Action does not enhance but attenuates predicted touch

Xavier Job[1] and Konstantina Kilteni[1,2]*

[1]Department of Neuroscience, Karolinska Institute, Stockholm, Sweden. [2]Department of Sensorimotor Neuroscience, Donders Institute, Radboud University, Netherlands

Abstract

Dominant motor control theories propose that the brain predicts and attenuates the somatosensory consequences of actions, referred to as somatosensory attenuation. Support comes from psychophysical and neuroimaging studies showing that touch applied on a passive hand elicits attenuated perceptual and neural responses if it is actively generated by 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 touch simultaneously with the passive hand (somatosensory enhancement) and by further attributing attenuation 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. We further assessed somatosensory perception in the absence of any predictive cues in a condition that turned out to be essential for interpreting the experimental findings. In three preregistered experiments, we demonstrate that action does not enhance the predicted touch (Experiment 1), that the previously reported "enhancement" effects are driven by the reference 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 and 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

somatosensory attenuation; prediction; cancellation; sharpening; enhancement

Introduction

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 [1–3]. For example, the brain predicts the upcoming touch as one reaches toward an object. These predictions allow for the correction of motor errors without relying on sensory feedback that suffers from intrinsic delays [4], thereby improving the estimation of the current state of our body by combining the predicted touch with the actual sensory input [5–7]. These predictions *attenuate* the perception of the self-generated input (sensory reafference) compared to that of externally generated input [8–10] and infer whether the cause of the sensory input is the self or the environment [11–13]. 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 [14]. 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 [15,16]. 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 [17–19]. 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 [20,21], more sensitive to low-level visual features that are in line with prior expectations [22,23], and show greater biases when perceiving visual events that are congruent with our expectations [24,25]. Such effects are thought to result from mechanisms that increase the "gain" of expected information by altering the weights of different sensory signals [26]. Thus, the enhancement model proposes that we amplify the perceptual representations of expected compared to unexpected sensory input.

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.*, self-generated touch) is perceived as weaker or less ticklish [27–41] and evokes attenuated somatosensory cortical activation [42–46] compared to touch of identical intensity applied on the passive hand that is externally generated. In contrast, evidence 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) [47]. 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 [48].

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 [12,17,36,49,50]. Clarifying how predictions about the sensory consequences of our movements affect our perception is fundamental to understanding the interaction between perception and action [7,16,51] but also for clinical and neurobiological theories of psychosis spectrum disorders, such as schizophrenia [46,52–58] and schizotypy [41], as well as functional movement disorders [59], Parkinson's disease [60] and ageing [61].

The present study aimed to contribute to this debate by directly contrasting the enhancement and attenuation models within the same paradigm. To this end, the same force discrimination task employed in earlier studies reporting attenuation [27,28,30,31,36,41,62–64] and enhancement [47] 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 novelty compared to previous studies [28,47] 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. Indeed, it was this baseline condition that turned out to be critical for distinguishing between attenuation and enhancement effects. All studies and analysis plans were preregistered on the Open Science Framework prior to data collection (**Methods)**.

Results

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 distinguish between effects of attenuation or enhancement (**Figure 1A**).

During the force-discrimination task, participants judged the intensity of a '*test'* force and 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 cylindrical probe attached to a lever driven by a DC electric motor. In each trial, participants reported which force they felt was stronger (the *test* or the *comparison*). The intensity of the *test* force was fixed at 2 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 or 3 N). In the *contact* condition, participants moved their right index finger towards their left index finger after an auditory cue and actively tapped on a force sensor placed on top of, but not 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 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 would always make contact between their fingers (through the probe) in this condition. In the *no-contact* condition, following the same auditory cue, participants moved their right 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 distance of their active finger as it approached their left index finger to trigger the *test* force, similar to [28,47]. The distance threshold was set such that the position of the right index finger when triggering the *test* force was equivalent to that in the *contact* condition. Participants were told that they would never make contact between their fingers. Before the experiment, participants were trained to make similar movements with their right index finger in the *contact* and *no-contact* 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 verbally reported their judgement (**Methods**).

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 (**Methods**). According to the attenuation model (**Figure 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 a predicted consequence of the action of the right hand. However, regarding the *no-contact* condition, 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 [27,44,65–69]. Instead, a bimanual sensorimotor context is needed such as during bimanual object manipulation and bimanual contact of the hands (Blakemore et al., 1998). Thus, while touch in the *no-contact* condition is *self-generated* in the sense that it is a consequence of one's movement, the efference copy and the sensory feedback are inconsistent with the sensorimotor context of touching oneself; in this case, the context of applying force on one's finger with another finger. In other words, the attenuation model suggests that not

any voluntary movement will attenuate upcoming sensory input. 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 [47], then higher PSEs in the *no-contact* 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 made contact (*contact* condition) (**Figure 1D, E, F**): the PSEs were significantly lower in the *contact* condition than in the *baseline* condition ($W = 422.00$, $p < 0.001$, $rrb = 0.82$, $CI^{95} = [0.08\ 0.25]$). Similarly, the PSEs were significantly lower in the *contact* condition than in the *no-contact* condition ($W = 441.00$, $p < 0.001$, $rrb = 0.90$, $CI^{95} = [0.13\ 0.26]$ (**Figure 1D, E, G**). Critically, however, in the comparison that contrasts the hypotheses of the two models, the *no-contact* condition did not produce any significant change in the perceived magnitude of the touch compared to the *baseline* condition ($W = 187.00$, $p = 0.360$, $rrb = -0.20$, $CI^{95} = [-0.08\ 0.030]$) (**Figure 1D, E, H**). A Bayesian factor analysis provided moderate support for the absence of any difference (BF_{01}=3.58). (See also **Supplementary Material** for individual fits and additional 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.

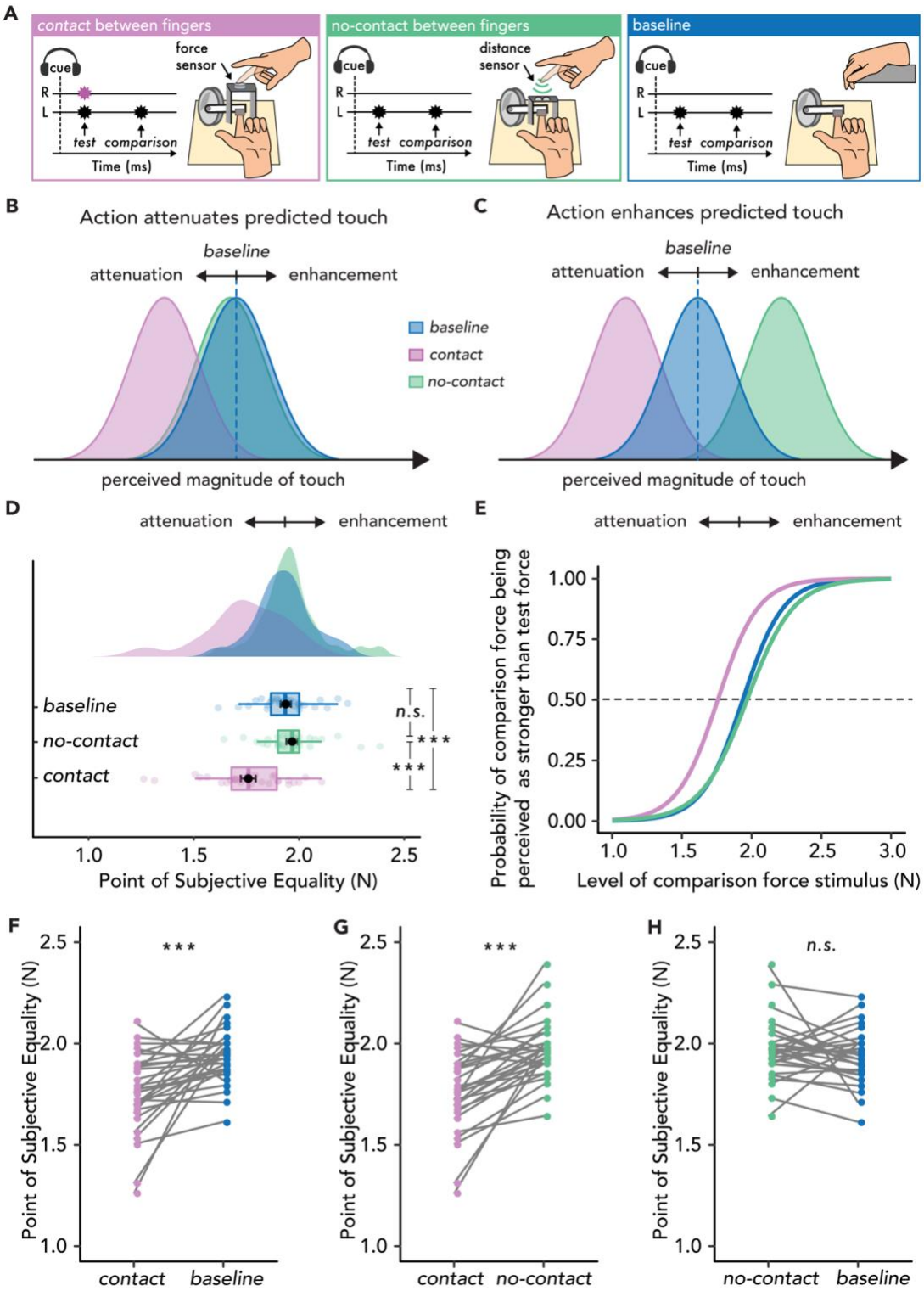


Figure 1. Experimental methods, hypotheses, and results of Experiment 1. A. In the *contact* condition (magenta), participants tapped with their right index finger (R) on a force sensor placed above the probe that delivered a *test* force of 2 N to their left index finger (L), followed by a

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 ± 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.

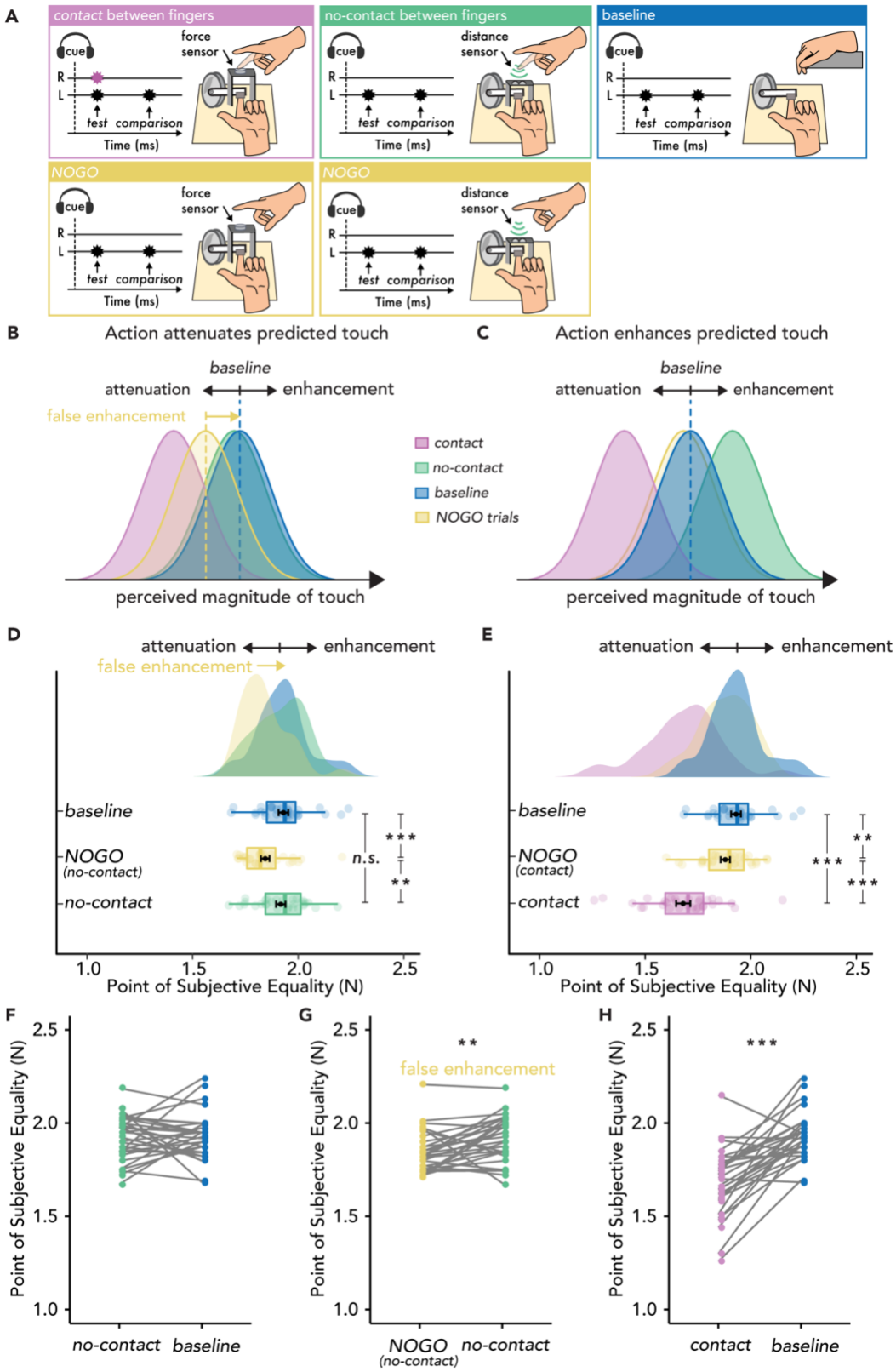
Having found no evidence for somatosensory enhancement in Experiment 1, Experiment 2 aimed to understand the potential source of the previously reported enhancement effects [47]. One critical methodological difference between Experiment 1 and previous evidence for enhancement concerns the *baseline* condition, as Thomas et al. [47] compared the participants' perception in the *no-contact* 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 [71–73] and the hand that would receive touch if the movement was executed [69]; moreover, such conditions result in a competition for attentional resources to inhibit the motor response with processes that encode sensory stimuli into memory [74–76] (*e.g.*, the *test* force in this paradigm). Therefore, if the motor inhibition condition used by Thomas et al. [47] 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. [47] (**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**) (**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 ($t(29) = 6.79$, $p < 0.001$, $d = 1.24$, $CI^{95} = [0.18\ 0.33]$) (**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 moderate evidence for the absence of any effects ($BF_{01} = 4.69$). Importantly, the PSEs in the *NOGO* (motor inhibition) trials were significantly lower than the *baseline* condition both for the *contact NOGO* ($t(29) = 2.99$, $p = 0.006$, $d = 0.55$, $CI^{95} = [0.02\ 0.09]$) and the *no-contact NOGO* trials ($t(29) = 4.44$, $p < 0.001$, $d = 0.81$, $CI^{95} = [0.05\ 0.13]$) (**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 ($t(29) = -2.98$, $p = 0.006$, $d = -0.54$, $CI^{95} = [-0.12\ -0.02]$), mimicking an 'enhancement' effect. Finally, PSEs were significantly lower in the *contact* trials than in the NOGO trials ($t(29) = 5.91$, $p < 0.001$, $d = 1.08$, $CI^{95} = [0.13\ 0.27]$), 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 [47] 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.


A
contact between fingers
no-contact between fingers
baseline
NOGO
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cue
force sensor
distance sensor
R
L
test
comparison
Time (ms)
B
Action attenuates predicted touch
C
Action enhances predicted touch
baseline
attenuation
enhancement
false enhancement
contact
no-contact
baseline
NOGO trials
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D
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Point of Subjective Equality (N)
F
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H
Point of Subjective Equality (N)
no-contact
baseline
NOGO (no-contact)
contact

264

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.

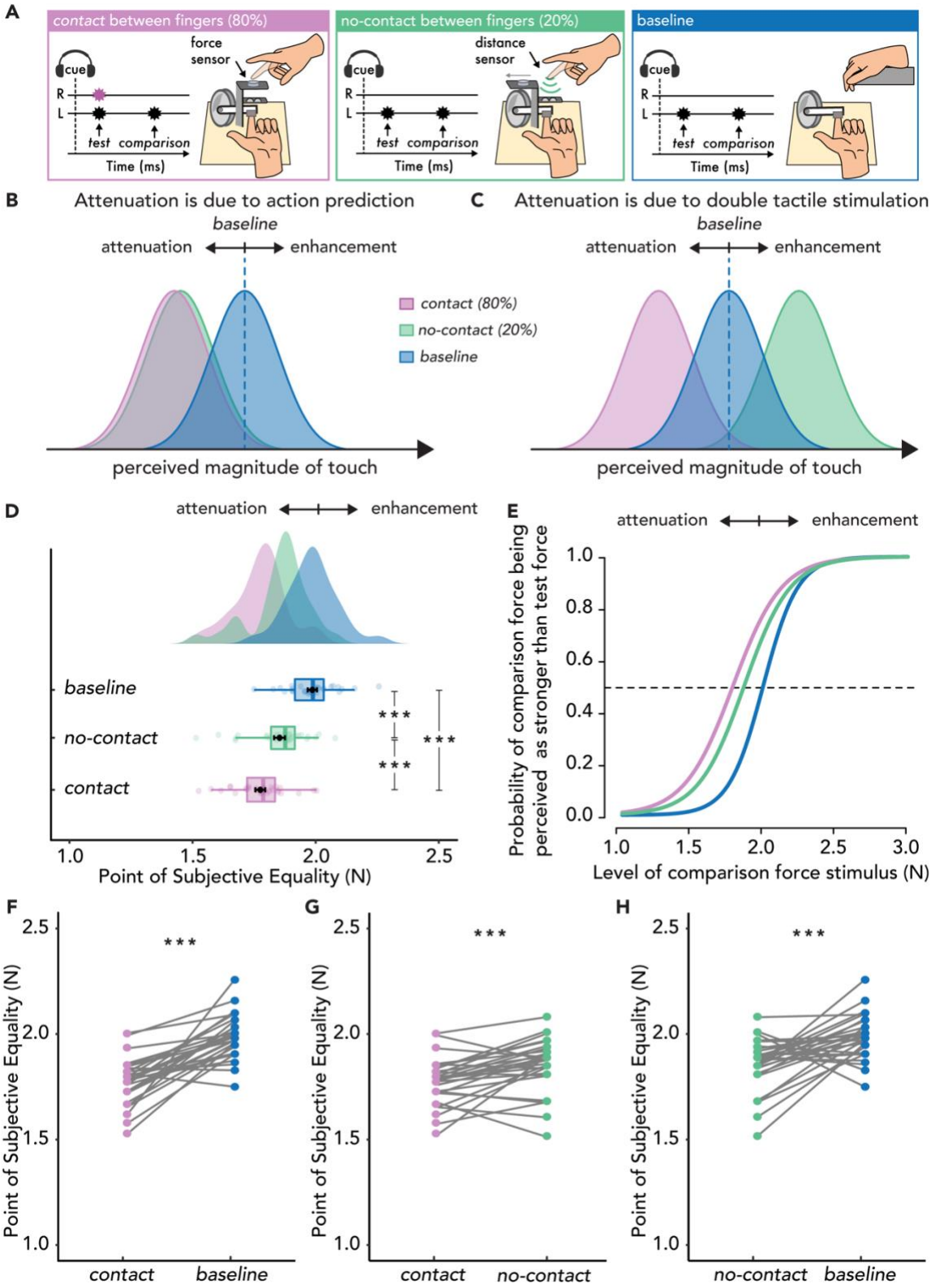
Within the framework of internal forward models, the absence of attenuation in the *no-contact* conditions of Experiments 1 and 2 is expected, given the lack of a sensorimotor context conducive to perceiving the touch as self-generated: when contact is never made, the forces applied on the passive left 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%, *no-contact* 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 ($t(29) = 8.06$, $p < 0.001$, $d = 1.47$, $CI^{95} = [0.16\ 0.27]$) and lower in the *no-contact* condition than in the *baseline* condition ($t(29) = 4.45$, $p < 0.001$, $d = 0.81$, $CI^{95} = [0.07\ 0.20]$). 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 ($t(29) = 3.94$, $p < 0.001$, $d = 0.72$, $CI^{95} = [0.04\ 0.12]$) (**Figure 3G)** (see also **Supplementary Material** for individual fits and additional analyses). The difference in the magnitude of attenuation 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 [47,49].

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. In Experiments 1 and 2 attenuation was only observed in the *contact* conditions, whereas attenuation was also observed in the *no-contact* condition of Experiment 3, where participants expected that they would make contact (i.e., the sensorimotor context was conducive to predicting self-touch). Thus, larger differences between the PSEs in the *contact* and *no-contact* conditions were observed for Experiments 1 and 2 compared to Experiment 3. To further strengthen 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 ($F(2, 87) = 8.05$, $p<0.001$, $\eta p2 = 0.156$), with Bonferroni corrected post hoc comparisons indicating significant differences between Experiments 1 and 3 ($t(2, 87) = 3.10$, $p = 0.008$, $d = 0.80$, CI [0.03 0.23]) as well as Experiments 2 and 3 ($t(2, 87) = 3.76$, $p < 0.001$, $d = 0.97$, CI [0.06 0.26]), but no significant differences between Experiments 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-contact* trials elicited attenuated perception only when the sensorimotor context allowed for a prediction of self-touch (Experiment 3) and not when the action was only arbitrarily associated with the touch (Experiments 1 and 2).


A
contact between fingers (80%)
no-contact between fingers (20%)
baseline
force sensor
distance sensor
cue
R
L
test
comparison
Time (ms)
B
Attenuation is due to action prediction
C
Attenuation is due to double tactile stimulation
baseline
attenuation
enhancement
contact (80%)
no-contact (20%)
baseline
perceived magnitude of touch
D
attenuation
enhancement
baseline
no-contact
contact
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1.0
1.5
2.0
2.5
Point of Subjective Equality (N)
E
attenuation
enhancement
Probability of comparison force being perceived as stronger than test force
1.0
0.8
0.6
0.4
0.2
0.0
1.0
1.5
2.0
2.5
3.0
Level of comparison force stimulus (N)
F
G
H
Point of Subjective Equality (N)
2.5
2.0
1.5
1.0
contact
baseline
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342

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

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 [47] for such comparisons). To this end, a *baseline* condition of pure somatosensory exafference (*i.e.*, externally generated touch) was included in all the present experiments that allowed us to distinguish the direction of the effects.

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 (*no-contact* 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. [28], 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. [47], 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 [47], 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 [73], reduced perceived amplitude for tactile stimuli under the mere expectation to move [71,77], and reduced encoding of sensory stimuli following motor inhibition [74,75,78]. 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 (*no-contact* 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%). This pattern of results can be explained by the attenuation model, which suggests that self-generation of a stimulus is in itself not sufficient for predictive attenuation, but that the action and it's predicted sensory feedback are consistent with touching one's own body [70]. Thus, a sensorimotor context that closely resembles tapping directly on the left index finger with the right (self-touch) was critical for predictive attenuation [28]. The findings of Experiment 3 also contradict the suggestion that attenuation on a passive hand reflects a nonpredictive gating of tactile input during movement of the active hand [47,49]. Indeed, several earlier studies showed gating effects only on the moving limb (movement effector) and not on the passive limb [79–84], and we have also recently shown that experimental paradigms identical to the one used in the present study produce attenuation effects but not gating effects on the passive hand [36]. Overall, the results suggest that attenuation effects are driven by action prediction and not the simultaneous tactile stimulation of the two hands. 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" [85]), and it is within these sensorimotor contexts that the brain forms predictions about the somatosensory consequences on multiple body parts [70].

Interestingly, the magnitude of attenuation was greater in the *contact* compared to the *no-contact* condition by approximately 35% in Experiment 3. This could suggest that the attenuation effect observed in the *contact* condition arises from multiple sources, one being the motor-based prediction and another source being the simultaneous touch on the active hand. However, this interpretation is inconsistent with the findings that somatosensory attenuation has been previously observed in the absence of simultaneous tactile

stimulation, for example, when imagining but not executing the right hand movement [69] or just before the hands make contact [27]. Similarly, no somatosensory attenuation is observed in the absence of action prediction, even if the two hands received simultaneous tactile stimulation; for example, the passive displacement of the right hand towards the left hand that is accompanied by double touch [31] or the mere delivery of simultaneous tactile stimulation on both hands [27] does not produce attenuation. Instead, our finding that the magnitude of attenuation was greater in the *contact* than the *no-contact* condition in Experiment 3 may instead reflect a decrease of attenuation in the *no-contact* trials, 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 [86–89]. 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[90], facilitated encoding of information into working memory [91] as well as changes in the allocation of attentional resources in a postdictive manner (for a review of effects of novelty on cognition see[92]).

Some authors have criticised the comparison of perceived intensity of sensory stimuli in self-generated and externally generated conditions [17,93,94]. A frequent criticism is that 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. Secondly, it has been argued that somatosensory attenuation findings may be driven by dual-task requirements [17] present only in self-generated conditions that could increase the working memory load or result in a shift of attention towards the active hand. A similar criticism has been suggested in which the mere movement of the active hand in self-generated conditions can result in a nonpredictive gating of tactile input. However, these explanations can also be ruled out, given that dual-task requirements and movement of the active hand were present in the *contact* and *no-contact* conditions of all three experiments without concomitant attenuation effects. Indeed, if dual-task requirements, or the mere presence of movement during the perceptual task, was sufficient to cause attenuation effects, then attenuation would have been observed in the *no-contact* conditions of Experiments 1 and 2. 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).

How can the findings that action prediction attenuates touch be reconciled with those showing that expectations outside the domain of action improve sensory perception [17]? 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* [95]. 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 [96,97] 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 [98]. 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.

It is important to emphasize that this study investigated the perception of self-generated touch during an action directed toward one's own body. Thus, perception was assessed on a passive body part that was the target of a movement of an active body part (*i.e.*, moving the right hand to touch the static left hand). This focus was chosen because extensive previous research has shown deteriorated performance when detecting or discriminating touch (both self-generated and externally generated) delivered on a moving limb, a phenomenon referred to as movement-related *gating* [99–103]. By assessing somatosensory perception on a static limb, we were able to isolate the effect of action prediction on somatosensory perception from other perceptual phenomena related to the movement *per se* including movement-related gating [36,99,104–108]. However, it is interesting to note that during the active exploration of objects through touch, referred to as *active touch*, self-generated touch also occurs, albeit only on the moving limb. Studies on active touch have observed improved perception of object features, such as texture or edge orientation when actively exploring an object [109,110] compared to passive exposure [111,112]. At first, the improved perception observed during active touch might appear paradoxical to observations of movement-related gating and predictive attenuation effects: if anything, active touch should result in worse perception than passive touch. However, it has been shown that humans optimize their exploratory movements to minimize these effects and maximize the quality of their sensory feedback. For example, it is known that the degree of gating decreases as movement speed slows [101,113,114] and it has been shown that participants optimize the speed of movement during active touch to avoid high speeds associated with tactile gating [115]. Similarly, when exploring objects through active touch, weaker forces are typically applied (e.g. < 1 N [116,117]) that elicit less attenuation than stronger forces, as shown in the classic force-matching task [118]. Thus, differences in the task context might primarily influence how one moves (e.g., the act of swatting a fly from one's arm versus feeling for a bump on one's skin), which can have disparate ensuing effects on perception depending on the movement kinematics.

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 [119–123]). For example, crickets and mice suppress auditory reafferent signals but maintain their sensitivity to external sounds [124–127], the weakly electric fish attenuates its electrosensory reafference to respond to externally generated electrical signals [128,129], and primates attenuate their vestibular reafference and activate vestibular-related reflexes only when the vestibular input is exafferent [130–132]. 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.

Methods

Participants

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 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). 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 [30,36]. Handedness was assessed using the Edinburgh Handedness Inventory [133]. All experiments were approved by the Swedish Ethical Review Authority (registration no. 2021-03790). Participants provided written informed consent and were compensated for their time.

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 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 experiments (**Main Text***)* and the kinematics across experiments (Supplementary Materials).

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 (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 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 or the second. A second identical force sensor within an identical cylindrical probe ("active force sensor") was placed on top of, but not in contact with, the probe of the left index finger.

Force-discrimination task

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 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 or 3 N). In all the conditions, the forces were delivered by the same motor, to precisely control their magnitude, however the source of the force was manipulated across conditions such that the force was triggered by the participants contact with a force sensor (*contact* condition), their finger movement (*no-contact* condition) or automatically by the stimulus computer (*baseline* condition).

Experimental design and procedures

<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 [27,30,31]. Each trial began with an auditory cue (100 ms duration, 997 Hz) followed by the *test* force delivered to the participant's 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 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 left index finger and actively tapped on the active force sensor placed on top of, but not in contact 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 and 1200ms after the *test* force. As in our previous studies[36,41,134], participants were asked to tap, neither too weakly nor too strongly, with their right index finger, "as if tapping the screen of their smartphone". This instruction was provided to ensure that the relationship between the force they applied with their right index finger on the force sensor and the force they received on their left index finger by the motor (2 N) remained approximately constant throughout the experiment, thereby establishing perceived causality[15,135]. Indeed, it has been previously shown that the magnitude of attenuation remains unaffected by halving or doubling the gain between the force applied by the active finger and the force delivered on the passive hand[15]. This should not be surprising given that when one finger transmits a force through an object to another finger, the resulting force depends also on the object properties (e.g., shape, material, contact area) and the angle at which the finger contacts the object.

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 the 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 *no-contact* 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 the 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 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.

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 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. 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 in 350 trials in total per participant. The order of the blocks was fully counterbalanced across participants.

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 1and 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 to 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.

Preprocessing of psychophysical trials.

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. The kinematic analysis also excluded all trials excluded by the psychophysical fits.

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.

Experiment 3

Experiment 3 included 10080 trials in total (30 participants * 224 contact trials + 56 no-contact 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. The kinematic analysis also excluded all trials excluded by the psychophysical fits.

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

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

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

We extracted two parameters of interest: the Point of Subjective Equality (PSE) ($PSE = -\frac{\beta 0}{\beta 1}$), which represents the intensity at which the *test* force felt as strong as the *comparison* force (p = 0.5) and quantifies the perceived intensity, and the JND ($JND = \frac{\log(3)}{\beta 1}$), which reflects the participants' discrimination ability. Before fitting the responses, the values of the applied comparison *forces* were binned to the closest value 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 McFadden's R squared measures ranging between 0.602 and 0.979.

Normality of data and statistical comparisons.

We used R [136], JASP [137] and MATLAB (2020b) to analyze our data. The normality of the PSE and the JND data distributions, as well as the kinematic information data distributions were assessed using Shapiro-Wilk tests. 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% confidence intervals (CI^{95}) for each statistical test. Effect sizes are reported as the Cohen's *d* for t-tests or the matched rank biserial correlation *rrb* for the Wilcoxon signed-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 effects, to provide information about the level of support

for the null hypothesis compared to the alternative hypothesis (BF_{01}) based on the data. We interpret a factor between 1/3 and 3 as "anecdotal evidence"[138,139], indicating that support for either the preferred or null hypotheses is insufficient. 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 significance, and the Q-Q plot of the standardized residuals indicated approximately normally distributed residuals. Post-hoc tests were made using Bonferroni corrections. All tests were two-tailed.

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Author Contributions

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

Declaration of interests

The authors declare no competing interests.

Data availability

Data (PSEs and JNDs) are publicly available along with preregistered analyses plans on the OSF (Experiment 1: https://osf.io/9jkqt, Experiment 2: https://osf.io/hs8au & Experiment 3: https://osf.io/gk).

Code availability

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

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