or medication to treat such conditions, were criteria for exclusion. 875 The sample size of each Experiment was decided prior to data collection based on our 876 877 previous studies using the same task (Kilteni et al., 2019; Kilteni & Ehrsson, 2022). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). 878 879 All experiments were approved by the Swedish Ethical Review Authority (registration 880 no. 2021-03790) and participants were compensated for their time.

#### 881 **Pre-registration of experiments**

The method and analysis plan for each experiment was pre-registered on the Open
Science Framework (OSF) prior to data collection (Experiment 1 <u>https://osf.io/9jkqt</u>,
Experiment 2 <u>https://osf.io/hs8au</u>, Experiment 3 <u>https://osf.io/gkwu7</u>).

#### 885 Modifications/additions to the pre-registered plan

The only modification from the pre-registered plan was a reduction in the number of trials administered in Experiment 3. Following initial piloting, it was deemed appropriate to reduce the overall length of the task by including fewer trials (see *Methods Details*). Two additional ANOVAs were also conducted to compare the results across the three experiments (**Main Text**) and the kinematics across experiments (Supplementary Materials).

#### 892 **METHODS DETAILS**

#### 893 **Experimental setup**

894 Participants sat comfortably on a chair with their arms placed on a table. The left hand rested palm up, with the index finger placed on a molded support. On each trial, a motor 895 (Maxon EC Motor EC 90 flat; Switzerland) delivered two forces (the test force and the 896 *comparison* force) on the pulp of the left index finger through a cylindrical probe (25 mm 897 898 height) with a flat aluminum surface (20 mm diameter) attached to a lever on the motor. A force sensor (FSG15N1A, Honeywell Inc.; diameter, 5 mm; minimum resolution, 0.01 899 N; response time, 1 ms; measurement range, 0-15 N) within the probe recorded the 900 901 forces applied on the left index finger. Following the presentation of the two forces, participants were asked to verbally report which of the two forces felt stronger - the first 902 or the second. A second identical force sensor within an identical cylindrical probe 903

904 ("active force sensor") was placed on top of, but not in contact with, the probe of the left905 index finger.

#### 906 **Force-discrimination task**

907 Participants judged the intensity of a *test* force and a *comparison* force (100 ms duration each) separated by a random interval between 800ms and 1200ms in a two-alternative 908 909 forced choice (2AFC) task. The intensity of the test force was  $2 \square N$ , while the intensity of 910 the comparison force was systematically varied among seven force levels (1, 1.5, 1.75, 2, 911 2.25, 2.5 or  $3\Box N$ ). In all the conditions, the forces were delivered by the same motor, in order to precisely control their magnitude, however the source of the force was 912 913 manipulated across conditions such that the force was triggered by the participants 914 contact with a force sensor (contact condition), their finger movement (no-contact condition) or automatically by the stimulus computer (baseline condition). 915

#### 916 **Experimental design and procedures**

917 <u>Experiment 1</u>

There were three conditions in Experiment 1 presented in three blocks separately: the *baseline* (i.e. externally generated touch) condition, the *contact* condition, and the *no-contact* condition.

In the *baseline* condition, participants did not move their limbs but passively received a *test* and the *comparison* force on the left index finger. This *baseline* condition was used to assess the participants' somatosensory perception in the absence of any movement (Bays et al., 2005; Kilteni et al., 2019, 2020). Each trial began with an auditory cue (100 ms duration, 997 Hz) followed by the *test* force delivered to the participants' left index finger 800 ms after the cue by the motor. The *comparison* force was then delivered at a random interval between 800 ms and 1200 ms after the *test* force.

In the *contact* condition, participants started each trial by holding their right index finger 928 approximately 10 cm above their left index finger. The start position was marked with a 929 visual marker placed next to their right index finger while the final position was the probe 930 931 of the active force sensor. The same auditory cue was presented as in the *baseline* condition, but participants now moved their right index finger downwards towards their 932 933 left index finger and actively tapped on the active force sensor placed on top of, but not in 934 contact with, the probe. The participant's active tap on the force sensor triggered the 935 motor to apply the *test* force on their left index finger (threshold 0.2 N). The tap of their 936 right index finger triggered the test force on their left index finger with an intrinsic delay 937 of 36 ms. The *comparison* force was then delivered at a random interval between 800ms and 1200ms after the test force. 938

In the *no-contact* condition, the participants started each trial by holding their right index finger 10 cm above their left index finger, identically to the *contact* condition. For this block, the active force sensor was removed and replaced by a distance sensor that detected the position of their right index finger. The distance sensor was placed on top of,

but not in contact with, the probe. Following the same auditory cue, participants moved 943 944 their right index finger towards their left index finger. To restrict the participants' right index finger movement within similar movement ranges as in the *contact* condition and 945 946 avoid contact with the distance sensor placed underneath, a second visual marker 947 indicated the final position of the right index finger above the distance sensor (5 cm from 948 the marker indicating the initial position). The distance sensor was connected to an 949 Arduino microcontroller that controlled a servo motor. The servo motor and the force sensor were placed 2 meters away from the participants' hands and hidden from view. 950 951 Once the distance sensor detected that the position of the right index finger became 952 smaller than a preset threshold, it triggered the servo motor that hit the force sensor and triggered the *test* force. We accounted for the additional delay of the distance sensor by 953 954 setting the position threshold for the distance sensor slightly higher than the lowest 955 position the participants were asked to reach with their right index finger. Therefore, the test force would be delivered at a similar timing to the participants' right index finger 956 957 endpoint between the *contact* and *no-contact conditions*. This position threshold was set 958 based on significant pilot testing prior all experiments. Indeed, there was a minimal time difference between the two setups across experiments (17 ms average delay) with the no-959 *contact* condition leading, rather than lagging the *contact* one (see **Supplementary** 960 **Materials**). The *comparison* force was delivered at a random interval between 800ms 961 and 1200ms after the *test* force. Therefore, in the *no-contact* condition, there was no 962 touch on the right index finger simultaneously with the *test* force on their left index 963 964 finger.

Before the experiment, participants were trained to make similar movements with their 965 966 right index finger in the *contact* and *no-contact* conditions, emphasis was placed on restricting their right index finger movements to between the two visual markers in the 967 no-contact condition. The 3D position of the right index finger was recorded using a 968 969 Polhemus Liberty tracker (240 Hz). Kinematic information was used to compare the movements between the *contact* and *no-contact* conditions and to reject any trials in 970 971 which the participant did not trigger the test stimulus with their movement, or trials in 972 which the participant did not move as instructed in the training (see below). Participants were administered white noise through headphones to mask any sounds made by the 973 974 motor to serve as a cue for the task. The loudness of the white noise was adjusted such 975 that participants could clearly hear the auditory tones of the trial.

Each block consisted of 70 trials resulting to 210 trials per participant. Thus, the
proportion of *contact* and *no-contact* trials was the same (50-50%). The order of the
conditions was fully counterbalanced across participants.

979 Experiment 2

The 2-AFC task was identical to that of Experiment 1. In Experiment 2, there were five conditions in total: the *baseline* condition, the *contact* condition, the *no-contact* condition, and two additional NOGO conditions (*NOGO contact* and *NOGO no-contact*). Trials of the NOGO conditions were pseudo-randomly intermixed with trials of the *contact* and *no-contact* conditions respectively (GO trials). The five conditions were

985 presented in three separate blocks: the *baseline*, *contact* (GO and NOGO trials) and *no-*986 *contact* (GO and NOGO trials) blocks.

In the *contact* block, 50% of trials began with an auditory "GO" cue (100 ms duration 987 high tone of 2458 Hz) instructing participants to tap the active force sensor to trigger the 988 989 test force (identically to the contact condition of Experiment 1). On the remaining 50% of trials an auditory "NOGO" cue (100ms duration low tone of 222 Hz) instructed 990 participants to withhold their movement and the test force was then delivered 800ms 991 992 following the NOGO cue. The *no-contact* block was identical to the *contact* block, except 993 that the *test* force was triggered by the position of the right index finger without contact 994 with the force sensor (identically to the *no-contact* condition of Experiment 1). The cue 995 tone in the baseline block was the same as the cue tone in the NOGO trials (100 ms 996 duration low tone of 222 Hz).

997 Therefore, this design replicated the experimental design of Thomas et al. (Thomas et al., 998 2021) with the additional inclusion of the *baseline* (i.e. externally generated touch) 999 condition. As in Experiment 1, we recorded the 3D position of the right index finger and 1000 the registered kinematic information was used to compare the movements between the contact and no-contact conditions and reject any trials in which the participant did not 1001 trigger the *test* stimulus with their movement, trials in which the participant did not move 1002 1003 as instructed in the training (see below), and trials in which the participants moved while instructed not to do so by the auditory cues (NOGO trials). As in Experiment 1, 1004 1005 participants were administered white noise and the loudness of the white noise was 1006 adjusted such that participants could clearly hear the GO and NOGO auditory cues of the 1007 trial.

The *baseline* block consisted of 70 trials, and the *contact* and *no-contact* blocks consisted
of 70 GO trials and 70 NOGO trials each, resulting to 350 trials in total per participant.
The order of the blocks was fully counterbalanced across participants.

1011 Experiment 3

The 2-AFC task and the experimental conditions (baseline, contact, and no-contact) were 1012 1013 identical to those of Experiment 1, except for the following. *Contact* trials (80%) were 1014 now pseudo-randomly intermixed with no-contact trials (20%) within the same block. 1015 The force sensor was now attached to a plastic platform that could be automatically 1016 retracted by a servo motor, depending on the trial type. Upon retraction, a distance sensor placed underneath the platform was revealed. In the *contact* trials, participants tapped the 1017 force sensor to trigger the *test* force identically to Experiments 1 and 2. In the *no-contact* 1018 1019 trials, the platform was automatically retracted before trial onset, unbeknownst to the 1020 participant. This led participants to unexpectedly miss the active force sensor and instead trigger the *test* force only by the position of their right index finger. In all conditions, the 1021 1022 participants' vision was occluded, and white noise was administered via headphones to prevent any visual or auditory cues indicating that the force sensor had been retracted in 1023 no-contact trials. The baseline block was identical to that of Experiments 1 and 2. 1024

1025 In Experiment 3, the number of trials was reduced from 70 to 56 to shorten the total 1026 experiment time to less than 90 minutes, similar in the Experiment 2. Thus, there were 56 1027 *no-contact* trials (20%) and 224 contact trials (80%). Similarly, there were 56 trials in the 1028 *baseline* condition. This resulted to 336 trials per participant. The order of the two blocks 1029 was fully counterbalanced across participants.

# 1030 QUANTIFICATION AND STATISTICAL ANALYSIS

- 1031 **Preprocessing of psychophysical trials.**
- 1032 Experiment 1

Experiment 1 included 6300 trials in total (30 participants \* 70 trials \* 3 conditions). Twenty-nine (29) trials were excluded (0.5%) because of 1 missing response, 4 trials in which the force was not applied correctly (1.85 N < *test* force < 2.15 N), and 24 trials because the *test* force was not triggered when moving towards the distance sensor. All trials excluded by the psychophysical fits were also excluded in the kinematic analysis.

1038 Experiment 2

Experiment 2 included 10500 trials in total (30 participants \* 70 trials \* 5 conditions). One-hundred fourteen (114) trials were excluded (1.1%) because of 2 missing responses, 6 trials in which the force was not applied correctly (1.85 N < *test* force < 2.15 N), 44 trials because the *test* force was not triggered when moving towards the distance sensor and 62 trials because the finger moved on a NOGO trial. All trials excluded by the psychophysical fits were also excluded in the kinematic analysis.

1045 Experiment 3

Experiment 3 included 10080 trials in total (30 participants \* 224 contact trials + 56 nocontact trials + 56 baseline trials). Two-hundred twenty-four (29) trials were excluded (2.42%) because of 29 missing responses, 86 trials in which the force was not applied correctly (1.85 N < *test* force < 2.15 N), 81 because the test force was not triggered when moving towards the distance sensor and 48 because the finger contacted the distance sensor on *no-contact* trials. All trials excluded by the psychophysical fits were also excluded in the kinematic analysis.

# 1053 **Preprocessing of kinematic recordings.**

1054 All kinematic trials were co-registered with the force trials through Transistor-Transistor Logic (TTL) signals sent by the motor to both file outputs. The kinematic recordings 1055 were corrected for any distortion in the Polhemus sensor from the force sensor and 1056 1057 distance sensor based on measurements made with and without the force/distance sensors within the same space. Exclusion of trials based on the kinematics was done by assessing 1058 1059 whether the test force was delivered after the position of the active finger reached its minimum value on the vertical plane. Trials in which the force was delivered after the 1060 minimum value had been reached were rejected. For experiment 2, trials in which the 1061 1062 active finger moved more than 1 cm following a NOGO cue were also rejected.

#### 1063 Fitting of psychophysical responses

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

1066 
$$p = \frac{e^{\beta 0 + \beta 1x}}{1 + e^{\beta 0 + \beta 1x}}$$
 (Equation 1)

1067

1068 We extracted two parameters of interest: the Point of Subjective Equality (PSE) (*PSE* = 1069  $-\frac{\beta_0}{\beta_1}$ ), which represents the intensity at which the *test* force felt as strong as the 1070 *comparison* force (p = 0.5) and quantifies the perceived intensity, and the JND (*JND* = 1071  $\frac{\log (3)}{\beta_1}$ ), which reflects the participants' discrimination ability. Before fitting the 1072 responses, the values of the applied comparison *forces* were binned to the closest value 1073 with respect to their theoretical values (1, 1.5, 1.75, 2, 2.25, 2.5 or 3 N).

For all participants and all conditions, the fitted logistic models were very good, withMcFadden's R squared measures ranging between 0.735 and 1.000.

#### 1076 Normality of data and statistical comparisons.

1077 We used R (R Core Team, 2022), JASP (JASP Team, 2022) and MATLAB (2020b) to analyze our data. The normality of the PSE and the JND data distributions, as well as the 1078 kinematic information data distributions were assessed using Shapiro-Wilk tests. 1079 1080 Depending on the data normality, pairwise comparisons between conditions were performed by using either a paired t-test or a Wilcoxon signed-rank test. We report 95% 1081 confidence intervals  $(CI^{95})$  for each statistical test. Effect sizes are reported as the 1082 Cohen's d for t-tests or the matched rank biserial correlation rrb for the Wilcoxon signed-1083 1084 rank tests. In addition, a Bayesian factor analysis using default Cauchy priors with a scale of 0.707 was performed for all statistical tests that led to not statistically significant 1085 effects, to provide information about the level of support for the null hypothesis 1086 compared to the alternative hypothesis  $(BF_{01})$  based on the data. We interpret a factor 1087 1088 between 1/3 and 3 as "anecdotal evidence" (Quintana & Williams, 2018; van Doorn et al., 2021), indicating that support for either the preferred or null hypotheses is insufficient. 1089 1090 For the Analysis of Variance (ANOVA, see **Supplementary Material**), homogeneity of variance was assessed using Levene's test for Equality of Variances, which did not reach 1091 significance, and the Q-Q plot of the standardized residuals indicated approximately 1092 1093 normally distributed residuals. Post-hoc tests were made using Bonferroni corrections. All tests were two-tailed. 1094

#### 1095 **References**

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#### 1408 SUPPLEMENTARY MATERIAL

#### 1409 Just Noticeable Difference (JND) analysis

From the psychophysical fits, we extracted the just noticeable difference (JND), which 1410 represents the participants' force discrimination capacity between conditions. In 1411 Experiment 1, the JNDs did not significantly differ between any of the conditions (all p 1412 1413 values > 0.05). In Experiment 2, the JNDs were not significantly different between 1414 conditions (p values > 0.05), except in the contact condition, where the JNDs were 1415 significantly higher than in the *baseline* condition (t(29) = -2.52, p = 0.017, d = -0.46, d = -0.46) $CI^{95} = [-0.06 - 0.01], BF_{01} = 0.355)$ . Finally, in Experiment 3, the JNDs were significantly 1416 lower in the baseline condition than in the contact condition (t(29) = -3.61, p < .001, d = -1417 0.66,  $CI^{95} = [-0.09 - 0.02], BF_{01} = 0.034)$  and the *no-contact* condition (t(29) = -2.77, p = -2.77)1418 0.010, d = -0.51,  $CI^{95} = [-0.08 - 0.01]$ ,  $BF_{01} = .213$ ), but there were no significant 1419 differences in the JNDs between the *contact* and *no-contact* conditions (t(29) = -0.65, p =1420 0.521. d = -0.12,  $CI^{95} = [-0.04 \ 0.02]$ ,  $BF_{01} = 4.233$ ). Thus, in contrast to the PSEs, there 1421 were no significant differences in the JNDs between the contact and no-contact 1422 1423 conditions in any of the three experiments, demonstrating that the two conditions yielded 1424 the same discrimination capacity.

#### 1425 Kinematic analysis

To ensure that the movements in both the *contact* and *no-contact* conditions were comparable, participants were trained to make the same movement with their right index finger between two visual markers positioned 5 cm apart in Experiments 1 and 2. This training was not required for Experiment 3, in which participants were blindfolded and unaware that the distance sensor had been retracted on *no-contact* trials.

Given that the right index finger movement ends on impact with the force sensor in the 1431 1432 contact condition but not in the *no-contact* condition, the kinematics of the finger movements are likely to differ between conditions. The active finger was slightly closer 1433 to the passive finger at the time of the *test* force in the *contact* compared to the *no-contact* 1434 1435 condition in Experiments 1 and 2 (by less than 5 mm). Specifically, in Experiment 1, the 1436 position of the right index finger at the time of the *test* force was marginally closer to the left index finger in the contact condition than in the no-contact condition (mean 1437 difference = 2.32 mm, s.e.m. = 1.14: t(29) = -2.04, p = 0.051, d = 0.37,  $CI^{95} = [-0.74]$ 1438 0.01],  $BF_{01} = 0.845$ . In Experiment 2, the position of the right index finger at the time of 1439 1440 the *test* force was slightly closer to the left index finger in the *contact* condition than in the *no-contact* condition (mean difference = 4 mm, s.e.m. = 1.8: t(29) = -2.29, p = 0.030, 1441 1442  $d = 0.42, CI^{95} = [-0.79 - 0.04], BF_{01} = 0.550$ . In Experiment 3, participants were unaware that they would miss the force sensor in the *no-contact* trials, so with no force sensor to 1443 1444 stop the movement, their right index finger continued further downwards. Here, the 1445 position of the right index finger at the time of the *test* force was closer to the left index 1446 finger in the *no-contact* condition than in the *contact* condition (mean difference = 25.7 mm, s.e.m. = 2.0: t(29) = 12.79, p < .001, d = 2.34,  $CI^{95} = [1.63, 3.03]$ ,  $BF_{01} < 0.001$ . 1447 Critically, the closer position of the right index finger to the left index finger in the no-1448 1449 contact trials compared to the contact trials cannot explain the attenuation findings in the

*no-contact* condition since the attenuation in the *contact* trials was actually stronger
compared to that in the *no-contact* trials (Main Text).

1452 It could be argued that our differences between the *contact* and *no-contact* conditions across experiments are driven by differences in the timing of the two setups. This 1453 explanation is unlikely since we observed robust attenuation in the *no-contact* condition 1454 of Experiment 3 but not in Experiments 1 and 2 while the setups remained the same. To 1455 further control that the attenuation observed in the *no-contact* condition of Experiment 3 1456 1457 but not in the *no-contact* conditions of Experiments 1 and 2 was not driven by timing 1458 differences in the participants' movement between experiments, we calculated the time the *test* force was delivered in the *contact* and *no-contact* conditions with respect to their 1459 1460 movement end point (*i.e.*, the force sensor press in the *contact* condition and the lowest 1461 vertical position in the *no-contact* condition). On average, the *test* force was applied 24 1462 ms earlier in the *no-contact* compared to the *contact* condition in Experiment 1 (s.e.m. = 1463 4.20), 11 ms earlier in the *no-contact* compared to the *contact* condition in Experiment 2 1464 (s.e.m. = 4.53) and 15 ms earlier in the *no-contact* compared to the *contact* condition in 1465 Experiment 3 (s.e.m. = 2.67). An ANOVA revealed a significant main effect of 1466 Experiment (F(2, 87) = 3.32, p = 0.041,  $\eta p = 0.071$ ), with Bonferroni corrected post hoc 1467 comparisons indicating significant differences between Experiment 1 and Experiment 2  $(t(2, 87) = -2.50, p = 0.043, d = 0.65, CI [0.62 26.83], BF_{01} = 0.500)$ . Importantly, there 1468 1469 were no significant differences between neither Experiments 1 and 3 (t(2, 87) = -1.80, p = -1470 0.226, d = 0.47, CI [-3.21 22.99],  $BF_{01} = 0.744$ ), nor Experiments 2 and 3 (t(2, 87) = -1471 0.69, p = 1.000, d = -0.18, CI [-16.93 9.27],  $BF_{01} = 3.051$ ) demonstrating that the attenuation observed in Experiment 3 cannot be attributed to time differences between the 1472 participants' movement and the received touch. 1473

# 1474 Supplemental Figure S1



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Figure S1. Fitted logistic models based on the participants' responses under each conditionof Experiment 1.





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1480 Figure S2. Fitted logistic models based on the participants' responses under each condition

1481 of Experiment 2.

#### **Supplemental Figure S3** 1482



1483

1484 Figure S3. Fitted logistic models based on the participants' responses under each condition 1485 of Experiment 3.