

Efference copy is necessary for the attenuation of self-generated touch

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Abstract

A self-generated touch feels less intense than an external touch of the exact same intensity. According to a prevalent computational theory of motor control, this attenuation occurs because the brain uses internal forward models to predict the somatosensory consequences of our movements using a copy of the motor command, i.e., the efference copy. These tactile predictions are then used to suppress the perceived intensity of the actual tactile feedback. Despite being highly influential, the core assumption of theory has never been tested; that is, whether the efference copy is necessary for somatosensory attenuation. A possible alternative hypothesis is that a predictable contact of two of one's own body parts is sufficient. Using a psychophysical task, we quantified the attenuation of touch applied on the participants' left index finger when the touch was triggered by the active or passive movement of the participants' right index finger and when it was externally generated in the absence of any movement. We observed somatosensory attenuation only when the touch was triggered by the voluntary movement of the participants' finger. In contrast, during the passive movement, the intensity of the touch was perceived to be as strong as when the touch was externally triggered. In both active and passive movement conditions, the participants showed the same discrimination capacity. Electromyographic recordings confirmed minimal activity of the right hand during the passive movement. Together, our results suggest that the efference copy is necessary for computing the somatosensory predictions that produce the attenuation of self-generated touch.

Keywords

Somatosensory attenuation; efference copy; passive movements; internal models; sensorimotor predictions

43 **Introduction**

44 Somatosensory attenuation refers to the phenomenon wherein a self-generated touch feels
45 weaker than an externally generated touch of the same intensity. Several behavioral
46 experiments have shown that participants judge a tap or a stroke delivered on their relaxed
47 hand as less intense when the touch is produced by the active movement of their other hand
48 compared to when it is produced externally by a motor (Bays *et al.*, 2005; Blakemore *et al.*,
49 1999; Kilteni *et al.*, 2019). Similarly, when participants were asked to match external forces
50 applied to their relaxed index fingers by reproducing the same forces with their other index
51 fingers through bimanual action simulating direct contact between the digits (force-matching
52 task), they produced stronger forces than the ones required; this is because the self-generated
53 forces are being perceptually attenuated (Kilteni *et al.*, 2018; Kilteni and Ehrsson, 2017b; a;
54 Shergill *et al.*, 2003).

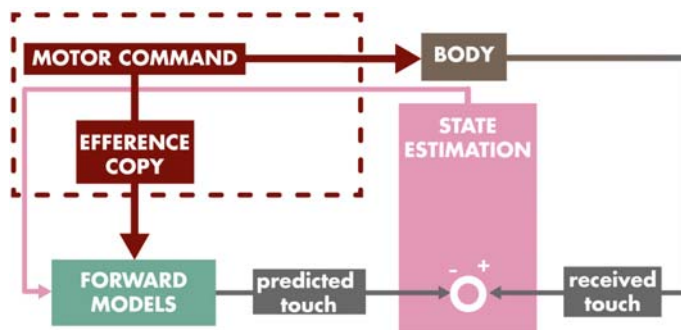
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56 Motor control theories suggest that somatosensory attenuation arises from the same predictive
57 processes that the brain uses when planning and executing movements, the so-called internal
58 models. Accordingly, when we perform a movement, the internal model uses a copy of the
59 motor command (i.e., the efference copy) to predict the sensory (including the
60 somatosensory) consequences of our movements. These predictions are then used to
61 compensate for the intrinsic delays in receiving sensory feedback (Davidson and Wolpert,
62 2005; Franklin and Wolpert, 2011; Kawato, 1999) but also to attenuate the self-generated
63 somatosensory signals and thus to increase the salience of any externally generated tactile
64 information (Bays and Wolpert, 2007; Blakemore *et al.*, 2000). The internal models have
65 been suggested to be located in the cerebellum (Shadmehr *et al.*, 2010; Shadmehr and
66 Krakauer, 2008; Therrien and Bastian, 2018; Wolpert *et al.*, 1998), and neuroimaging studies
67 on somatosensory attenuation have indeed revealed cerebellar activity when comparing
68 conditions that include externally generated touches with those that include self-generated
69 touches (Blakemore *et al.* 1998; Kilteni and Ehrsson *Under Review*).

70
71 The importance of the efference copy for somatosensory attenuation is well established within
72 the motor control community. Indeed, all previously mentioned behavioral studies of
73 somatosensory attenuation (Bays *et al.*, 2006, 2005; Bays and Wolpert, 2008; Kilteni *et al.*,
74 2018, 2019; Kilteni and Ehrsson, 2019, 2017b; a; Palmer *et al.*, 2016; Shergill *et al.*, 2005,
75 2014, 2003; Walsh *et al.*, 2011; Wolpe *et al.*, 2016) use conditions with voluntary movement,
76 and it is generally assumed that it is the efference copy associated with the voluntary motor
77 commands that is critical for the attenuation phenomenon to occur. However, this assumption
78 has not been directly tested. This is problematic because the experimental conditions that
79 produce somatosensory attenuation not only involve efference copy but also the *prediction*
80 and the *perception* of self-touch. For example, in the classic force-matching task, when
81 participants press one index finger against the other and somatosensory attenuation is
82 observed, this includes the efference copy, the prediction of contact between the hands and
83 the perceptual experience from the bimanual interaction. Thus, a parsimonious alternative
84 model for somatosensory attenuation is that the mere prediction and perception of self-touch
85 between two of one's own body parts could be the critical factor that triggers the phenomenon
86 and not the efference copy.

87

88 To the best of our knowledge, the results of all previously published studies on sensory
89 attenuation using bimanual force-matching tasks would be consistent with this alternative
90 view. In line with this, if a distance is introduced between the two fingers that makes both
91 unlikely and non-feasible the physical contact of the digits in the force-matching task, the
92 attenuation is eliminated or significantly reduced (Bays and Wolpert, 2008; Kilteni and
93 Ehrsson, 2017b). Moreover, it is the *prediction* and *perception* of self-touch that is important,
94 not the actual contact between the hands; this was demonstrated in experiments where the
95 participants experienced the illusion where a plastic right hand seen to press against their left
96 hand was thought to be their own right hand (rubber hand illusion), which led to an
97 attenuation of the forces even though their real hand was kept at a distance from the right
98 hand (Kilteni and Ehrsson, 2017a). Furthermore, the stronger the illusion that the participants
99 experienced was, the stronger the attenuation of the self-produced forces. Further support on
100 the importance of the prediction of self-touch can be found in the study of Bays et al. (2006)
101 who observed somatosensory attenuation also when the participants' hands unexpectedly
102 failed to touch each other. All these findings have previously been interpreted in a theoretical
103 model in which the internal model uses both the efference copy and information about the
104 sensory state of the body to compute the likelihood of self-touch and the associated
105 attenuation (Blakemore *et al.*, 2000; Kilteni and Ehrsson, 2017a) (**Figure 1**). According to the
106 alternative theory, however, the brain would attenuate self-touch through sensory predictions
107 that are purely based on (i) the sensory state of the body, indicating that one hand is (likely)
108 directly touching the other hand, and (ii) the belief that the touch is caused by this single event
109 of the two own body parts contacting each other (**Figure 1**). This generalized predictive
110 mechanism does not consider the efference copy as a prerequisite, and it relates to the
111 predictive coding theory that state that the brain forms predictions based on its prior beliefs
112 and continuously updates them to minimize any error between the predicted and the incoming
113 sensory information (Friston, 2005, 2009; Rao and Ballard, 1999). Moreover, this theory is
114 supported by earlier observations that neural responses become suppressed after the repeated
115 presentation of a stimulus (repetition suppression) or after the presentation of an expected
116 stimulus (for a review see (Grotheer and Kovács, 2016)). Importantly, this theory would not
117 necessarily speak against the internal models' theory, but it would favor a universal predictive
118 mechanism underlying all multisensory bodily events, including somatosensory attenuation
119 that is not necessarily based on motor signals; the predictions of this mechanism could be
120 more finely tuned when a motor command is available.

121



122

123 **Figure 1. A theoretical model for somatosensory attenuation.** According to the efference
124 copy-based theoretical model, during the active movement of the right hand to touch the left
125 hand, a copy of the motor command discharged to the right hand (the efference copy) is sent
126 to the forward model that predicts the next state (e.g., position) of the right hand as well as the
127 sensory consequences associated with that state (e.g., proprioceptive input). Similarly, the
128 next state of the left hand is predicted, although this should remain motionless. Predicted and
129 incoming information are combined in the state estimation process. If the predicted positions
130 of the two hands are close, touch is additionally predicted and thus the incoming touch is
131 attenuated. According to the alternative hypothesis describing a general predictive mechanism
132 underlying somatosensory attenuation in the absence of the efference copy, during the passive
133 movement of the right hand towards the left hand, there is no motor command and, thus, no
134 efference copy (dark red part is absent from the model). The incoming sensory input (e.g.,
135 proprioception) is used in combination with prior beliefs from the forward models (“where I
136 expect my hand to be”) to estimate the states of the two hands. The estimated states are fed
137 back to the forward models. As before, if the predicted states of the two hands are close, touch
138 is predicted and the incoming touch becomes attenuated. The present study investigated
139 whether the motor command and thus the efference copy (the part of model denoted by the
140 dark red dotted line) is a prerequisite of this predictive attenuation mechanism to dissociate
141 between these two models.

142

143 Here, we used a psychophysics paradigm (Bays *et al.*, 2005; Kilteni *et al.*, 2019) to
144 quantitatively compare somatosensory attenuation in conditions with active and passive
145 movements to directly test the hypothesized necessary role of the efference copy in the
146 attenuation of self-touch and thus to distinguish between the two alternative hypotheses
147 discussed above. The passive movement of one index finger to touch the other lacks the
148 efference copy but does involve the prediction and perception of self-touch. Therefore, if
149 somatosensory attenuation is observed only when the touch is produced by a voluntary
150 movement (active movement), this would indicate that the efference copy is necessary and it
151 would speak in favor of the internal models’ theory. Alternatively, if somatosensory
152 attenuation is also observed during a passive movement, this would support the generic
153 multisensory predictive model of attenuation.

154

155 **Materials and Methods**

156 ***Participants***

157 After providing written informed consent, thirty participants (15 women and 15 men, 29
158 right-handed and 1 left-handed) aged 18-39 years participated in the present study. The
159 sample size was decided based on a previous study using the same task (Kilteni *et al.*, 2019).
160 Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). The
161 Swedish Ethical Review Authority (<https://etikprovningmyndigheten.se/>) approved the study
162 (no. 2016/445-31/2, amendments 2018/254-32 and 2019-03063).

163

164 ***Materials and Procedures***

165 Participants were asked to place their left index finger inside a molded support while their
166 right arm comfortably rested on top of a set of sponges. In each trial, a DC electric motor
167 (Maxon EC Motor EC 90 flat; manufactured in Switzerland) delivered two taps (the test tap
168 and the comparison tap in **Figure 2a-c**) on the pulp of the participants' left index finger
169 through a cylindrical probe (25 mm height) with a flat aluminum surface (20 mm diameter)
170 attached to the motor's lever. A force sensor (FSG15N1A, Honeywell Inc.; diameter, 5 mm;
171 minimum resolution, 0.01 N; response time, 1 ms; measurement range, 0–15 N) was placed
172 within the probe to record the forces applied on the left index finger (red sensor in **Figure 2a-**
173 **c**).

174

175 In the *active movement* condition (**Figure 2a**), participants were asked to actively tap with
176 their right index finger a force sensor (same specifications as above) placed on top of (but not
177 in contact with) the probe upon an auditory 'go' cue (blue sensor in **Figure 2a-c**). Participants
178 were asked to tap the sensor after the 'go' cue, neither too hard nor too softly but "as strongly
179 as when they tap the surface of their smartphone". Their active tap on the force sensor
180 triggered the test tap with an intrinsic delay of 36 ms (threshold set to 0.15 N).

181

182 In the *passive movement* condition (**Figure 2b**), participants were asked to rest their right
183 index finger on top of a plastic surface that was placed on top of (but not in contact with) the
184 sensor for the right index finger. Upon an auditory 'go' cue, a servomotor (Hitec HS-81)
185 retracted this surface away, and the participants' right index finger freely fell on the
186 underlying sensor. As before, the passive tap on the force sensor (> 0.15 N) triggered the test
187 tap with a minimal (36 ms) delay. Significant training took place before this condition to
188 ensure that the participants did not resist the action and did not produce any large muscular
189 activity, as well as to confirm that the finger fell freely on the sensor. To minimize the
190 elicitation of any motor reflexes due to surprise, the passive movement condition was
191 designed to be as predictable as possible by retracting the surface always at the same time
192 after the 'go' cue.

193

194 In the *no movement* condition (**Figure 2c**), participants kept their right hand on top of the
195 sponges. After the auditory 'go' cue, the test tap was applied to the participants' left index
196 finger.

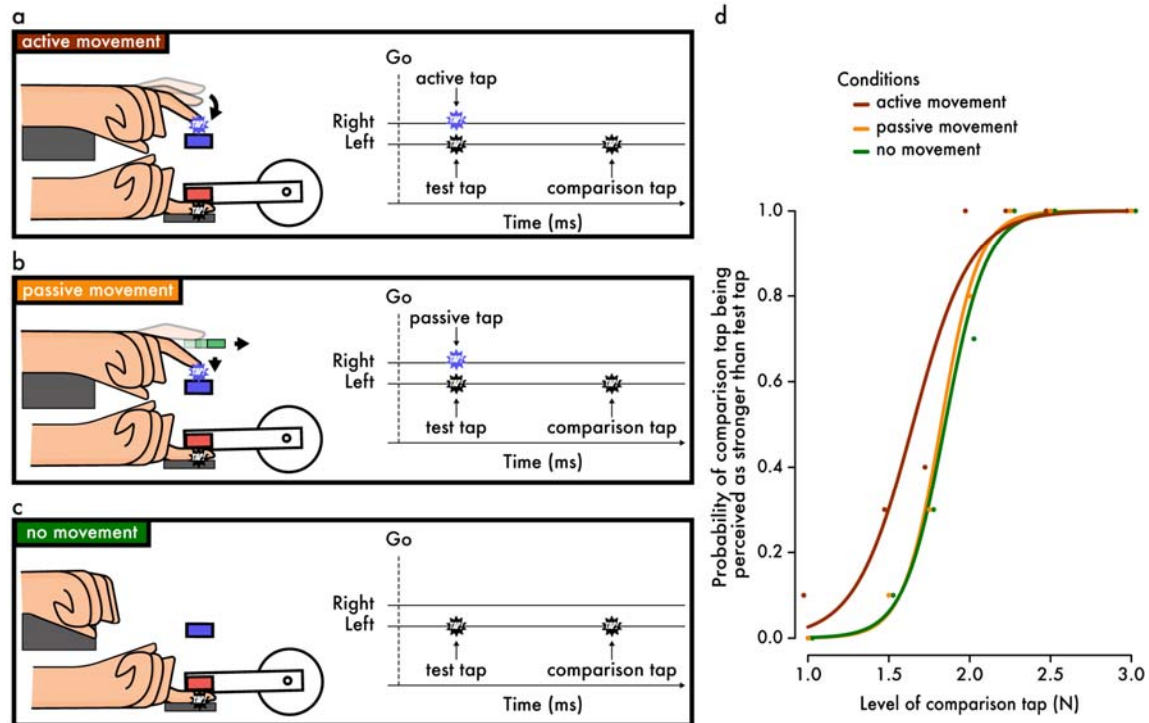
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198 In all conditions, the view of the pulp of the left index finger was occluded, and participants
199 were asked to fixate on a cross placed on a wall 2 m opposite them. A force of 0.1 N was
200 constantly applied on the participants' left index finger to avoid overshooting in the
201 experimental forces. Any sounds created by the motor, by the right hand's tap, or by the
202 servomotor were precluded by administering white noise to the participants through a pair of
203 headphones. No feedback was provided to the participants. EMG was recorded from the right
204 first dorsal interosseous muscle (FDI) (see below for details). The order of conditions was
205 fully counterbalanced across participants. The experiment lasted 60 minutes approximately.

206

207 After the end of the three conditions, all participants were asked whether they spontaneously
208 performed motor imagery during the passive movement condition. We asked this question to

209 exclude the putative concern that participants would spontaneously engage in mental
210 simulation in this condition, which would produce somatosensory attenuation through an
211 efference copy-based mechanism (Kilteni *et al.*, 2018).



212 **Figure 2. Experimental setup, design and analysis.** In all three conditions, the participants
213 received two taps on their relaxed left index finger (a test tap and a comparison tap), and they
214 were requested to indicate which tap felt stronger. In the active movement condition (a), the
215 participants actively tapped a force sensor with their right index finger (blue sensor). This
216 active tap simultaneously triggered the test tap on the participants' left index finger. In the
217 passive movement condition (b), the participants' right index finger was left to fall on the
218 force sensor (blue sensor) and passively tap it. This passive tap simultaneously triggered the
219 test tap on the participants' left index finger. In the no movement condition (c), the
220 participants remained relaxed, and the test tap was externally triggered. (d) Data from a
221 representative participant. For each condition, the participant's responses were fitted with
222 psychometric curves, and the point of subjective equality (PSE) and the just noticeable
223 difference (JND) were extracted. We have horizontally jittered the points to avoid their
224 overlapping.
225

226

227 *Psychophysics*

228 Each condition involved 70 trials. The test tap was set to 2 N, while the intensity of the
229 comparison tap was systematically varied among seven different force levels (1, 1.5, 1.75, 2,
230 2.25, 2.5 or 3 N). The two taps had a 100 ms duration, and the delay between them was
231 random (800 – 1500 ms). On every trial, participants had to verbally indicate which tap on
232 their left index finger felt stronger: the first (test) or the second (comparison). They were told
233 that they should not try to balance their responses (50% first and 50% second) and they were
234 asked to guess when the intensity of the two taps felt very similar.

235

236 For each condition, the participants' responses were fitted with a generalized linear model
237 using a *logit* link function (Equation 1, **Figure 2d**).

238

239
$$p = \frac{e^{\beta_0 + \beta_1 X}}{1 + e^{\beta_0 + \beta_1 X}} \text{ (Equation 1)}$$

240

241 Two parameters of interest were extracted: the point of subjective equality ($PSE = -\frac{\beta_0}{\beta_1}$),

242 which represents the intensity at which the test tap felt as strong as the comparison tap ($p =$

243 0.5) and which quantifies the attenuation, and the just noticeable difference ($JND = \frac{\log(3)}{\beta_1}$),

244 which reflects the participants' sensitivity for the force discrimination.

245

246 During the data collection, trials during which the right index finger was seen not to fall

247 properly were rejected and repeated to reach 70 trials per condition. After the data collection,

248 twenty-six force trials (26 of 6300, 0.4%) were rejected: in five trials, the responses were

249 missing; in three trials, the intensity of the test tap (2 N) was not applied correctly; and in

250 eighteen, the passive movement was not properly performed as instructed. These 26 trials

251 were also rejected from the EMG. Before fitting the responses, the values of the applied

252 comparison taps were binned to the closest value with respect to their theoretical values (1,

253 1.5, 1.75, 2, 2.25, 2.5 or 3 N).

254

255 ***EMG acquisition and preprocessing***

256 Surface EMG was recorded using the Delsys Bagnoli electromyography system (DE-2.1

257 Single Differential Electrodes) from the belly of the right FDI muscle after cleaning the skin

258 with alcohol. The EMG reference electrode was placed either on the left clavicle or on the

259 superior anterior iliac spine. The signals were analog bandpass filtered between 20 and

260 450 Hz, sampled at 2.0 kHz and amplified (gain = 1000). EMG data were preprocessed

261 in MATLAB. A bandstop filter was used to suppress the 50 Hz powerline interference, and

262 the DC offsets of the signals were removed.

263

264 ***EMG analysis***

265 For each trial, we calculated the root mean square (RMS) of the EMG signal during the time

266 window from the 'go' cue to the test tap. The window length in the *active movement*

267 condition depended on the participants' reaction time to tap the sensor and was 716.8 ± 186.8

268 ms (mean \pm sd). For the *passive movement* condition, the duration of the windows could

269 slightly change depending on how the participants placed the finger on the surface and was

270 287.1 ± 36.7 ms. Finally, in the *no movement* condition, the duration of the windows was

271 fixed at 599.8 ± 0.2 ms. We averaged the RMS activity across all (70) trials and then

272 compared the mean RMS across participants between the three conditions.

273

274 During data collection, trials in which the participants did not relax their right index finger (in

275 the *passive* and *no movement* conditions) or where there was visibly larger EMG activity

276 during the test tap compared to the comparison tap (for the *passive* condition) were rejected

277 and repeated. For one participant, the EMG data from the *active movement* condition were not
278 registered; thus, the EMG analysis was performed with 29 subjects.

279

280 *Statistical analysis*

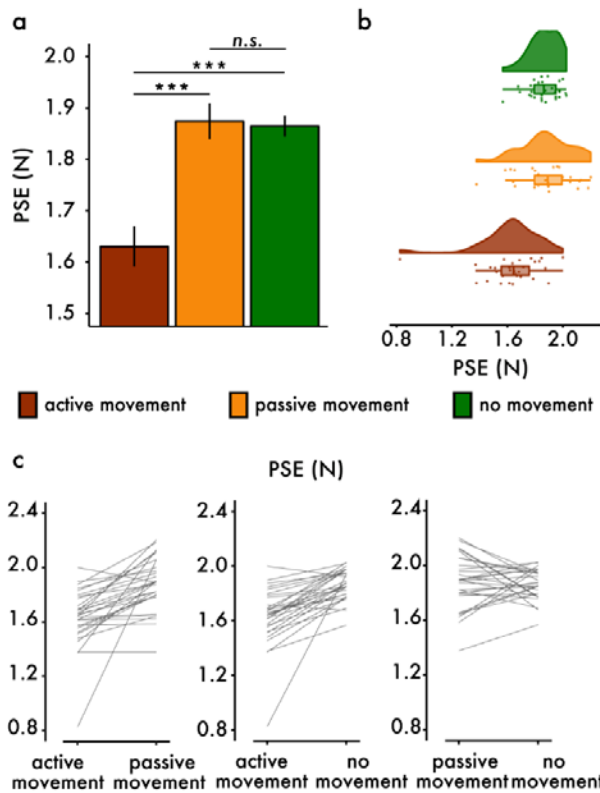
281 Data were analyzed using R (Core Team, 2018) and JASP (JASP Team 2019). The normality
282 of the PSE, the JND and the EMG data distributions was checked using the Shapiro-Wilk test.
283 Depending on their normality, we performed planned comparisons using either a paired t-test
284 or a Wilcoxon signed-rank test. We report 95% confidence intervals (CI^{95}) for each statistical
285 test. Effect sizes are given by Cohen's d if the data were normally distributed or by the
286 matched rank biserial correlation r_{rb} if the data were not normally distributed. In addition, a
287 Bayesian factor analysis using default Cauchy priors with a scale of 0.707 was carried out to
288 provide information about the level of support for the alternative hypothesis compared to the
289 null hypothesis (BF_{10}) given the data. Finally, a correlation was tested using Kendall's Tau-b
290 coefficient τ_B given that the data were not normally distributed. All tests were two-tailed.

291

292 **Results**

293 **Figure 3** shows the average and individual PSEs extracted for each condition, as well as the
294 individual differences per pair of conditions. In agreement with previous studies (Bays *et al.*,
295 2005; Kiltner *et al.*, 2019), a tap that was self-generated through a voluntary movement
296 (*active movement* condition) felt significantly weaker compared to an externally generated
297 identical tap (*no movement* condition): Wilcoxon signed rank test, $n = 30$, $V = 6$, $p < 0.001$,
298 $CI^{95} = [-0.268, -0.156]$, $r_{rb} = -0.974$, $BF_{10} > 14246$. This is the classic phenomenon of
299 somatosensory attenuation. Importantly, the self-generated tap (*active movement* condition)
300 was significantly attenuated compared to the tap of the same intensity that resulted from
301 passive movement (*passive movement* condition): Wilcoxon signed rank test, $n = 30$, $V = 8$, p
302 < 0.001 , $CI^{95} = [-0.286, -0.144]$, $r_{rb} = -0.966$, $BF_{10} > 1325$. Notably, the perception of the tap
303 that resulted from passive movement (*passive movement* condition) did not significantly differ
304 from that of the externally generated tap (*no movement* condition), and the Bayesian analysis
305 indicated that the level of perceived force was similar in the two conditions: paired t-test, $n =$
306 30 , $t(29) = 0.26$, $p = 0.799$, $CI^{95} = [-0.064, 0.083]$, Cohen's $d = 0.047$, $BF_{10} = 0.20$.
307 Collectively, these results suggest that only the somatosensory feedback from the self-
308 generated taps is attenuated.

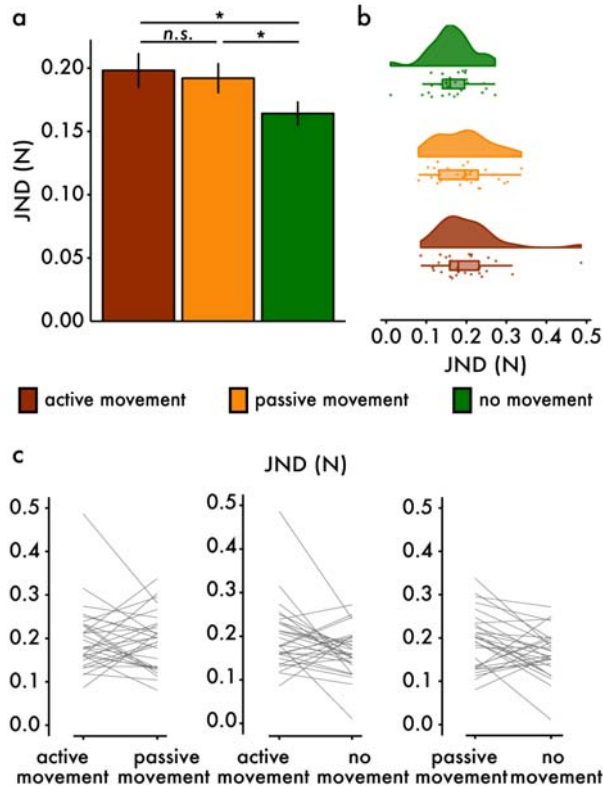
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310
 311 **Figure 3. Results on the points of subjective equality (PSEs).** (a) Bar graphs show the
 312 PSEs (mean \pm se) per condition (***) $p < 0.001$, n.s. not significant). Only the *active*
 313 *movement* condition produced somatosensory attenuation. In contrast, no changes were
 314 detected in the PSEs between the *passive movement* and the *no movement* condition. (b)
 315 Raincloud plots (Allen *et al.*, 2019) show the raw PSEs as well as their distribution per
 316 condition. (c) Line plots illustrate the participants' paired responses per combination of
 317 conditions.

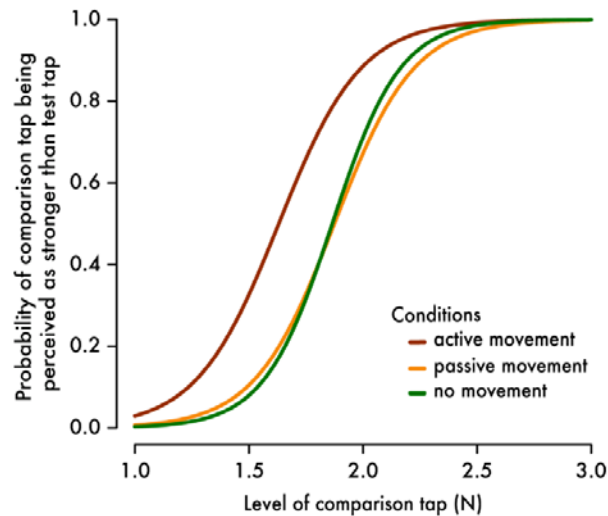
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 319 **Figure 4** shows the average and individual JNDs extracted for each condition, as well as the
 320 individual differences per pair of conditions. Participants showed similar response
 321 sensitivities in the force discrimination task between the *active movement* and the *passive*
 322 *movement* conditions, ruling out the possibility that one condition was more or less difficult
 323 than the other: paired t-test, $n = 30$, $t(29) = 0.42$, $p = 0.680$, $CI^{95} = [-0.024, 0.036]$, Cohen's d
 324 $= 0.076$, $BF_{10} = 0.211$. Both the *active movement* (paired t-test, $n = 30$, $t(29) = 2.25$, $p =$
 325 0.032 , $CI^{95} = [0.003, 0.065]$, Cohen's $d = 0.411$, $BF_{10} = 1.706$) and *passive movement*
 326 conditions (paired t-test, $n = 30$, $t(29) = 2.11$, $p = 0.044$, $CI^{95} = [0.001, 0.055]$, Cohen's $d =$
 327 0.384 , $BF_{10} = 1.323$) showed significantly lower discrimination capacities than the *no*
 328 *movement* condition. The Bayesian analysis did not provide any conclusive support for the
 329 existence of such differences ($BF_{10} < 2$ in both cases) and thus, one should be cautious on
 330 interpreting the frequentist analysis. Nevertheless, if these JND differences do exist, they
 331 indicate that the movement of the right index finger per se, either voluntary or not,
 332 deteriorates the discrimination performance on the left index finger. This because in both
 333 *active* and *passive* movement conditions, the participants had to direct their attention to both
 334 hands (i.e., the movement of the right index and the force discrimination task on the left

335 index), while in the *no movement* condition, the participants directed their attention only to
336 the left index finger. Another related factor could be the presence of sensory feedback on the
337 right index finger simultaneous to the sensory feedback on the left hand in the movement
338 conditions that could render the task slightly more demanding.
339



340
341 **Figure 4. Results on the just noticeable difference (JNDs).** (a) Bar graphs show the JNDs
342 (mean \pm se) per condition ($*p < 0.05$, *n.s.* not significant). The *active* and *passive movement*
343 conditions showed higher JND than the *no movement* condition. In contrast, no changes were
344 detected in the JNDs between the *active* and *passive movement* condition. (b) Raincloud plots
345 (Allen *et al.*, 2019) show the raw JNDs as well as their distribution per condition. (c) Line
346 plots illustrate the participants' paired responses per combination of conditions.
347

348 **Figure 5** shows the group psychometric functions per condition using the corresponding
349 mean PSE and JND (see also **Appendix Supplementary Figure S1** for all individual fits).
350 Somatosensory attenuation was produced only during a self-generated (voluntary) movement.
351

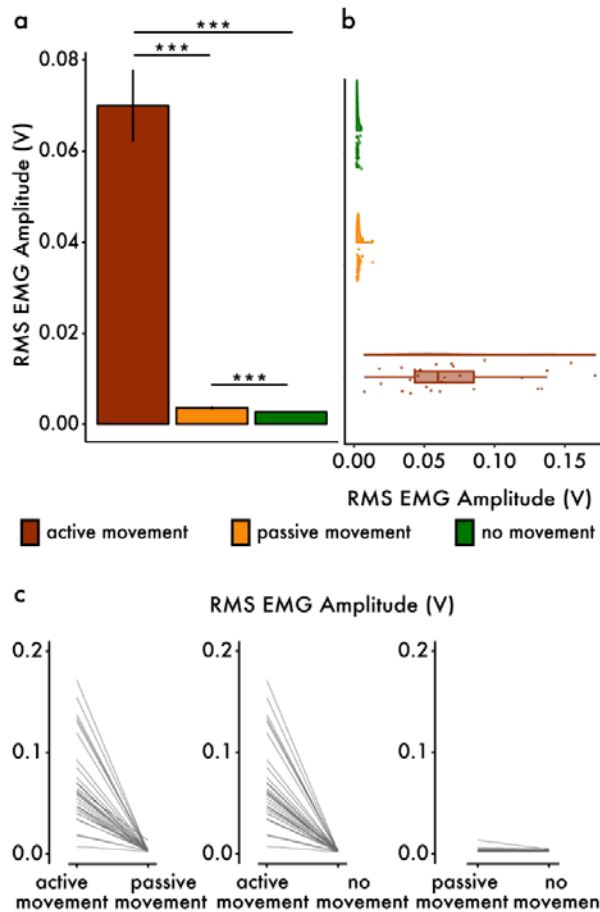


352
353 **Figure 5. Group psychometric functions per condition.** The plots were generated using the
354 mean PSE and the mean JND across the thirty participants per condition. Significant
355 attenuation with respect to the *no movement* condition was observed only in the *active*
356 *movement* condition.

357
358 It should be noted that the *active* and *passive movement* conditions differed not only in terms
359 of the efferent signals discharged to the right index finger for pressing but also in terms of the
360 afferent somatosensory feedback received from the right index finger; that is, the force that
361 was applied by the sensor to the right index finger, opposite to the pressing force. The
362 participants pressed stronger forces with their right index finger during the *active* ($mean \pm sd$:
363 1.210 ± 0.790 N) than during the *passive movement* condition (0.431 ± 0.134 N): Wilcoxon
364 signed rank test, $n = 30$, $V = 455$, $p < 0.001$, $CI^{95} = [0.441, 0.988]$, $r_{rb} = 0.957$, $BF_{10} > 3145$.
365 To rule out the unlikely possibility that passive movements did not produce somatosensory
366 attenuation because of the reduced force and somatosensory feedback from the right index
367 finger, we tested for a relationship between the forces the participants pressed on the sensor
368 (passive tap, Figure 2) and their PSEs in the passive condition. As we expected, no
369 relationship was found: $n = 30$, $T = 205$, $\tau_B = -0.057$, $p = 0.671$, $CI^{95} = [-0.279, 0.164]$, with
370 the Bayesian analysis favoring the null hypothesis: $BF_{10} = 0.259$. We further performed the
371 same analysis with the JNDs; no relationship was found between the JND in the passive
372 movement condition and the somatosensory feedback from the right index finger: $n = 30$, $T =$
373 235 , $\tau_B = 0.080$, $p = 0.547$, $CI^{95} = [-0.201, 0.362]$, with the Bayesian analysis favoring again
374 the null hypothesis: $BF_{10} = 0.284$.

375
376 Next, we analyzed the EMG data to test whether participants were relaxed during the passive
377 movement condition. **Figure 6a** and **b** shows the average and individual RMS activity
378 calculated per condition, and **Figure 6c** illustrates the individual differences per pair of
379 conditions. Validating our experimental manipulation, analysis of the RMS activity revealed
380 significantly higher activity in the *active movement* condition compared to the *no movement*
381 condition (Wilcoxon signed rank test, $n = 29$, $V = 435$, $p < 0.001$, $CI^{95} = [0.048, 0.084]$, $r_{rb} =$
382 1 , $BF_{10} > 4.48 \times 10^6$) and the *passive movement* condition (Wilcoxon signed rank test, $n = 29$,

383 $V = 435$, $p < 0.001$, $CI^{95} = [0.046, 0.084]$, $r_{rb} = 1$, $BF_{10} > 3.27 \times 10^6$). The *passive movement*
384 condition did reveal small EMG activity compared to the *no movement* condition (Wilcoxon
385 signed rank test, $n = 29$, $V = 394$, $p < 0.001$, $CI^{95} = [0.0003, 0.001]$, $r_{rb} = 0.811$, $BF_{10} =$
386 8.257), but this increase was $\cong 70$ times smaller compared to the increase in the *active*
387 *movement* condition (**Figure 6c**). Thus, we conclude that the participants were able to relax in
388 the passive condition and that the experimental comparison of active versus passive finger
389 movements was successfully implemented in our paradigm.
390



391
392 **Figure 6. Results on the EMG RMS amplitude.** (a) Bar graphs show the mean RMS
393 amplitude (\pm SE) per condition ($*** p < 0.001$). (b) Raincloud plots show the raw amplitudes
394 as well as their distributions per condition. (c) Line plots show the participants' paired
395 responses per combination of conditions.

396
397 Finally, with respect to the motor imagery question, none of the thirty participants reported
398 performing motor imagery during the passive movement condition. This excludes the
399 possibility that the *passive movement* condition was confounded with motor simulation and
400 thus with efference copies – a factor that could drive somatosensory attenuation *per se*
401 (Kilteni *et al.*, 2018).

402

403 Discussion

404 The present study found that touch applied on a static left index finger gets attenuated only
405 when it results from the active movement of the right index finger, not when it results from
406 the passive movement of the right index finger or when it is applied in the absence of any
407 movement. Specifically, the perceived intensity of a touch that results from the passive
408 movement of the right index finger was comparable to that of an externally generated touch.
409 These findings favor the interpretation based on the internal models and suggest that the
410 efference copy is necessary for the attenuation of self-generated touch. According to this
411 theory, during the *active movement* condition, a copy of the motor command sent to the right
412 hand (the efference copy) is used to predict the next state (e.g., position) of the hand and its
413 expected sensory consequences associated with that state (Bays and Wolpert, 2008;
414 Blakemore *et al.*, 2000; Wolpert and Flanagan, 2001; Wolpert and Ghahramani, 2000). Since
415 the predicted end-position of the right index finger falls very close to that of the relaxed left
416 index finger, touch is predicted on this left finger as well (Kilteni and Ehrsson, 2017b). The
417 actual touch (here, the test tap) is attenuated once it is received since it has been predicted
418 based on the efference copy from the motor command to the right index finger. From a
419 computational perspective, the present study demonstrates that it is the voluntary direct
420 contact of the two body parts that is critical for somatosensory attenuation and not the mere
421 contact or close proximity between the two involved body parts produced by the
422 (active/passive) movement. This supports the internal model theory of sensory attenuation and
423 speaks against the general multisensory predictive hypothesis.

424
425 We first discuss three methodical issues: (i) were the active and passive tasks comparable in
426 terms of performance on the discrimination task and the predictability of touch? (ii) was the
427 passive task free of efference copies? and (iii) could small differences in tactile feedback from
428 the right index finger between the active and the passive movement conditions influence the
429 somatosensory attenuation on the left index? With respect to the first question, it is important
430 to stress that there were no task differences between the *active* and *passive movement*
431 conditions that could influence the participants' responses in the force discrimination task.
432 First, the two conditions had similar JNDs, suggesting that the participants' performance
433 sensitivity did not differ between the two conditions (**Figures 3 and 4**). Second, we designed
434 the *passive movement* condition to minimize any surprises and make it as predictable as
435 possible, similar to the *active movement* condition. Specifically, in the *passive movement*
436 condition, the platform was always retracted at the same time to facilitate the anticipation of
437 the timing of the hands' contact and to strengthen the causal link between the passive
438 displacement of one finger and the somatosensory input of the other finger – as in the *active*
439 *movement* condition. With respect to the sensory predictability, an earlier study on the
440 unloading task (Diedrichsen *et al.*, 2003) showed that anticipatory adjustments are present
441 only when the efference copy is available; in contrast, no adjustments were observed in the
442 absence of a voluntary movement, even when the predictability of the sensory stimulus was
443 high. Therefore, in the present study the absence of attenuation in the passive movement
444 condition suggests that the motor system cannot predict the consequences of an involuntary
445 movement as precisely as those of a voluntary one because of the lack of efference copy.

446

447 With respect to the second question, it is noteworthy that the *passive movement* condition did
448 yield some muscular activity compared to the *no movement* condition, but its magnitude was
449 much (approximately 70 times) smaller than the one elicited in the *active movement*
450 condition. This weak muscular activity in the passive condition could represent reflexes for
451 automatic postural stabilization or stretch reflexes (Doemges and Rack, 1992) rather than
452 voluntary motor commands. Importantly, this interpretation is in line with the fact that we did
453 not observe any reliable somatosensory attenuation in the passive condition. Another related
454 putative concern is that the participants might spontaneously start to imagine active
455 movements in the passive condition. We know that imagery of voluntary self-touch can lead
456 to somatosensory attenuation, presumably by engaging the efference copy when internally
457 simulating the action (Kilteni et al. 2018). As an extra precaution to rule out this unlikely
458 scenario, we asked our participants to indicate whether they performed motor imagery during
459 the passive movement, and they all denied doing so. Therefore, we can exclude the possibility
460 that participants mentally simulated an active movement in the passive condition (Kilteni *et*
461 *al.*, 2018). Thus, we think it is reasonable to conclude that the passive condition was free of
462 efferent copies, at least to the extent that matters for the interpretation of the results.

463
464 The third concern was that the *passive movement* condition also differed from the *active*
465 *movement* condition in terms of the somatosensory feedback received from the *right* index
466 finger because the subjects pressed smaller forces with their right index finger in the *passive*
467 compared to the *active movement* condition. We did not find any evidence that this reduced
468 feedback could hinder somatosensory attenuation during passive movements. Further
469 evidence comes from a previous somatosensory attenuation study that used the same
470 psychophysics task as the present study; in the study of Bays et al. (2005) participants did not
471 move their right index finger but they received a tap from an upward force pulse at the same
472 time they received the tap on their left index finger that was of similar magnitude. Despite the
473 enhanced somatosensory feedback, the participants did not show any attenuation. Moreover,
474 an earlier study on the force-matching task found no effect on somatosensory attenuation by
475 different relationships (gains) between the forces participants pressed with their right index
476 finger and the forces they received on their left index finger, as long as this relationship were
477 stable (Bays and Wolpert, 2008). This further corroborates the hypothesis that the
478 somatosensory feedback from the right index finger *per se* is not critical for somatosensory
479 attenuation on the left index finger in the bimanual force matching task.

480
481 It is interesting to consider the present results together with the findings that were recently
482 reported by Kilteni et al. (2018) on somatosensory attenuation during motor imagery. Motor
483 imagery corresponds to internally simulating movement without executing it, which involves
484 producing a central motor command and thus efference copy. In that study, Kilteni et al.
485 (2018) asked their participants to imagine pressing their right index finger against their left
486 index finger through a sensor while they simultaneously received a force on their left index
487 finger. The experimenters observed that when the tactile consequences of the imagined
488 movement matched the received touch in terms of space and time, the touch was attenuated to
489 the same extent as when the participants actually executed the movement. This result suggests
490 that the efference copy is sufficient for somatosensory attenuation when the sensory

491 predictions derived from the efference copy are spatiotemporally congruent with the actual
492 somatosensory feedback. Importantly, the present results add to this by suggesting that the
493 efference copy is not only sufficient but also *necessary* for sensory attenuation of self-touch,
494 which has important bearings on the computational models of sensory attenuation.

495
496 The difference between active and passive movements in terms of perceptual stability and
497 sensory processing has been shown in modalities other than touch. For example, in their
498 seminal observations within the visual domain, first Descartes and later Helmholtz (1867)
499 noted that when we actively move our eyes, the world seems stable; in contrast, when we tap
500 the side of our eyeball to ‘passively’ change the retinal image, the world appears to be
501 moving. That is, the visual consequences of this passive displacement are processed
502 differently from those produced by active eye movements. Similarly, in primates, it has been
503 systematically shown that the vestibular consequences of active head movements are
504 significantly attenuated, in striking contrast to vestibular information received during passive
505 head movements (see (Cullen, 2012) for a review). Our findings provide evidence that a
506 similar distinction applies in the somatosensory domain as well: only touches that result from
507 an active and not from a passive movement become attenuated.

508
509 Efference copy-related circuits have been revealed in several species across the animal
510 kingdom (Crapse and Sommer, 2008), suggesting that predictive signals computed from the
511 motor command might constitute a generalized strategy for biological organisms to
512 differentiate self-generated from externally generated information. The present study showed
513 that only active movements allow the computations of somatosensory predictions that
514 produce attenuation. This finding reaffirms that action might constitute the most efficient way
515 to distinguish ourselves from others.

516

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522

523 **Author Contributions**

524 Konstantina Kilteni and H. Henrik Ehrsson conceived and designed the experiment.
525 Konstantina Kilteni and Patrick Engeler collected together the data of the experiment.
526 Konstantina Kilteni conducted the statistical analysis. Konstantina Kilteni and H. Henrik
527 Ehrsson wrote the manuscript, and Patrick Engeler read and approved the final version.

528

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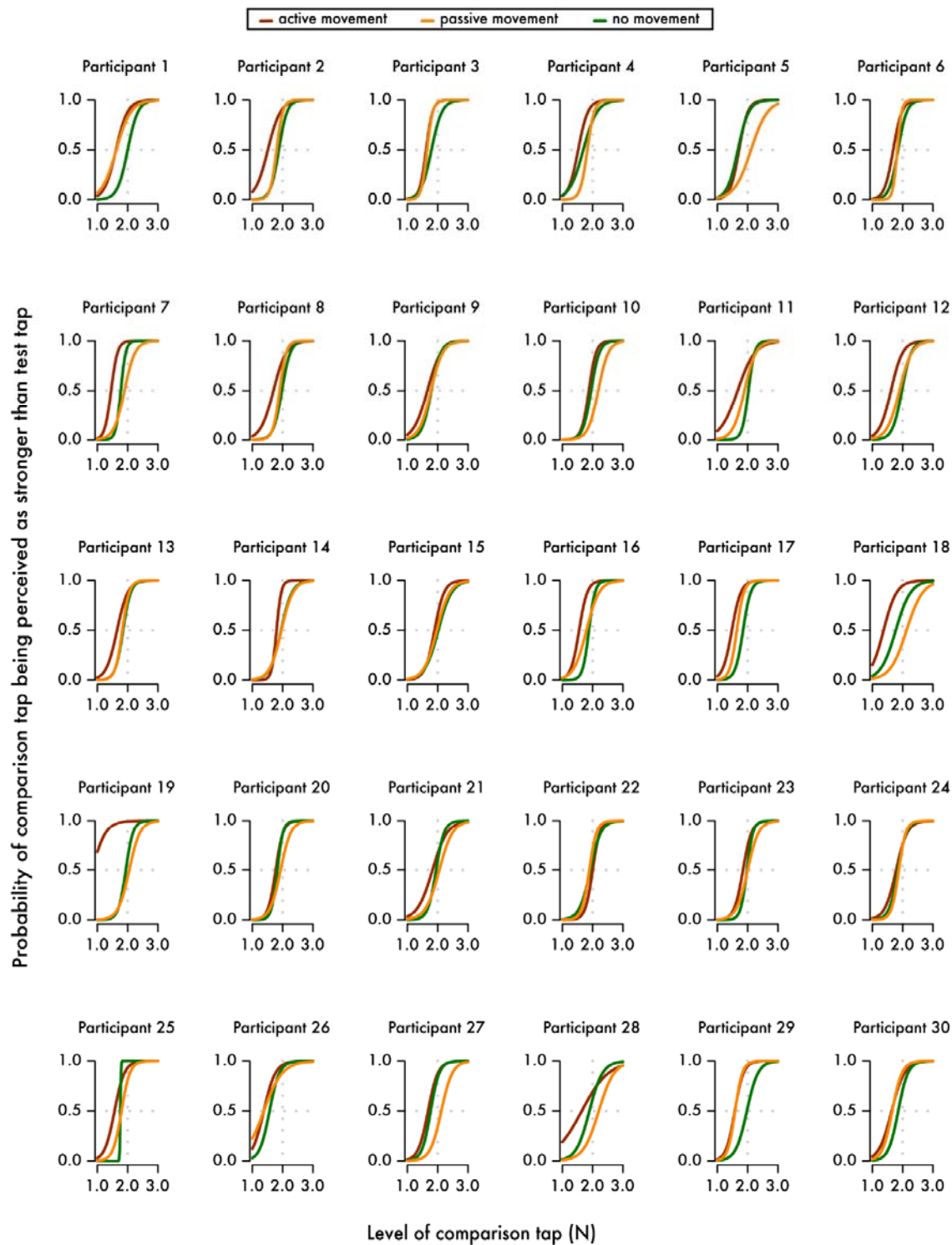
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631 **Appendix**



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634 **Supplementary Figure S1. Individual fits per condition.** Horizontal gray dotted lines
635 indicate the 50% probability of the comparison tap being perceived as stronger than the test
636 tap (PSE), while the vertical gray dotted lines indicate the true intensity of the test tap (2 N).