Action does not enhance but attenuates predicted touch

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Abstract

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Dominant motor control theories propose that the brain uses efferent information to predict and attenuate the somatosensory consequences of actions, referred to as sensory attenuation. Support for this model comes from psychophysical and neuroimaging studies showing that touch applied on a passive hand elicits attenuated perceptual and neural 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 challenged this view by providing psychophysical evidence that the perceived intensity of 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 attributing attenuation effects to the double tactile stimulation of the hands upon contact. Here, we directly contrasted the hypotheses of the attenuation and enhancement models regarding how action influences somatosensory perception by manipulating whether the active hand contacts the passive hand. In three preregistered experiments, we demonstrate 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 (Experiment 2), and that self-generated touch is robustly attenuated regardless of whether the two hands make contact (Experiment 3). Our results provide conclusive evidence that action does not enhance but attenuates predicted touch. These findings prompt a reappraisal of recent experimental findings upon which theoretical frameworks proposing a perceptual enhancement by action prediction are based.

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.

Keywords

31 somatosensory attenuation; prediction; cancellation; sharpening; enhancement

Introduction

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Dominant motor control theories propose that the brain uses an internal forward model in combination with a copy of the motor command (efference copy) to predict the sensory consequences of our movements (McNamee & Wolpert, 2019; Shadmehr et al., 2008; Daniel M Wolpert & Flanagan, 2001). For example, the brain predicts the upcoming touch as one reaches towards an object. These predictions allow for the correction of 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 by combining the predicted touch with the actual sensory input (Scott, 2004; Shadmehr et al., 2008; Todorov & Jordan, 2002). These predictions attenuate the perception of the self-generated input (sensory reafference) compared to that of externally generated input (Davidson & Wolpert, 2005; Franklin & Wolpert, 2011; D. M. Wolpert & Kawato, 1998) and infer whether the cause of the sensory input is the self or the environment (Brown et 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 touch of others (S.-J. Blakemore, Wolpert, et al., 2000). The attenuation of sensory 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 perception of more informative externally generated stimuli (Bays & Wolpert, 2012; McNamee & Wolpert, 2019). Thus, the attenuation model proposes that we dampen perceptual representations of expected self-generated stimuli to reduce redundancy and to highlight behaviourally relevant unexpected externally generated stimuli.

In contrast, an alternative theoretical framework proposes that predictions, including those arising from our motor commands, should not attenuate but instead enhance sensory signals, thereby allowing for sharper (i.e., more accurate) representations of predicted compared to unpredicted sensory events (Press et al., 2020; Press & Yon, 2019; You et al., 2020a). This *enhancement* account – also referred to as the sharpening account - 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 North Pole, one expects to see a polar bear rather than an elephant) and that these predictions should bias our perception towards our expectations. The proposal mainly stems from experimental research outside the domain of action and argues that weak, noisy, or ambiguous sensory input that is in line with prior expectations should be enhanced to achieve, on average, more accurate representations. For example, we are more biased to report the presence of visual events that are statistically likely to occur rather than unlikely events (Chalk et al., 2010; Wyart et al., 2012), more sensitive to lowlevel visual features that are in line with prior expectations (Stein & Peelen, 2015; Teufel et al., 2018), and show greater biases when perceiving visual events that are congruent with our expectations (Hudson, Nicholson, Ellis, et al., 2016; Hudson, Nicholson, 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 (Summerfield & de Lange, 2014). Thus, the enhancement model proposes that we amplify the perceptual representations of expected compared to unexpected sensory input.

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In the somatosensory domain, evidence supporting the attenuation model has repeatedly 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 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 et al., 2022; Weiskrantz et al., 1971; Wolpe et al., 2016) and evokes attenuated 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 intensity applied on the passive hand that is externally generated. In contrast, one study 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 active hand never receives touch simultaneously with the passive hand (i.e., hands do not 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 gating processes caused by the simultaneous double tactile stimulation of the two hands (Press et al., 2022).

The attenuation (or cancellation) and enhancement (or sharpening) models present strikingly different hypotheses regarding how action influences the perception of sensory input and are supported by contradictory experimental evidence, leading to debates 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 enhancement findings (Thomas et al., 2022) and directly contrasting them with earlier attenuation findings (Bays et al., 2006) which used similar experimental manipulations 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 al., 2005, 2006; Kilteni et al., 2019, 2020, 2021, 2022; Kilteni & Ehrsson, 2022) and enhancement (Thomas et al., 2022) was used to determine (a) whether movement of the right hand enhances or attenuates the perceived magnitude of touch applied on the left hand when the two hands do not make contact (Experiments 1 and 2) and (b) whether 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 about whether action prediction "attenuates" or "enhances" the perception of the 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 passively received externally generated touch, with which we compared the participants' perception in all experimental conditions. Consequently, if participants perceive a touch as less or more intense during action than in the absence of action, we can infer that the received touch was attenuated or enhanced, respectively. This is a critical methodological detail compared to previous studies (Bays et al., 2006; Thomas et al., 2022) because if such baseline conditions are missing, the same patterns of results can be incorrectly attributed to "attenuation" or "enhancement": for example, if one condition produces less attenuation than another, it may be interpreted as enhancement, and vice versa. All studies and analysis plans were preregistered on the Open Science Framework prior to data collection (STAR Methods).

Results

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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 (no-
- contact 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

During the force-discrimination task, participants judged the intensity of a 'test' force and

- distinguish between effects of attenuation or enhancement (**Figure 1A**).
- 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 $2\square N$, while the intensity of the *comparison* force was systematically varied among seven force levels $(1, 1.5, 1.75, 2, 2.25, 2.5 \text{ or } 3 \square \text{N})$. 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
- 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

verbally reported their judgement (STAR Methods).

conditions. Finally, in the *baseline* condition (externally generated touch), participants

were told to relax their right hand, and each trial began with the same auditory cue

followed by the test force delivered to the participants' left index finger 800 ms after the

cue. In all trials, the *comparison* force was delivered after the *test* force, and participants

- 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

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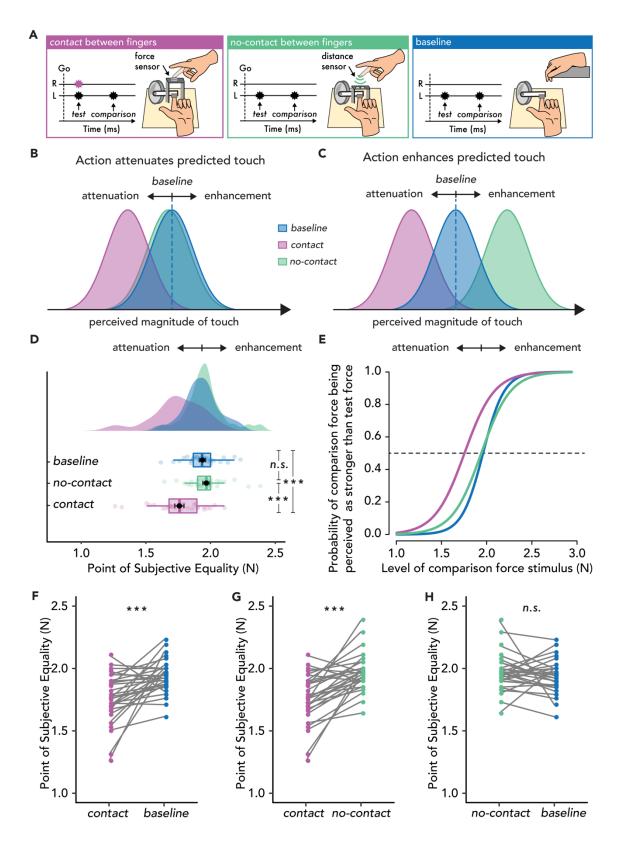
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1B), attenuation of the somatosensory input on the left hand in the *contact* condition compared to the baseline condition should be observed (i.e., lower PSEs) due to the test force being predicted from the action of the right hand. Moreover, earlier studies have shown that the mere movement of one hand is not sufficient to produce predictions of somatosensory input simultaneously applied on the other hand (Bays et al., 2005; Kilteni 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 manipulation and bimanual contact of the hands (Blakemore et al., 1998). Based on this, neither attenuation nor enhancement should be observed in the *no-contact* condition (i.e., 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 nocontact condition compared to the baseline condition should be observed (Figure 1C). Finally, since the enhancement model proposes that attenuation effects are attributed to unspecific (nonpredictive) gating effects caused by the simultaneous tactile stimulation of 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 action enhances the received touch when the index fingers of the two hands do not make 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.



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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 above the probe that delivered a test force of 2 N to their left index finger (L), followed by a comparison force randomly varying between 1 and 3 N. In the no-contact condition (green), participants approached a distance sensor with their right index finger, which triggered the test force on their left index finger, thus receiving no touch on their active finger. In the baseline condition (blue), participants relaxed both hands and passively received the forces on their left index finger. 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 in the no-contact condition (green) should be perceived similarly to that in the baseline (blue). C. Hypotheses based on the enhancement model. Touch in the no-contact condition (green) should be perceived as stronger than in the baseline (i.e., enhanced) (blue), but touch in the contact condition (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 difference that the attenuation model attributes these effects to action prediction, while the enhancement model attributes these effects to the simultaneous touch on the active hand. D-H. Data are colour-coded per condition. **D.** Box plots show the median and interquartile ranges for the PSE values per condition, 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. No enhancement effects were observed in the *no-contact* condition. **E.** Group psychometric functions for each condition. The leftward shift of the curves in the contact condition indicates attenuated PSE values compared to the other two conditions. F-H. Line plots for individual participant PSE values illustrating significantly lower PSEs for the contact versus baseline (F) and no-contact (G) conditions, but no significant differences in the PSE values between no-contact and baseline (H). (***p < .001)

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

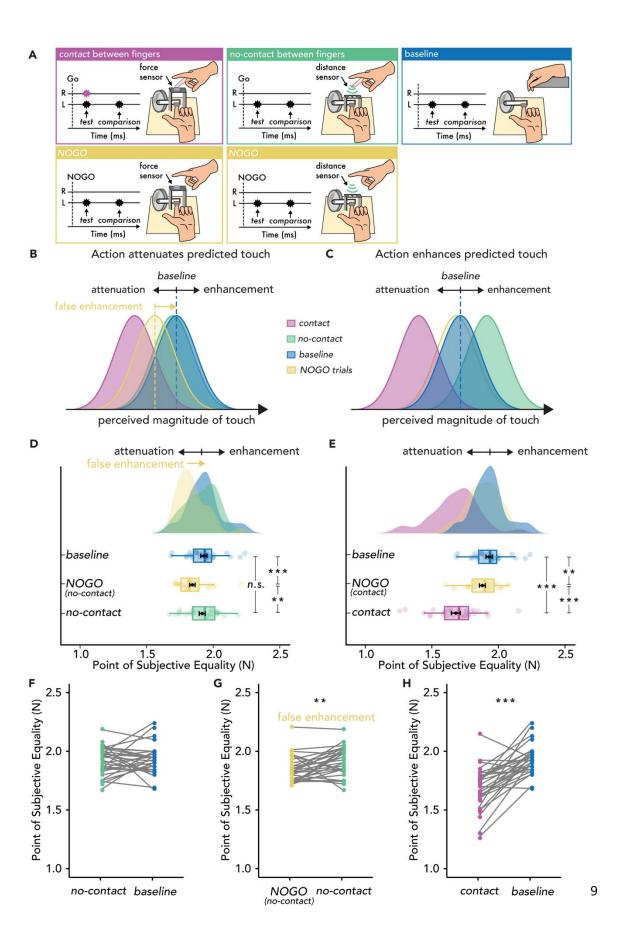
Having found no evidence for somatosensory enhancement in Experiment 1, Experiment 2 aimed to understand the potential source of the previously reported enhancement effects (Thomas et al., 2022). One critical methodological difference between Experiment 1 and the experiment of Thomas et al. (Thomas et al., 2022) concerns the baseline condition, as Thomas et al. (Thomas et al., 2022) compared the participants' perception in the nocontact condition to a condition where the participants prepared their right index movement but received a NOGO cue to inhibit the movement, and it was that comparison that revealed enhancement effects. However, motor inhibition (i.e. planning the hand 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 & Haggard, 2007) and the hand that would receive touch if the movement was executed (Kilteni et al., 2018); moreover, such conditions result in a competition for attentional resources to inhibit the motor response with processes that encode sensory stimuli into memory (Chiu & Egner, 2015b, 2015a; Yebra et al., 2019) (e.g., the test force in this 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 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 participants were cued to withhold their movement, identical to the design of Thomas et al. (Thomas et al., 2022) (**Figure 2A**). Participants were trained to make similar movements with their right index finger in the *contact* and *no-contact* trials. An externally generated touch condition was also included as an action-free *baseline* 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 inhibition condition (*i.e.*, NOGO trials) should be found compared to the *baseline*, which would then lead to apparent enhancement effects upon comparison with the *no-contact* trials (**Figure 2B, C**) (**STAR Methods**).

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 significant attenuation (i.e., lower PSEs) compared to the baseline condition (t(29) = 6.79, p < 0.001, d = 1.24, $CI^{95} = [0.18 \ 0.33]$, $BF_{01} < 0.001$) (**Figure 2E & H**). Once again, there was no enhancement in the no-contact trials compared to the baseline condition $(t(29) = 0.45, p = 0.658, d = 0.08, CI^{95} = [-0.05, 0.07])$ (Figure 2D & F), and 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 lower than the baseline condition both for the contact NOGO (t(29) = 2.99, p = 0.006, d)=0.55, $CI^{95} = [0.02 \ 0.09]$, $BF_{01} = 0.136$) and the no-contact NOGO trials (t(29) = 4.44, p) $< 0.001, d = 0.81, CI^{95} = [0.05 \ 0.13], BF_{0I} = 0.005)$ (Figure 2D, E & G). This demonstrates that NOGO trials resulted in a suppression of perceived touch on the left hand. Critically, this led to an apparent increase in the PSE from the *no-contact* trials to the NOGO trials in the no-contact block $(t(29) = -2.98, p = 0.006, d = -0.54, CI^{95} = [-0.12]$ -0.02], $BF_{01} = 0.139$), mimicking an 'enhancement' effect. Finally, PSEs were significantly lower in the contact trials than in the NOGO trials (t(29) = 5.91, p < 0.001, d=1.08, $CI^{95} = [0.13 \ 0.27]$, $BF_{01} < 0.001$), while the NOGO trials in the *contact* and *no*contact blocks did not significantly differ $(t(29) = 1.58, p = 0.126, d = 0.29, CI^{95} = [-0.01,$ 0.08], $BF_{01} = 1.697$). (See also **Supplementary Material** for individual fits and 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.



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

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 relative frequency was manipulated within the same block (contact trials: 80%, nocontact trials: 20%) (Figure 3A). The force sensor the participants tapped in the contact trials was now attached to a platform that could be automatically retracted. In the contact trials, participants tapped the force sensor to trigger the test force identically to 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 contact with the sensor but still trigger the test force only by the position of their right index finger. Participants' vision was occluded so that they could not know whether the 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 form predictions about the somatosensory consequences of their movement in most of the 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 contrast, if attenuation is a nonpredictive process caused by the mere simultaneous tactile 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 to the baseline condition, regardless of whether contact was made (Figure 3D, E, F & H): the PSEs were significantly lower in the contact condition than in the baseline condition $(t(29) = 8.06, p < 0.001, d = 1.47, CI^{95} = [0.16 \ 0.27], BF_{01} < 0.001)$ and lower in the no-contact condition than in the baseline condition (t(29) = 4.45, p < 0.001, d = 0.81, $CI^{95} = [0.07 \ 0.20], BF_{01} = 0.004$). The magnitude of attenuation was larger in the *contact* condition than in the no-contact condition, with significantly lower PSEs in the contact condition than in the *no-contact* condition $(t(29) = 3.94, p < 0.001, d = 0.72, CI^{95} = [0.04])$ 0.12], $BF_{01} = 0.016$) (Figure 3G) (see also Supplementary Material for individual fits and additional analyses). It should be mentioned however that the difference in the attenuation magnitudes was modest (

35%). These findings indicate that the perceived intensity of touch on the passive left hand was significantly attenuated both when the active hand received touch or not, thereby ruling out the possibility that attenuation is merely due to simultaneous tactile stimulation (Thomas et al., 2022).

 The results of Experiment 3 emphasise the predictive nature of somatosensory attenuation, which is observed only when the sensorimotor context allows the formation of such predictions. To further strength our interpretation we performed an ANOVA on the difference in the PSEs between the *contact* and *no-contact* conditions across all three experiments. The ANOVA revealed a significant main effect of Experiment (F(2, 87) = 8.05, p<0.001, $\eta p = 0.156$), with Bonferroni corrected post hoc comparisons indicating significant differences between Experiments 1 and 3 (t(2, 87) = 3.10, t(2, 87) = 0.008, t(2, 87) = 0

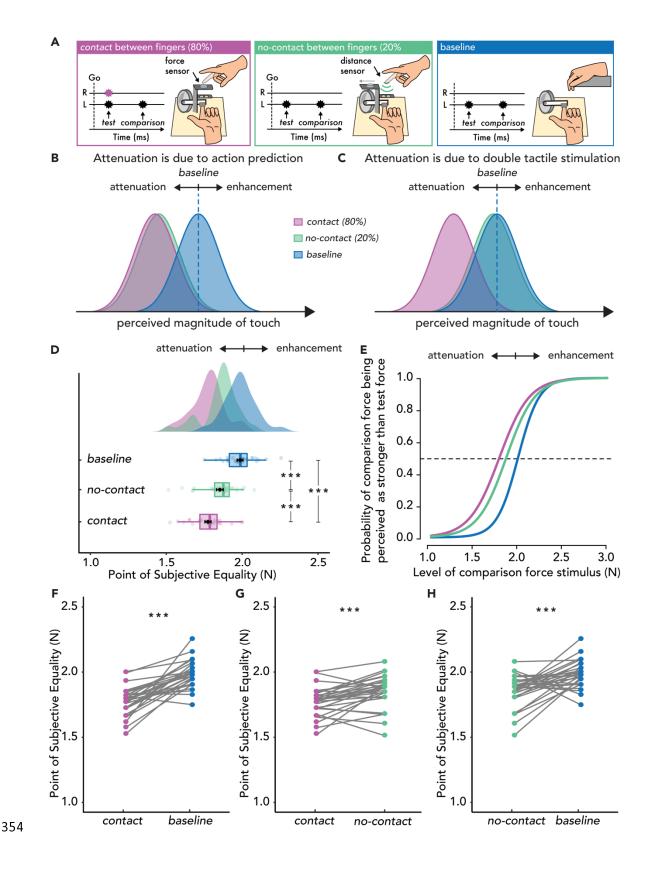


Figure 3. Experimental methods, hypotheses, and results of Experiment 3. A. The contact (magenta) and *no-contact* (green) conditions were identical to those of Experiment 1, with the only difference being their relative proportion (contact trials 80%, no-contact trials 20%). In the no-contact trials, the force sensor was automatically retracted, unbeknownst to the participant, revealing the distance sensor placed below. The baseline condition (blue) was identical to that of Experiments 1 and 2. **B.** Hypotheses based on the attenuation model. If attenuation is due to action prediction, then the perceived magnitude of touch should be reduced in both the contact (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 active hand, then the perceived magnitude of touch should be reduced only in the contact 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 plots show the median and interquartile ranges for the PSE values per condition, black circles and error bars show the mean PSE ± 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 the curves in the *contact* and *no-contact* conditions indicates attenuated PSE values compared to the baseline. F. Line plots for individual participant PSE values illustrating significantly lower 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 < 0.001)

Discussion

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

Before discussing the findings, it is important to emphasise that to draw conclusions about whether perception is attenuated or enhanced in an experimental condition including action, it is necessary to include a baseline condition without action. Only comparing conditions that include action prevents differentiating a genuine effect of 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 predicted with unpredicted somatosensory stimuli during action (see (Thomas et al., 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 experiments that allowed us to distinguish the direction of the effects.

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The results of Experiment 1 showed a robust attenuation of the touch applied on the 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 (nocontact condition). In contrast, the perceived intensity of touch in the no-contact condition was similar to that of the baseline (i.e., externally generated touch). These 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 contact, but do not replicate those of Thomas et al. (Thomas et al., 2022), who observed enhancement of touch in a no-contact condition. Experiment 2 further investigated the 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 condition in which the touch was applied rapidly following a cue to inhibit the movement (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, 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) compared to baseline perception. This is in line with previous evidence showing reduced amplitude of somatosensory evoked potentials for tactile stimuli presented shortly following a cue to inhibit a movement (Hoshiyama & Sheean, 1998), reduced perceived amplitude for tactile stimuli under the mere expectation to move (Voss et al., 2006, 2008), and reduced encoding of sensory stimuli following motor inhibition (Chiu & 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 following the cue to inhibit the movement that leads to an apparent enhancement. In contrast, by including a novel externally generated touch condition as a baseline that involved neither motor planning nor response inhibition, it became clear that there were no enhancement effects.

Experiment 3 demonstrated that action attenuates the predicted touch even if the active hand does not receive simultaneous tactile stimulation with the passive hand. When 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 found. This suggests that an arbitrary mapping between the movement of the right hand 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 attenuation was observed, even when the active hand unexpectedly missed the contact (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). This finding contradicts the suggestion that attenuation on a passive hand reflects a 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 (movement effector) and not on the passive limb (Chapman et al., 1987; Cohen & Starr, 1987; Colino et al., 2014; Papakostopoulos et al., 1975; Pertovaara et al., 1992; Rushton et al., 1981), and we also recently showed that experimental paradigms identical to the one used in the present study produce attenuation effects but not gating effects on the passive hand (Kilteni & Ehrsson, 2022).

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

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, 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. This concern can be ruled out since in all three experiments, the stimulus in the baseline (i.e., externally generated touch) condition was delivered at a fixed timepoint (800 ms after the cue); therefore, participants could predict it in the absence of motor-based 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 conditions that could increase the working memory load or result in a shift of attention 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 experiments without concomitant attenuation effects. Finally, alternative explanations based on differences in other psychophysical parameters, movement kinematics or timings between experiments can also be ruled out (see Supplementary Material for additional analyses).

Overall, the results suggest that attenuation effects are driven by action prediction and not the double tactile stimulation of the two hands. Somatosensory attenuation has been 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 the hands make contact (Bays et al., 2005). Similarly, no somatosensory attenuation is observed in the absence of action prediction, even if the two hands received double tactile 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 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

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).

How can the findings that action prediction attenuates touch be reconciled with those showing that expectations outside the domain of action improve sensory perception (Press et al., 2020)? While it is difficult to directly compare these lines of research 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 why action prediction may not have the same effect on perception as prediction mechanisms outside the domain of action. First, research on action-based predictions concerns ubiquitous associations between actions and their sensory consequences that we are continually exposed to throughout the lifespan. For example, we are constantly exposed to associations between our motor behaviours and their tactile consequences 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 arbitrary associations between stimuli that are typically learned only during the time 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, & Aarts, 2019; Dogge, Custers, Gayet, et al., 2019) for discussion). Second, higher-level expectations, such as explicit prior knowledge that a specific sensory event is likely, might not operate in the same way as lower-level action predictions; for example, it has been proposed that action-based predictions inhibit expected stimuli, while sensory expectations potentiate the expected sensory inputs (de Lange et al., 2018). Most importantly, from a theoretical perspective, attenuating the predicted sensory consequences of actions does not necessarily mean that the brain forms inaccurate representations of the world but instead indicates a flexible strategy that prioritises more informative externally generated events.

Debates between researchers supporting attenuation or enhancement are useful and fruitful for scientific dialogue and advancement. The present study revisited recent findings on somatosensory enhancement during action and showed that when the 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 alignment with animal studies showing that action attenuates the predicted sensory consequences (for reviews, see (Brooks & Cullen, 2019; Crapse & Sommer, 2008; Cullen, 2004; Schneider & Mooney, 2018; Straka et al., 2018)). For example, crickets 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 & Hedwig, 2003; Schneider et al., 2018), the weakly electric fish attenuates its electrosensory reafference to respond to externally generated electrical signals (Cullen, 2004; Sawtell, 2017), and primates attenuate their vestibular reafference and activate vestibular-related reflexes only when the vestibular input is exafferent (Brooks et al., 2015; Cullen, 2012; Roy, 2004). To this end, the results of the present study prompt a

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

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535 **Author Contributions**

- 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**

The authors declare no competing interests.

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STAR Methods

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KEY RESOURCES TABLE

Key resources table

RESOURCE	SOURCE	IDENTIFIER
Preregistered studies		
Pre-registered experimental designs, methods and analyses	Open Science Framework (OSF)	Experiment 1: https://osf.io/9jkqt Experiment 2: https://osf.io/skau Experiment 3: https://osf.io/gkwu7
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/analog/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

RESOURCE AVAILABILITY

Lead contact

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- 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.

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.

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

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Participants

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- 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
- 872 20-37, 29 right-handed and 1 left-handed) and thirty naive adults participated in
- Experiment 3 (12 female, aged 21-40, 29 right-handed, 1 ambidextrous, 1 left-handed).
- 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.
- The sample size of each Experiment was decided prior to data collection based on our
- previous studies using the same task (Kilteni et al., 2019; Kilteni & Ehrsson, 2022).
- Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971).
- All experiments were approved by the Swedish Ethical Review Authority (registration
- no. 2021-03790) and participants were compensated for their time.

Pre-registration of experiments

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

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
- 890 experiments (Main Text) and the kinematics across experiments (Supplementary
- 891 Materials).

METHODS DETAILS

Experimental setup

- 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
- 896 (Maxon EC Motor EC 90 flat; Switzerland) delivered two forces (the test force and the
- comparison force) on the pulp of the left index finger through a cylindrical probe (25 mm
- 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
- N; response time, 1 ms; measurement range, 0–15 N) within the probe recorded the
- 901 forces applied on the left index finger. Following the presentation of the two forces,
- 902 participants were asked to verbally report which of the two forces felt stronger the first
- 903 or the second. A second identical force sensor within an identical cylindrical probe

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

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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
- 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,
- 2.25, 2.5 or $3 \square N$). 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
- manipulated across conditions such that the force was triggered by the participants
- ontact with a force sensor (contact condition), their finger movement (no-contact
- condition) or automatically by the stimulus computer (baseline condition).

Experimental design and procedures

- 917 <u>Experiment 1</u>
- There were three conditions in Experiment 1 presented in three blocks separately: the
- 919 baseline (i.e. externally generated touch) condition, the contact condition, and the no-
- 920 contact condition.
- 921 In the baseline condition, participants did not move their limbs but passively received a
- 922 test and the comparison force on the left index finger. This baseline condition was used
- 923 to assess the participants' somatosensory perception in the absence of any movement
- 924 (Bays et al., 2005; Kilteni et al., 2019, 2020). Each trial began with an auditory cue (100
- 925 ms duration, 997 Hz) followed by the *test* force delivered to the participants' left index
- 926 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
- approximately 10 cm above their left index finger. The start position was marked with a
- visual marker placed next to their right index finger while the final position was the probe
- 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
- 933 left index finger and actively tapped on the active force sensor placed on top of, but not in
- ontact with, the probe. The participant's active tap on the force sensor triggered the
- motor to apply the *test* force on their left index finger (threshold 0.2 N). The tap of their
- right index finger triggered the test force on their left index finger with an intrinsic delay
- of 36 ms. The *comparison* force was then delivered at a random interval between 800ms
- 938 and 1200ms after the *test* force.
- In the *no-contact* condition, the participants started each trial by holding their right index
- 940 finger 10 cm above their left index finger, identically to the *contact* condition. For this
- 941 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 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 avoid contact with the distance sensor placed underneath, a second visual marker indicated the final position of the right index finger above the distance sensor (5 cm from the marker indicating the initial position). The distance sensor was connected to an 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. Once the distance sensor detected that the position of the right index finger became 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 setting the position threshold for the distance sensor slightly higher than the lowest 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 endpoint between the *contact* and *no-contact conditions*. This position threshold was set 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 nocontact condition leading, rather than lagging the contact one (see Supplementary **Materials**). The *comparison* force was delivered at a random interval between 800ms and 1200ms after the test force. Therefore, in the no-contact condition, there was no touch on the right index finger simultaneously with the test force on their left index finger.

Before the experiment, participants were trained to make similar movements with their 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 *no-contact* condition. The 3D position of the right index finger was recorded using a 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 which the participant did not trigger the test stimulus with their movement, or trials in 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 motor to serve as a cue for the task. The loudness of the white noise was adjusted such 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
- 978 conditions was fully counterbalanced across participants.

Experiment 2

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

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

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

Therefore, this design replicated the experimental design of Thomas et al. (Thomas et al., 2021) with the additional inclusion of the *baseline* (i.e. externally generated touch) condition. As in Experiment 1, we recorded the 3D position of the right index finger and 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 trigger the *test* stimulus with their movement, trials in which the participant did not move 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, participants were administered white noise and the loudness of the white noise was adjusted such that participants could clearly hear the GO and NOGO auditory cues of the 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 identical to those of Experiment 1, except for the following. Contact trials (80%) were now pseudo-randomly intermixed with *no-contact* trials (20%) within the same block. The force sensor was now attached to a plastic platform that could be automatically 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 force sensor to trigger the *test* force identically to Experiments 1 and 2. In the *no-contact* trials, the platform was automatically retracted before trial onset, unbeknownst to the 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 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 no-contact trials. The baseline block was identical to that of Experiments 1 and 2.

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

QUANTIFICATION AND STATISTICAL ANALYSIS

1031 Preprocessing of psychophysical trials.

1032 Experiment 1

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- 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,
- 1041 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

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- Experiment 3 included 10080 trials in total (30 participants * 224 contact trials + 56 no-
- 1047 contact trials + 56 baseline trials). Two-hundred twenty-four (29) trials were excluded
- 1048 (2.42%) because of 29 missing responses, 86 trials in which the force was not applied
- 1049 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.

Preprocessing of kinematic recordings.

- 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
- were corrected for any distortion in the Polhemus sensor from the force sensor and
- 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
- 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
- minimum value had been reached were rejected. For experiment 2, trials in which the
- active finger moved more than 1 cm following a NOGO cue were also rejected.

Fitting of psychophysical responses

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

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

- We extracted two parameters of interest: the Point of Subjective Equality (PSE) (PSE =1068
- $-\frac{\beta 0}{\beta 1}$), which represents the intensity at which the *test* force felt as strong as the 1069
- comparison force (p = 0.5) and quantifies the perceived intensity, and the JND (JND =1070
- $\frac{\log (3)}{\beta_1}$), which reflects the participants' discrimination ability. Before fitting the 1071
- responses, the values of the applied comparison forces were binned to the closest value 1072
- 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, with 1074
- 1075 McFadden's R squared measures ranging between 0.735 and 1.000.

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
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- 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

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SUPPLEMENTARY MATERIAL

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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, $CI^{95} = [-0.06 - 0.01]$, $BF_{01} = 0.355$). 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 =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.

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**).

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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 explanation is unlikely since we observed robust attenuation in the *no-contact* condition of Experiment 3 but not in Experiments 1 and 2 while the setups remained the same. To further control that the attenuation observed in the *no-contact* condition of Experiment 3 but not in the *no-contact* conditions of Experiments 1 and 2 was not driven by timing 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 movement end point (i.e., the force sensor press in the contact condition and the lowest vertical position in the *no-contact* condition). On average, the *test* force was applied 24 ms earlier in the *no-contact* compared to the *contact* condition in Experiment 1 (s.e.m. = 4.20), 11 ms earlier in the *no-contact* compared to the *contact* condition in Experiment 2 (s.e.m. = 4.53) and 15 ms earlier in the *no-contact* compared to the *contact* condition in Experiment 3 (s.e.m. = 2.67). An ANOVA revealed a significant main effect of Experiment $(F(2, 87) = 3.32, p = 0.041, \eta p = 0.071)$, with Bonferroni corrected post hoc 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 were no significant differences between neither Experiments 1 and 3 (t(2, 87) = -1.80, p =0.226, d = 0.47, CI [-3.21 22.99], $BF_{01} = 0.744$), nor Experiments 2 and 3 $(t(2, 87) = -1)^{-1}$ 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 participants' movement and the received touch.

Supplemental Figure S1

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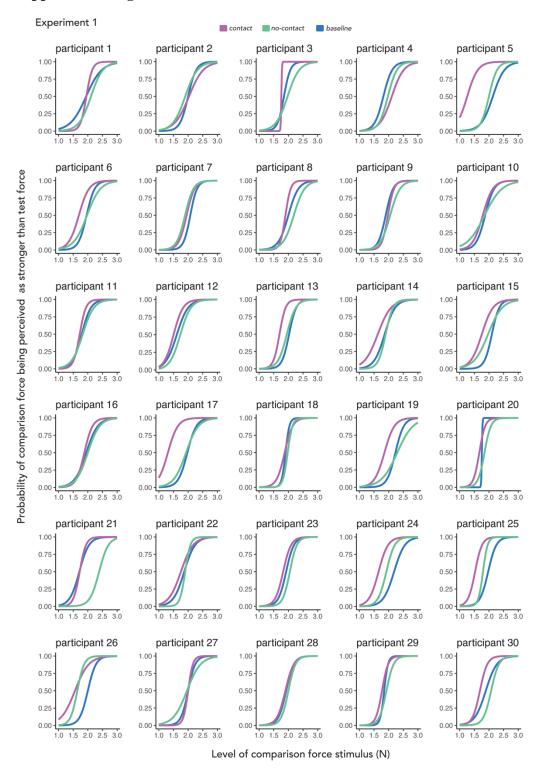


Figure S1. Fitted logistic models based on the participants' responses under each condition of Experiment 1.

Supplemental Figure S2

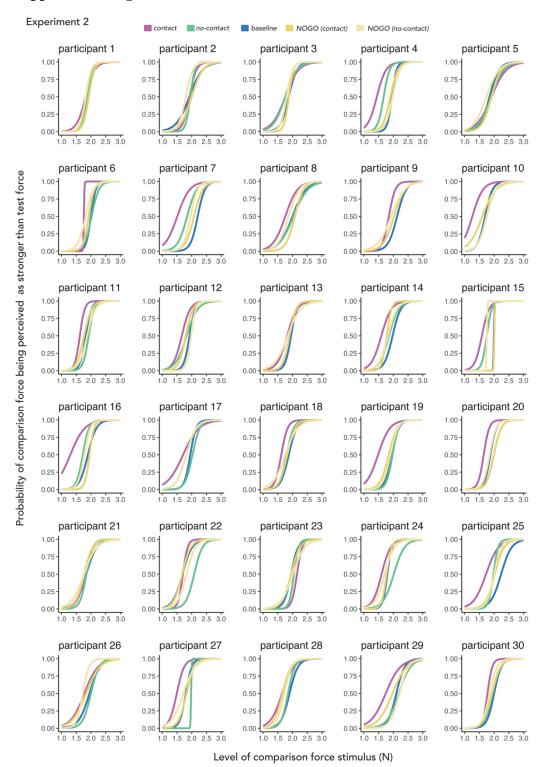


Figure S2. Fitted logistic models based on the participants' responses under each condition of Experiment 2.

Supplemental Figure S3

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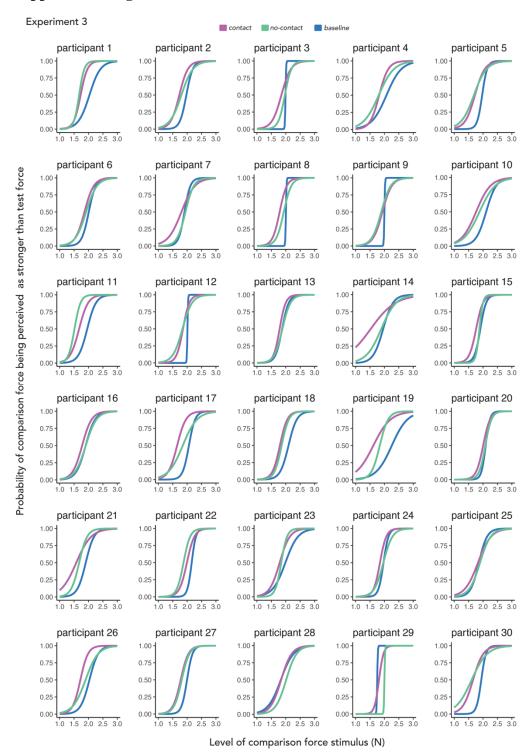


Figure S3. Fitted logistic models based on the participants' responses under each condition of Experiment 3.