

1 Constructing spatial perception through self-touch

2

3 **Running Title:** Constructing spatial perception through self-touch

4

5 A. Cataldo^{1,2†*}, L. Dupin^{3,4‡}, H., Dempsey-Jones¹, H. Gomi⁵, P. Haggard^{1,2,4}

6

7 ¹ Institute of Cognitive Neuroscience, University College London, Alexandra House 17 Queen

8 Square, London WC1N 3AZ, UK

9 ² Institute of Philosophy, University of London, Senate House, Malet Street, London WC1E 7HU,

10 UK.

11 ³ Institut de Psychiatrie et Neurosciences de Paris, INSERM U1266 – Université de Paris, Paris,

12 France.

13 ⁴ Chaire Blaise Pascal de la Région Ile de France, Laboratoire de Neurosciences Cognitives et

14 Computationnelles, Département d'Etudes Cognitives, Ecole Normale Supérieure, Paris.

15 ⁵ NTT Communication Science Laboratories, Nippon Telegraph and Telephone Corporation,

16 Atsugi, Japan.

17 * Corresponding author: Institute of Philosophy, University of London, Senate House, Malet

18 Street, London WC1E 7HU, United Kingdom. Tel.: +44 (0)20 7664 4865. Email address:

19 antonio.cataldo@sas.ac.uk

20 † Equal contribution.

23 **Abstract (140/150)**

24 Classical accounts of spatial perception are based either on the topological layout of
25 sensory receptors, or on implicit spatial information provided by motor commands. In
26 everyday self-touch, as when stroking the left arm with the right hand, these elements are
27 inextricably linked, meaning that tactile and motor contributions to spatial perception
28 cannot readily be disentangled. Here, we developed a robot-mediated form of self-touch
29 in order to decouple the spatial extent of active or passive movements from their tactile
30 consequences. Participants judged the spatial extent of either the movement of the right
31 hand, or of the resulting tactile stimulation to their left forearm. Across five experiments,
32 we found bidirectional interference between motor and tactile information. Crucially,
33 both directions of interference were stronger during active than passive movements. Thus,
34 voluntary motor commands produced stronger integration of multiple signals relevant to
35 spatial perception.

36

37 **MAIN TEXT**

38 **Introduction (1188)**

39 Successful interactions with the environment depend on accurate spatial representations of
40 both the external world and of our body acting upon it. The coding of space is, therefore,
41 an essential requirement for both motor and perceptual systems. Reaching actions, for
42 example, rely on classifying spatial locations into near (e.g., reachable) vs. far space (1, 2),
43 and on computing movement vectors to bring the hand to the target location. Similarly,
44 localising tactile stimuli impinging on the skin requires body-centered reference frames
45 based on accurate representations of both the skin relative to the underlying body, and the
46 positions of body parts in space (3).

47 Self-touch is arguably one of the earliest and most ubiquitous spatial experiences.
48 Fetal hand-to-face movements occur in utero from 13 weeks, and the uterine environment
49 makes for frequent interlimb contact (4). After birth, several forms of self-touch
50 behaviours persist through childhood and into adulthood, including incidental contact
51 between the hands during bimanual object handling (e.g., tying shoelaces), grooming
52 actions, and functional self-stimulation (e.g., clapping hands to express approval, or to
53 keep warm; grasping a wounded body part). These self-touch behaviours all involve a
54 distinctive sensorimotor contingency between the neural information relating to the
55 moving body part and the stimulation sensed by skin receptors in the touched body part.
56 This situation, often termed *touchant-touché* (i.e., motor touching and sensory touched,
57 respectively) (5–7), results in highly correlated motor and sensory representations in the
58 brain, which has been linked to the development of self-awareness (6, 8) and body
59 representation (7, 9–12). For our purposes, the causal dependence between the motor
60 (*touchant*) and somatosensory (*touché*) components of self-touch means that spatial
61 features are coded twice, by distinct but related spatial codes for action and for perception

62 respectively. For example, if we slide our right index finger along our left forearm, the
63 movement we perform with the finger and the touch we feel on the arm both carry spatial
64 information. Further, this tight spatial relationship between movement and touch
65 contributes to their perceptual fusion into a single psychological event, so that movement
66 and touch are perceived as having the same spatial extent. The double sensation of
67 *touchant-touché* indeed forms a central element in phenomenological accounts of the
68 bodily self (6). However, few experimental studies have investigated the relative
69 contributions of motor and sensory information to this integrated percept.

70 Interestingly, self-touch is widely discussed in early discussions of spatial
71 perception. The origins of our “amodal and invariant sense of space” (13) are still a
72 matter of debate. Many neuroscientific discussions of spatial perception stress the orderly
73 topographic projections from receptor surfaces, such as the retina and skin, to the brain
74 (14, 15). However, if these projections are taken as explanations of spatial perception,
75 they may seem circular, since they apparently explain (external) space in terms of
76 (internal, neurotopographic) space. In contrast, *local sign* theories of space perception
77 instead explained the sensory quality that a stimulus has in virtue of where it is located
78 (i.e., its “thereness”) in terms of the motor commands required to orient to the stimulus.
79 Thus, perception of visual location was explained in terms of the saccadic motor
80 command required to fixate that location (16); while perception of tactile location was
81 explained in terms of the reaching movement required to touch that location (17, 18). On
82 this view, active self-touch provides an underpinning mechanism of space perception.
83 However, these descriptions were ultimately thought experiments, and were not
84 accompanied by extensive experimental evidence (17, 18).

85 In our example scenario of stroking the forearm with the finger, local sign theories
86 clearly predict that the spatial nature of the resulting percept comes from the motor

87 command to move the finger, and not from tactile, sensory signals from the skin region
88 that is stroked. Early hypotheses of motor dominance over sensory signals have continued
89 to be influential in psychology and neuroscience of perception, finding modern echoes in
90 theories such as perceptual enactivism (19), and active vision (20, 21).

91 Table 1 outlines some alternative theoretical accounts of how spatial percepts
92 might arise in self-touch. First, the brain might maintain completely independent spatial
93 representations for *touchant* (movement) and for *touché* (tactile sensation) (22, 23),
94 implying no interference between signals Table 1, Hypothesis A. Second, the motor
95 signal might dominate the tactile signal as suggested by local sign theories, or *vice versa*,
96 producing asymmetric interference between movement and touch in spatial perception
97 (17, 18), Table 1, Hypothesis B. Third, motor and tactile signals might fuse, either along
98 the lines of optimal multisensory integration (24), or suboptimally, to produce a single
99 spatial percept, Table 1, Hypothesis C. Each theory makes distinct predictions about the
100 weighting that the motor signal will have when participants are asked to report the spatial
101 perception of the touch, and *vice versa*. We will refer to this weighting measure of
102 interference or automatic integration as ω .

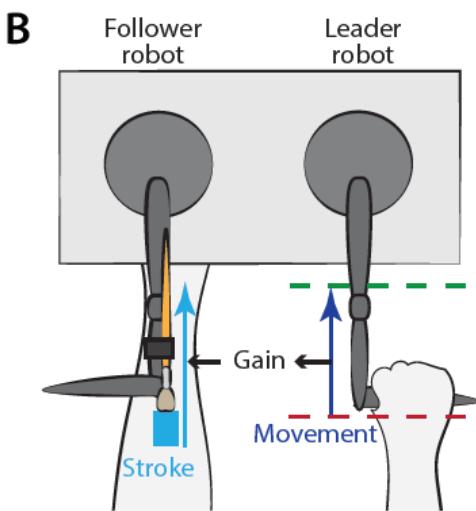
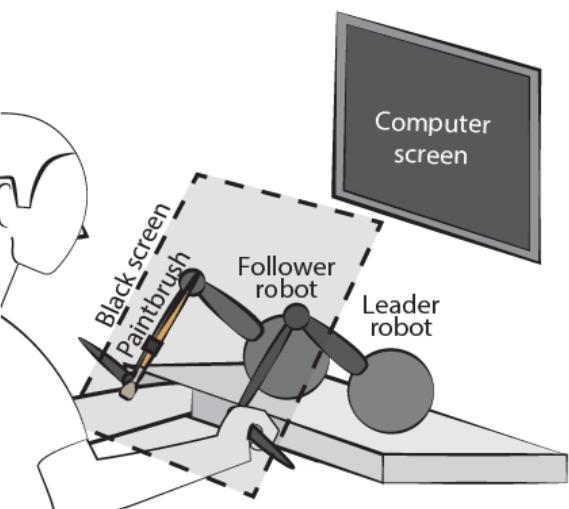
103 Here, we used two robots linked in a leader-follower configuration with a
104 computer-controlled gain between them, to achieve a laboratory version of the common
105 self-touch experience of stroking the left forearm with the right hand. Participants moved
106 the handle of the leader robot with their right hand and simultaneously felt a
107 corresponding stroke on the left forearm from a brush attached to the follower robot (see
108 Figure 1). The computer-controlled gain of the robot coupling allowed the tactile
109 stimulation to be shorter, equal, or longer in extent than the movement that caused it, thus
110 decoupling the normally fixed spatial relation between *touchant* and *touché*. We
111 investigated the patterns of interference between these signals by asking participants to

judge either the extent of the tactile stroke they felt (Experiment 1), or the extent of the movement they made (Experiment 2). Participants either actively moved their right hand, or it was passively moved. In the active self-touch condition, participants actively moved the leader robot with their right hand to induce self-touch on their other arm. In the passive self-touch conditions, instead, the participant held the robot with their right hand, while the experimenter passively moved it, again causing a matching self-touch stimulation of the participant's left forearm. Comparing our active and passive conditions allowed us to investigate the importance of voluntary action to spatial perception. Experiment 3 used a within-subject design, in which the same participants gave both movement judgements and touch judgements. This allowed a stronger within-participant test of asymmetric interference between movement and touch, an opportunity to correlate weights for movement judgements with those for touch judgements, and a direct test of optimal integration theories by relating each signal's weight to its precision. Finally, two control experiments looked at whether our results could be caused by effects on spatial extent judgement of the different velocities of movement and touch (the 'tau effect') (25) produced by changing the motor:tactile gain. To do this, we tested unimodal versions of each task, where participants either judged the extent of the tactile sensation without any concomitant movement (i.e. "touch only" condition, Experiment 4), or judged the extent of movement in absence of any tactile stimulation (i.e. "movement only" condition, Experiment 5). As both the control experiments involved unimodal judgements, interference from another signal could not have affected the results.

*** PLEASE INSERT TABLE 1 HERE ***

| Hypothesis | Weighting of movement on tactile extent perception | Weighting of touch on motor extent perception |
|--|--|---|
| A. Independent spatial coding of movement and touch | $\omega = 0$ | $\omega = 0$ |
| B. Motor dominance over tactile signals | $\omega = 1$ | $\omega = 0$ |
| C. Partial integration | $0 < \omega < 1$ | $0 < \omega < 1$ |

137 **Table 1.** Three alternative accounts of the relation between motor and tactile signals
138 during self-touch, and their predictions for the interference weighting between signals.



144 **Figure 1. Experimental setup and stimuli. A.** Participants moved the handle of the
145 leader robot with their right hand and simultaneously felt a corresponding stroke on the
146 left forearm from a brush attached to the follower robot. A black screen (black dashed
147 line) covered both the participants' arms and the robotic setup throughout the experiment.
148 **B.** The physical extent of right arm movement was modulated via two “virtual walls”
149 defining start (red dashed line) and stop (green dashed line) positions, which varied
150 between trials. The relation between the extent of movement (dark blue arrow) and touch
151 (light blue arrow) depended on the gain of the leader:follower robot coupling, which was
152 randomized across trials (see <https://tinyurl.com/yxf34yna> for a video of the setup).

153

154

155 **Results (1886)**

156 ***Overall performance***

157 Perceptual performance was generally good in all experiments. We found a monotonic
158 relation between perceived and actual spatial extent for both movement and touch
159 judgement conditions in both active and passive self-touch (see panels A and B in Figures
160 2-4 and Supplementary ANOVA Tables S1-5). Participants were thus able to perceive
161 spatial extent in all conditions.

162 Experimentally manipulating the motor:tactile gain allowed us to quantify the
163 effect of movement information on tactile perception and *vice versa*. Stronger effects of
164 gain manipulations correspond to stronger interference from the task-irrelevant signal on
165 the to-be-judged signal. We therefore used equation 1 (see Statistical Analysis) to
166 compute the weight of task-irrelevant information (i.e. weighting of movement extent
167 when the task was to judge tactile extent and vice versa) in each experimental condition
168 (judge touch/movement x active/passive) and in the unimodal control conditions. The
169 resulting weights (denoted by ω) for each participant and each experiment are given in the
170 Supplementary Materials.

171

172 ***Are touchant and touché independent?***

173 An account of independent spatial perception for action and tactile perception (22,
174 23) predicts no influence of movement on judgements of tactile extent, and no
175 influence of tactile extent on judgements of movement extent, as the motor:tactile
176 gain is varied (see Table 1A). Our measure of the weight of the task-irrelevant
177 sensation thus provides a summary measure of the effects of changing motor:tactile
178 gain.

179 Figure 2 A-B shows the mean perceived extents for each to-be-judged
180 information as a function of the actual extent and the gain applied to the task-
181 irrelevant information in Experiment 1 (i.e. “judge touch”; Figure 2A) and
182 Experiment 2 (i.e. “judge movement”; Figure 2B). The data were not normally
183 distributed (see Supplementary Table S11), and were therefore tested using the
184 Wilcoxon’s Sign Test (see Statistical Analysis section). We compared each
185 condition against 0 (where a ω of 0 would indicate no effect of the task-irrelevant
186 information, see Table 1, hypothesis A) and against 1 (where a ω of 1 would indicate
187 complete dominance of one signal over the other, e.g., Table 1, hypothesis B) within
188 each experiment, so we Bonferroni corrected for four comparisons per experiment,
189 giving $\alpha = 0.0125$ per test.

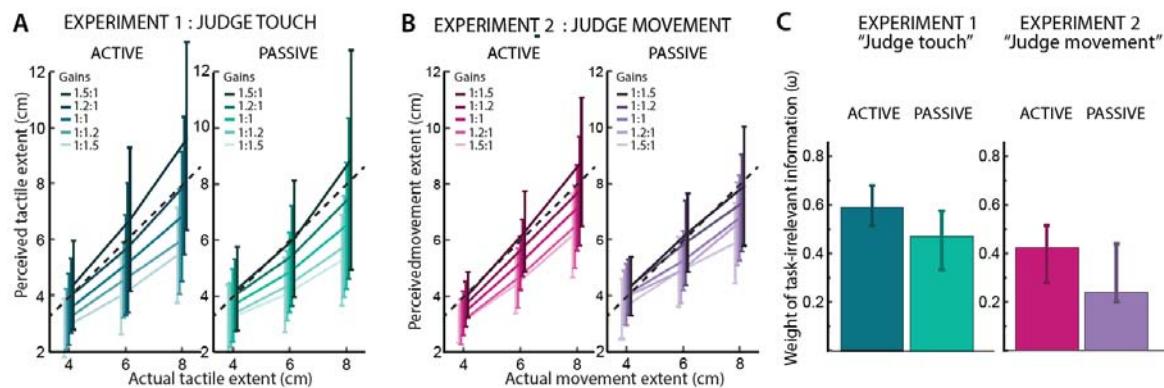
190 The weights (ω) of the task-irrelevant information (Figure 2C) were
191 significantly greater than 0 in both type of task and type of movement
192 (Experiment 1: Judge Touch – Active: median $\omega = 0.59$ [95% Confidence Interval of
193 the median = 0.52, 0.68]; Judge Touch – Passive: 0.47 [0.34, 0.58]; Experiment 2:
194 Judge Movement – Active: 0.42 [0.28, 0.52]; Judge Movement – Passive: 0.24 [0.21,
195 0.44]; test against 0, $Z < -3.059$, $p < 0.002$, $r < 0.883$, in all cases).

196 That is, when participants were instructed to judge the spatial extent of the
197 tactile stroking, they were nonetheless influenced by the extent of the movement, and
198 *vice versa*. Thus, the two components of self-touch strongly influenced each other,
199 even when task irrelevant. This finding clearly rejects a hypothesis of complete
200 independence between motor and somatosensory signals in extent perception (Table
201 1A).

202
203 *** PLEASE INSERT FIGURE 2 HERE ***

204

Figure 2



205
206 **Figure 2. Results from Experiment 1 and 2.** **A** Mean perceived tactile extent
207 (Experiment 1) as a function of actual stimulus extent, and gain applied to the task-
208 irrelevant information. **B** Mean perceived movement extent (Experiment 2) as a function
209 of actual movement extent and gain applied the task irrelevant information. Error bars in
210 **A-B** represent the Standard Deviation of the Mean (SD). **C** Median weights (ω) of the
211 task-irrelevant information (median was used because weights were not normally
212 distributed). The positive weights in both experiments show that motor information
213 influences tactile judgement even when task-irrelevant, and that tactile information
214 similarly influences judgements about movement. Error bars represent the 95% CIs for
215 the median (26).

216

217 ***Do motor signals dominate tactile perception in self-touch?***

218 Motor-based theories of space perception hold that motor signals dominate over
219 sensory signals (17, 18). Under this hypothesis, tactile stroking should thus have
220 little to nil influence on perception of movement (i.e., a weight $\omega = 0$ for touch in the
221 “judge movement” task, see Table 1A). Conversely, movement should strongly
222 influence, or even totally dominate tactile extent perception (i.e., a weight $\omega = 1$ for
223 task-irrelevant movement in the “judge touch” task, Table 1B). Our previous

224 analysis provides evidence against the first prediction of motor dominance theories,
225 by showing that the weights of tactile information were significantly higher than 0.
226 Similarly, contrary to the second hypothesis of the motor dominance theories, the
227 effect of movement on touch was significantly different from a prediction of total
228 dominance, since all ω s were significantly lower than 1 ($Z < -2.824$, $p < 0.005$, $r <$
229 0.88, in all cases; Bonferroni adjusted for four multiple comparisons: $\alpha = 0.0125$ per
230 test).

231 Thus, our results suggest that theories that reduce spatial perception to motor
232 signals cannot readily account for the bidirectional interference in spatial extent
233 perception during our self-touch manipulation.

234

235 ***Partial integration of motor and tactile information during self-touch***

236 The results of Experiments 1 and 2 suggest that both tactile and motor information
237 are partially integrated during self-touch. To investigate this partial integration
238 further, and to directly compare the weights of the irrelevant information in the two
239 tasks (“judge touch”, “judge movement”) we asked a new group of participants in
240 Experiment 3 to judge both movement and touch extents, in separate blocks. In
241 Experiments 1 and 2, direct comparison of weights would include an element of
242 inter-participant variability, because of the between-subjects comparison. Only three
243 motor:tactile gains were tested, but these spanned the same range as Experiments 1
244 and 2 (see Methods). Mean perceived to-be-judged extents for each gain are
245 presented in Figure 3A.

250

251

Figure 3

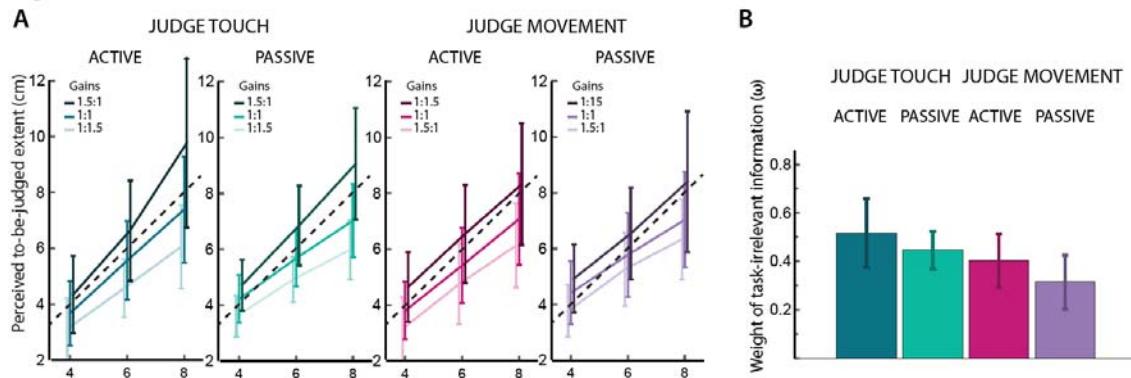


Figure 3. Results from Experiment 3. **A-B** Mean perceived extent of the target sensation as a function of actual stimulus extent, and gain applied to the task-irrelevant information in Experiment 3. Error bars represents the SD. **C** Mean weights (ω) of the task-irrelevant information in Experiment 3. Error bars represent the 95%CI of the mean.

First, we analysed Experiment 3 to replicate the results of Experiments 1 and 2. As the data were normally distributed (see Supplementary Table S6), we used t-tests to analyse the weights. As in the previous experiments, all weights ω were significantly greater than 0 ($t_{23} > 5.99$, $p < 0.001$, Cohen's $d > 1.22$, in all cases) and lower than 1 ($t_{23} < -10.001$, $p < 0.001$, Cohen's $d > 2.042$, in all cases, Bonferroni adjusted for two comparisons in each of four conditions, i.e., $\alpha = 0.0063$ per test) (see Figure 3B) (Judge Touch – Active: mean $\omega = 0.52$ [$\pm 95\%$ CI = 0.09]; Judge Touch – Passive: 0.45 [0.07, 0.17]. Judge Movement – Active: 0.4 [0.1, 0.24]; Judge Movement – Passive: 0.31 [0.11, 0.28]).

Next, to test for effects of type of judgement (movement extent, tactile extent) and type of movement (active, passive), and directly compare weights across these conditions, we used a 2×2 repeated measures ANOVA. The ANOVA showed a

269 significant main effect of type of Task ($F_{1,23} = 5.21, p = 0.032, \eta_p^2 = 0.19$) with a
270 greater weight of movement when participants had to judge touch (mean $\omega \pm 95\% \text{ CI}$:
271 0.48 ± 0.08) than *vice versa* (0.36 ± 0.10), indicating a directional asymmetry in the
272 interference between movement and touch signals. Moreover, there was also a
273 significant main effect of Movement type ($F_{1,23} = 10.1, p = 0.004, \eta_p^2 = 0.31$) with
274 higher weights, indicating stronger interference, when movement was active (mean ω
275 $\pm 95\% \text{ CI}$: 0.46 ± 0.08) than passive (0.38 ± 0.07). There was no significant
276 interaction between the two factors ($F_{1,23} = 0.17, p = 0.68$).

277 Finally, no correlation between the interference of movement on touch and of
278 touch on movement was found, in either active or passive conditions (see
279 Supplementary Figure S1 and explanatory text in Supplementary Material).
280 However, Active and Passive movement conditions in both tasks were strongly
281 correlated (see Supplementary Figure S2 and explanatory text in Supplementary
282 Material), suggesting that, within each task, the influence of irrelevant information
283 occurs due to some process that is common to active and passive conditions.

284 Thus, these results show strong and bidirectional, but asymmetrical
285 interference between the *touchant* and the *touché* sensations in self-touch. The
286 interference of movement on tactile extent judgements was greater than the
287 interference of touch on movement extent judgements.

288

289 *Self-touch as optimal integration*

290 Current theories of multisensory perception focus on optimal integration of multiple
291 sources of information (24). Each source is weighted according to its reliability or
292 precision (27–29). To test whether the weightings of tactile and movement signals in
293 self-touch are optimally integrated, we calculated participants' *precision* for each

294 condition of each experiment (see Statistical Analysis section and Table 2). If
295 optimal integration of tactile and motor information takes place in self-touch, then
296 our weighting values should directly follow from precision data, with precision data
297 showing the same significant main effects of task and movement as weightings, and
298 no interaction.

299 Yet, a 2 x 2 repeated measures ANOVA on the precision data of Experiment 3
300 showed no significant main effects (type of Task: $F_{1,23} = 1.37, p = 0.25$; type of
301 Movement: $F_{1,23} = 0.15, p = 0.71$) nor interaction ($F_{1,23} = 0.002, p = 0.96$). Similarly, we
302 did not find any difference in precision between the type of movement in Experiment 1
303 and 2 ($t_{11} = 0.06, p = 0.96$ and $t_{11} = 0.92, p = 0.38$ respectively using paired t-test), nor
304 between active and unimodal conditions in Experiments 4 and 5 ($t_{11} = 1.05, p = 0.32$ and
305 $t_{11} = 0.81, p = 0.41$ respectively using paired t-test). Thus, the weightings for interference
306 between movement and touch do not simply follow the precision of the component
307 signals.

308
309 *** PLEASE INSERT TABLE 2 HERE ***

| Experiment | Task | Condition | | |
|------------|-----------------------|----------------------------------|-----------------------------------|---------------------------|
| | | Active movement mean \pm SD | Passive movement mean \pm SD | Unimodal mean \pm SD |
| 1 | Judge Touch | 1.78 ± 1.19 | 1.77 ± 0.90 | |
| 2 | Judge Movement | 1.53 ± 0.49 | 1.39 ± 0.64 | |
| 3 | Judge Touch | 1.37 ± 1.01 | 1.33 ± 0.84 | |
| | Judge Movement | 1.21 ± 0.97 | 1.16 ± 0.57 | |
| 4 | Judge Touch | 1.8 ± 0.94 | | 2.14 ± 1.40 |
| 5 | Judge Movement | 0.94 ± 0.48 | | 1.08 ± 0.61 |

310
311

Table 2. Precision data (cm^{-2}) for each condition of each experiment.

312

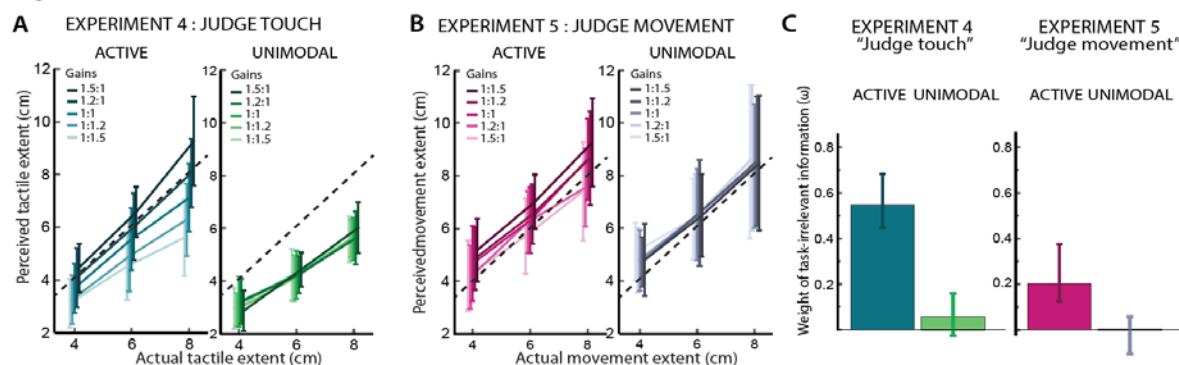
313 **Could the “tau effect” explain our results? Control experiments**

314 Since the movement durations of the leader and follower robots were matched,
315 changes in motor:tactile gain necessarily modify velocity of the tactile stroking
316 stimulus. Extent perception can be affected by the velocity or duration of the
317 stimulation, a phenomenon often referred to as “tau effect” (25). Because in our
318 design movement and touch began and ended together, a high motor:tactile gain
319 would result in both a greater tactile spatial extent *and* a higher tactile velocity, than
320 a low motor:tactile gain. We therefore investigated whether the effects of gain on
321 spatial extent perception truly reflected interference *between* the two different
322 signals, rather than influence of velocity on extent perception *within* a single sensory
323 channel. Therefore, we ran two additional control experiments to investigate
324 whether a tau effect could explain the results of Experiment 1-3.

325
326

327 *** PLEASE INSERT FIGURE 4 HERE ***

Figure 4



328
329

330 **Figure 4. Results from control Experiment 4 and 5. A-B** In Experiments 4 and 5, the
331 passive conditions were replaced with unimodal versions of the task where tactile (**A**) or
332 movement (**B**) sensations occurred in absence of task-irrelevant information. Error bars in
333 **A-B** represents SD. **C** Weights (ω) of the task-irrelevant information. Error bars
334 represent 95% CIs of the median.

335
336 The active movement conditions of Experiments 4 and 5 were identical to the
337 active conditions of Experiments 1 and 2, and to the corresponding conditions of
338 Experiments 1-3. In a second, “unimodal”, condition, participants were asked to
339 judge the tactile extent in absence of any movement (Control Experiment 4) or, to
340 judge the extent of the movement in absence of any tactile stimulation (Control
341 Experiment 5). In these conditions, any spatial perception is both unimodal and
342 unimanual, since only touch (Experiment 4) or only movement (Experiment 5) is
343 present, and thus there is no interference between movement and touch. If the
344 apparent influence of irrelevant signals in Experiments 1-3 was in fact due to an
345 artefact of the tau effect, then the tau effect should be equally present in unimodal
346 conditions, and our ω measure should again be greater than 0. Conversely, if the
347 interference in Experiments 1-3 indeed represents interference from irrelevant
348 information, rather than variations in the velocity of the judged signal, then ω in
349 unimodal conditions should show not be different from 0. Participants in Control
350 Experiments 4 and 5 judged spatial extents of touch, and of movement respectively,
351 in two conditions: a unimodal condition described above, and an active self-touch
352 condition replicating Experiments 1-3 (Figure 4A, B).

353 Data violated the normality assumption (see Supplementary Table S6), and
354 were therefore tested using the Wilcoxon’s Sign Test. In the “unimodal” conditions

355 of both experiments 4 and 5, weights were not significantly different from 0 (Judge
356 Touch – Unimodal: 0.06 [-0.03, 0.15], $Z = -1.80$, $p = 0.071$; Judge Movement –
357 Unimodal: 0.0005 [-0.11, 0.05], $Z = 0.078$, $p = 0.94$; see Figure 4C). Thus, we found
358 no significant evidence for a tau effect, and no reason to attribute the interference
359 effects of Experiments 1-3 to this source. The results for the active condition
360 replicated the effects of Experiment 1-3 (see Supplementary Results).

361

362 **Discussion (2149)**

363 Self-touch is widely thought to be an important psychophysiological event, but it has
364 rarely been studied experimentally. While other studies have examined the consequences
365 of self-touch (30, 31) and the processing of self-generated stimuli (32), our results provide
366 a systematic experimental manipulation of self-touch stimulation, and a novel focus on
367 spatial perception of self-touch events themselves.

368 We used an innovative method that allows variable coupling between two haptic
369 robots. We could thus break the direct relation, between hand movement and tactile
370 stimulation of another body part, that characterizes normal self-touch. Participants made
371 voluntary movements of their unseen right hand or were passively moved through an
372 equivalent trajectory. Crucially, they could not predict or decide in advance the amplitude
373 of these movements, which instead depended on haptic walls generated by the robot
374 interface. The movements directly caused a simultaneous, unseen stroking stimulus along
375 the left forearm, in the same direction as the movement, via a leader:follower robot
376 arrangement. The gain of the robotic coupling varied unpredictably across trials, so that
377 the spatial extent of movement and the spatial extent of touch could be decoupled, in
378 contrast to their strict correspondence during natural self-touch. When participants were
379 asked to report the spatial extent of their movement, their perceptual judgements were
380 strongly influenced by the tactile stimulus extent, and vice versa. This automatic
381 perceptual interference, in both directions, from an irrelevant signal was stronger when
382 participants made active movements than when they made passive movements. Control
383 experiments confirmed that these results reflected interference between representations of
384 extent, rather than a confound between extent and velocity introduced by our
385 manipulations of motor:tactile gain and leading to a tau effect. Overall, our results
386 provide robust experimental support for a degree of mutual interference between *touchant*

387 and *touché* during self-touch. In experiments 1-3 both *touchant* and *touché* signals were
388 always present, and always simultaneous, yet participants judged just one of these signals.
389 Our task thus required selective attention. The interference from the unattended signal can
390 be considered either as a limitation of selective attention, or as an automatic, pre-attentive
391 integration between the two signals. However, other studies reported minimal bilateral
392 interference (33), and even enhancement (34), in many somatosensory perceptual tasks
393 (see 35 for a review), making it unlikely that our results reflect general inability to direct
394 attention. Moreover, general effects of attention cannot readily explain the consistent and
395 strong differences in *touchant-touché* interference that we observed for active *vs* passive
396 movement – a point to which we will return below.

397 Several neurocognitive theories make contrasting predictions about perceptual
398 experience in *touchant-touché* scenarios. First, local sign theories (17, 18) perhaps have
399 the most direct relation to our self-touch scenario, because they specifically posit a
400 motoric basis for spatial percepts. These theories specifically predict a strong influence of
401 movement extent on tactile perception, without any reverse influence of touch on
402 movement (17, 18). In a strong version of this theory, the motor command signal simply
403 *is* the basis of spatial experience. The weightings of Figure 2C should then be 1 for
404 effects of active movement on touch, and 0 in all other conditions. Indeed, many theories
405 emphasise the dominant role of active motor signals in perception (24). Our results do not
406 support an account of total motor dominance, for two reasons. First, the effects of touch
407 on movement perception were clearly significant – even though they were less than the
408 effects of movement on touch perception. This occurred both when a voluntary motor
409 command was present, and, in our passive condition, when it was not. Thus, while
410 movement did influence touch more than touch influenced movement, as predicted by
411 local sign theory, the exclusive reduction of spatial perception to non-spatial, intensive

412 (i.e. based on intensity), as opposed to “extensive” (or based on extent), motor command
413 signals, was not confirmed.

414 Second, active motor commands lead to an increased bidirectional interference,
415 from touch to movement, as well as from movement to touch, relative to passive
416 movements. A key result of our study, replicated across Experiments 1-3, is thus an
417 increased integration between movement and tactile signals during active vs passive
418 movement, rather than a simple enhancement of motor dominance.

419 Self-touch is often cited in support of theories of motor-based space (36, 37).
420 Further, self-touch is considered a basis of bodily self-awareness and wider spatial
421 cognition (6, 8), i.e., that one’s own body is a volumetric spatial object within an external
422 world consisting of other objects. Our results cast doubt on the idea that motor commands
423 form the underpinning foundation of the experiences of tactile space, or of bodily self-
424 awareness, since tactile sensations had a strong reciprocal influence on awareness of
425 movement. Of course, we cannot exclude the possibility that tactile spatial perception
426 initially depends on movement, but later becomes an independent experience through
427 repeated motor-tactile association (17, 18). However, such associationist theories would
428 presumably predict that the primary original signal (motor) should continue to dominate
429 the secondary, associated signal (tactile) when both are present – yet we found robust
430 effects of tactile stimulation on perceived movement extent.

431 Could the array of tactile receptors in the skin then be alone sufficient for spatial
432 perception? This point is controversial: some theories deny the existence of a ‘tactile
433 field’ analogous to the visual field, and hold that the spatial properties of tactile sensation
434 do not reflect signals from tactile receptors themselves, but rather depend on movements
435 that generate specific patterns of tactile contact with external objects (38). Conversely, we
436 have previously shown that passive touch on an immobile skin surface is sufficient to

437 develop a rich spatial percept (39). Specifically, passive touch supported the same
438 processes of path integration and shape representation that are conventionally used to
439 identify cognitive maps of external space in the navigation literature (39).

440 Other neurocognitive theories also make predictions about self-touch.
441 Neurocomputational models of predictive motor control (32) suggest that perceptual
442 consequences of self-generated motor actions are suppressed, or at least attenuated, by
443 being cancelled against predictions of an internal model. On a strict version of this view,
444 the *touché* part of self-touch should generate no sensation at all – yet everyday experience
445 shows this is not the case. In our experiments, however, random trial-to-trial variation in
446 motor:tactile gain meant that tactile stimulation was not entirely predictable from the
447 motor activity. Nevertheless, motor prediction theories would struggle to explain our
448 finding that the sensory consequences of self-touch strongly influenced the perception of
449 voluntary movement extent.

450 Ideomotor theories of action (40) seem to make the opposite prediction, suggesting
451 that actions are mentally represented in terms of their external outcomes, rather than the
452 internal motor commands used to achieve those outcomes. On this view, one might
453 expect tactile signals to dominate self-touch perception, yet this was not found.

454 Finally, multisensory integration theories suggest that signals relating to a common
455 source are integrated to provide a single representation. Optimal integration theories
456 predict that more reliable (precise) signals should be more strongly weighted. Previous
457 observations of strong integration and coherence during *touchant-touché* sensations (6)
458 suggests these models might apply to self-touch. Our methods used automatic
459 interference of an irrelevant signal on a to-be-judged signal, rather than reports of a
460 common source event traditionally used to study optimal integration (24). Nevertheless,
461 the mutual influences on movement on touch perception and *vice versa* that we observed

462 did not appear to follow predictions of optimal integration theory. First, we found that
463 movement information was more highly weighted than tactile information in our main
464 Experiments 1-3. Optimal integration theory would predict this pattern to reflect a higher
465 precision for judgements of movement extent compared to tactile extent, but we observed
466 a (non-significant) difference in the opposite direction. Thus, while we did not formally
467 use multisensory integration framework for our study, the pattern of interference between
468 self-touch signals that we found points to suboptimal integration.

469 An interesting feature of our results was the greater bidirectional interference
470 between motor and tactile signals in active, compared to passive movement. Local sign
471 theories would predict a stronger influence of active compared to passive movement on
472 judgements of touch, but a weaker influence of touch on judgements of active compared to
473 passive movement. In fact, we found both increased influence of movement on tactile
474 judgement, and also increased influence of touch on movement judgement, for active
475 compared to passive conditions. The latter finding seems in stark contradiction to local
476 sign theory, and models of ‘motor-based space’ generally. While the increased
477 interference during active compared to passive movement was not originally predicted for
478 Experiments 1-2, the effect was strongly replicated using a larger sample size and a
479 within-participant design in Experiment 3. Our results thus suggest that presence of
480 voluntary motor commands led to an increased interaction between movement and tactile
481 signals, implying stronger automatic integration. At first sight, this might simply seem an
482 effect of selective attention to action. When participants must additionally focus on
483 controlling their right hand movement, they might be less able to attend to other signals
484 such as the tactile stimulation of the left hand. Stronger attentional demands of active *vs*
485 passive movement could potentially explain the stronger interference of active *vs* passive
486 movements on judgements of touch. However, those same attentional demands of active

487 movement cannot also explain the stronger interference from touch on judgements of
488 active compared to passive movements. Further, this hypothesis would predict low
489 precision of touch judgement in active vs. passive movement. However, we did not find
490 any significant effects of active versus passive movement on perceptual precision across
491 our five experiments.

492 Instead, we suggest that the presence of a voluntary motor command may promote
493 integration between multiple sensory and motor signals present in self-touch. A
494 distinctive feature of voluntary movement is its instrumentality: voluntary actions often
495 aim to achieve a specific outcome. Action and outcome are then represented as bound
496 together, as suggested by ideomotor and reinforcement learning theories (40–42). Such
497 binding processes imply a readiness-to-associate of voluntary action. By this we mean
498 that voluntary motor commands should readily integrate with signals carrying information
499 about the consequences of the action. Across three experiments, the presence of a
500 voluntary motor command lead to an increased influence of movement on touch, but also
501 to an increased influence of touch on movement. We therefore suggest that voluntary
502 actions have a distinctive psychological effect of promoting multisensory binding between
503 diverse signals, to produce more integrated, coherent representation of action events.
504 Previous studies have suggested similar integrative functions of voluntary action, in bodily
505 illusions (43) and in time perception (44). Our result adds a novel dimension to this
506 general view of the integrative nature of voluntary action. It may also explain how
507 voluntary action contributes to the experience of one's body as a coherent, unified self-
508 object, despite the striking diversity of sensory signals reaching the brain from the body.

509 Our study has several limitations. First, we studied only the *spatial* aspects of self-
510 touch. Our results cannot therefore address other important aspects of self-touch, such as
511 the self-other distinction (45). Second, we used a measurement framework based on

512 selective influence and interference between signals, rather than an optimal multisensory
513 integration framework. Therefore, we cannot formally establish whether *touchant* and
514 *touché* signals are integrated in a mathematical sense. An integration framework would
515 imply asking participants to report a *single* percept (e.g., “What was the extent of that self-
516 touch event?”), whereas our primary concern was to establish the different perceptual
517 contents associated with each individual component signal in the *touchant-touché*
518 situation. Nevertheless, the results of our study are consistent with a strong integration of
519 these signals, while suggesting that the integration process itself may be suboptimal.

520 To conclude, we reported several experiments on spatial perception during self-
521 touch. Novel experimental manipulations of the relationship between movement and touch
522 allowed us to investigate the contributions of each signal to spatial perception, and the
523 degree of interference between one signal and another. We found strong interference of
524 movement on judgements of touch, and also of touch on judgements of movement. While
525 motor signals dominated tactile signals in self-touch processing, classical local sign
526 theories and motor-based space theories are not consistent with the strong interfering
527 effects of tactile input on perceived extent of movement that we repeatedly found.
528 Further, interference effects in both directions were enhanced under active voluntary
529 movement, compared to passive movement. This suggests that a distinctive cognitive
530 consequence of the voluntary motor command is to promote a general integration of
531 multiple signals to synthesise representations related to the body, and thus produce a
532 coherent overall representation of the bodily self. In this sense, our results reveal a simple
533 sensorimotor basis for the intuition that voluntary action underlies the coherence and unity
534 of self-awareness. We have proposed that the voluntary motor command induces a
535 cognitive binding process that facilitates perceptual integration of multiple signals. The
536 mechanisms underlying this distinctive feature of volition, and its relation to phenomenal

537 self-models (46) remain unclear, but action-outcome learning is likely to provide a key
538 mechanism (47).
539

540 **Materials and Methods (2057)**

541 **Participants**

542 The sample size for experiment 1 ($n = 12$: 7 females, mean age \pm SD: 22.7 ± 3.1) was
543 decided a priori on the basis of previous similar studies (7, 12). To determine the sample
544 size for experiments 2-5, we performed a power analysis based on the results of
545 Experiment 1. The effect size for the main effect of the robotic gain manipulation in
546 experiment 1 was $\eta^2 = 0.722$ (see Supplementary ANOVA Table S1 in the Supplementary
547 Material), considered to be very large using Cohen's criteria (48). With an alpha = 0.05
548 and power = 0.8, the projected sample size indicated to demonstrate interference effects on
549 movement on touch perception and *vice versa* was 4 participants (G*Power 3.1.9.2
550 software) (49). We nevertheless set a sample size of $n = 12$ for Experiments 2, 4, and 5
551 (Experiment 2: 11 females, mean age \pm SD: 25.2; Experiment 4: 8 females, mean age \pm
552 SD: 24.4 ± 3.8 ; Experiment 5: 8 females, mean age \pm SD: 24.1 ± 3.6), and of $n = 24$ for
553 Experiment 3 (17 females, mean age \pm SD: 29.5 ± 13.2). Eighty-two healthy right-handed
554 volunteers were originally recruited for the study. Two participants were excluded because
555 of technical issues. Based on a priori exclusion criteria, eight further participants were
556 excluded during the training phase because they proved unable to use the robotic device to
557 produce smooth self-stimulation movements (see procedure below). The experimental
558 protocol was approved by the Research Ethics Committee of University College London
559 and adhered to the ethical standards of the Declaration of Helsinki. All participants were
560 naïve regarding the hypotheses underlying the experiment and provided their written
561 informed consent before the beginning of the testing, after receiving written and verbal
562 explanations of the purpose of the study.

563

564

565 ***Apparatus***

566 Figure 1 shows a schematic representation of the setup. Participants sat in front of a
567 computer screen with their left arm on a fixed moulded support, and their right arm on an
568 articulated armrest support (Ergorest, series 330 011, Finland). Both the participants'
569 arms and the robotic setup were covered by a horizontal screen and remained unseen
570 throughout the experiment. The sensorimotor self-touch stimulation was implemented
571 using two six-degrees-of-freedom robotic arms (3D Systems, Geomagic Touch X, South
572 Carolina, USA) linked as a computer-controlled leader-follower system. In this system,
573 any 3D-movement of the right-hand leader robot is reproduced by the follower robot. The
574 estimated lag between the robot trajectories was 2.5 ms (see Supplementary Methods for
575 details). The follower robot carries a paintbrush (12.7 mm width) that strokes the
576 participant's left forearm (see <https://tinyurl.com/yxf34yna> for a video of the setup). This
577 setup allowed us to manipulate the gain between the leader and the follower robots so as
578 to produce different combinations of motor and tactile displacements. For instance, if the
579 motor:tactile was set to 1:1.5 then every 1 cm movement of the leader (movement) robot
580 would cause 1.5 cm movement of the follower robot.

581 The extent of each movement in the anteroposterior direction was controlled by
582 two “virtual walls” created by the force-feedback system of the leader robots. That is,
583 participants would move the leader arm forward/backward until resistance from the force
584 feedback wall prevented them from moving further. This allowed the movement extent to
585 be randomized across trials.

586

587 ***Experimental design***

588 Experiments 1 and 2 tested, respectively, the effect of movement on tactile extent (judge
589 touch task) and vice versa (judge movement task). Each experiment had a 2 (movement

590 type: active, passive) x 3 (extent of the to-be-judged stimulus: 4, 6, 8 cm) x 5
591 (motor:tactile gains: 1.5:1, 1.2:1, 1:1, 1:1.2, 1:1.5) within subject design. The movement
592 type factor (active/passive) was blocked and counterbalanced across participants. The
593 spatial extent of the to-be-judged events (movement, or stroke) was randomised. Each of
594 the 30 possible combinations of these factors was experienced eight times, giving a total
595 of 240 trials per participant. The testing was divided into 16 blocks of 15 trials each, and
596 breaks were allowed between blocks.

597 Experiments 1 and 2 tested for the effects of movement extent on judgements of
598 tactile extent, and for the effects of tactile extent on judgements of movement extent,
599 respectively. Five levels of motor:tactile gain were tested, in randomized order.

600 Experiment 3 used a full within-subjects design with a 2 (judgement type: judge
601 movement, judge touch) x 2 (movement type: active, passive) x 3 (extent of the to-be-
602 judged stimulus: 4, 6, 8 cm) x 3 (motor:tactile gains: 1.5:1, 1:1, 1:1.5) paradigm. Each of
603 the resulting 36 conditions was repeated eight times, for a total of 288 trials per
604 participant. The testing was divided into 16 blocks of 18 trials each, and breaks were
605 allowed between blocks.

606 Experiments 4 and 5 aimed to control for the contribution of differential stimulus
607 velocity produced by the gain manipulation and were based on the same experimental
608 design as Experiments 1 and 2. In these experiments, the passive movement condition
609 was replaced with a purely unimodal, and unimanual condition in which participants
610 judged the extent of either touch (Experiment 4) or movement (Experiment 5) in absence
611 of any movement, or of any tactile stimulation respectively.

612

613 **Procedure**

514 Participants were familiarised with the experimental setup at the beginning of the
515 experiment, and received training before each condition. In the active movement
516 condition, participants were instructed to perform a back-and-forth movement of the right
517 hand from the far wall to the near wall, and then returning to the starting position (far
518 wall). Participants would move their hand forward/backward until they discovered the
519 position of the virtual walls on each trial, guided by the haptic feel of force when they
520 touched the wall. This was followed by a short auditory beep, as an additional cue they
521 had reached the wall. In the passive movement condition, the handle of the leader robot
522 was moved by the experimenter in the same back-and-forth trajectory described for the
523 active condition. Participants held the leader robot's handle with their right hand and
524 followed passively the movements produced by the experimenter. The unimodal
525 conditions (Experiments 4-5) were identical to the passive conditions in Experiments 1-2,
526 with the only exception that the participant kept the right, active movement hand
527 (Experiment 4) or the left, passive touch recipient hand (Experiment 5) on the desk, away
528 from the setup. Participants were, thus, judging the extent of touch in absence of
529 movement or vice versa.

530 Each training phase ended with a practice block of the spatial extent judgement
531 task. Participants were asked to focus only on the “to-be-judged” experience of the block
532 – either the extent of the right hand’s movement, or the extent of the stroke on the left
533 forearm, as appropriate – and to ignore the other sensation. After each active or passive
534 movement, the fixation cross on the screen was replaced by a line of a random length
535 (between 2 and 10 cm). Participants then used two foot-pedals (one which made the line
536 longer, and the other shorter) to adjust the length of the line on the screen. Their task was
537 to match the line on the screen to the extent of either the movement or the tactile
538 sensation, depending on condition. The fixation cross and judgement task line were

539 aligned with the participants' left arm in the case of the "judge touch" task, and with the
540 participants' right hand in the case of the "judge movement" task. After adjusting the
541 length of the line, participants clicked a button on the handle of the leader robot to confirm
542 their response and start a new trial.

543 In all trials of the practice block, movements and tactile feedback were 8 cm in
544 length, so the spatial extent of natural self-touch was consistent with movement extent, as
545 in typical self-touch. The main testing phase was identical to the training phase, except
546 that the gain between the leader and follower robots was systematically manipulated in
547 order to obtain different extents for movement and touch sensations. The gain varied
548 randomly across trials between the different gain values set in each experiment (see
549 above). Thus, although a general consistency between movement and tactile extents
550 remained, participants could not reliably predict movement extent from tactile extent or
551 vice versa. This allowed us to investigate the perceived extent of the to-be-judged
552 sensation (e.g. touch in the "judge touch" task), as a function of the task-irrelevant spatial
553 extent of the other, task-irrelevant event (e.g. movement in the "judge touch" task).

554

555 *Statistical analysis*

556 *Weight of task irrelevant information*

557 The main goal of this study was to test some of the most influential accounts of tactile
558 self-touch space perception using a self-touch paradigm. In particular, we contrasted the
559 theory of independent coding, motor dominance, and partial fusion between motor and
560 tactile spatial information. Each of these groups of theories makes clear predictions (see
561 Table 1) on how the sensory and motor components of self-touch would be weighted
562 according to the task demands (judge touch/judge movement) and the type of movement
563 (active/passive). First, a model based on independent spatial coding for action and

564 perception (22, 23) predicts that participants' extent judgements in each task should be
565 unaffected by the task-irrelevant information. Second, a strong motor-based theory of
566 space perception (17, 18) predicts a strong influence of movement on tactile extent (i.e. a
567 weight $\omega > 0$ for movement in the “judge touch” task), but much less, or zero, influence of
568 tactile stroking on perception of movement (i.e. a weight $\omega = 0$ for touch in the “judge
569 movement” task). Finally, a weight ω in between 0 and 1 would suggest partial
570 integration. This could be either optimal (24) or sub-optimal, depending on whether the
571 weighting is determined by the precision of each modality or not.

572 To test these hypotheses, we first used a regression approach to extract a summary
573 measure of sensitivity describing the relation between perceived and actual extent of
574 stimulus. In particular, we fitted the following model to quantify the effect of the task-
575 irrelevant extent information on the to-be-judged extent.

576 **JudgedExtent ~ ScaleIndiv ((1 - ω) ToBeJudgedExtent + ω TaskIrrelevantExtent)**

577 (1)

578 Where ScaleIndiv is an individual scaling factor to capture each participant's cross-modal
579 mapping from motor/tactile stimulation extent to visual line response, ω is the weight of
580 the task-irrelevant extent (TaskIrrelevantExtent) on the judged extent (ToBeJudgedExtent)
581 information. We did not fit any intercept in this model, since we assumed a judged extent
582 of zero in the absence of any actual spatial stimulation (50, for a similar approach in
583 perceptual judgement task, see 51). In this model, a weight $\omega = 0$ would correspond to the
584 situation where the participant would report the target extent independently from the task-
585 irrelevant information (e.g. no effect of movement on touch in the “judge touch” task).
586 Conversely, $\omega = 1$ would mean that the participants' to-be-judged extent perception is
587 entirely based on the task-irrelevant information and not at all on the to-be-judged

588 information. Finally, a weight between 0 and 1 would indicate the partial integration of
589 task-irrelevant information in judged extent. Fitting this model allowed us to calculate a
590 single summary numerical value from all the raw judgement data, capturing the influence
591 of movement on touch, and another value capturing the influence of touch and movement
592 (see Supplementary Material for individual weights for each participant in each
593 experiment).

594

595 ***Precision***

596 For each participant, and each condition, we computed the precision (Precision =
597 1/Standard Deviation) for each combination of extent and gain. Since our interest
598 focussed on the conditions, while extent and gain were effects of no interest, we then
599 averaged the precisions values across the different levels of extent and gain, to obtain
600 a single mean precision value for each participant and each condition. The mean
601 precision and its standard deviation over participants are shown in Table 2.

602

703 ***Normality of data***

704 Data from Experiments 1-2 and 4-5 violated the normality assumption (see Supplementary
705 Material), therefore the different predictions were tested with a series of Wilcoxon's Sign
706 tests contrasting the weight of the task-irrelevant information in the four conditions (type
707 of judgement x type of movement) against 0 or 1. Data from Experiment 3 were normally
708 distributed, thus the same analysis were conducted using a series of t-tests contrasting the
709 weight of the task-irrelevant information in the four conditions (type of judgement x type
710 of movement) against 0 or 1, and a 2 x 2 repeated measures ANOVA with factors of
711 Judgement type ("judge touch", "judge movement") and Movement type (active, passive).

712 **References**

- 713 1. G. Rizzolatti, L. Fadiga, L. Fogassi, V. Gallese, The space around us. *Science*. **277**, 190–191 (1997).
- 714 2. N. P. Holmes, C. Spence, The body schema and multisensory representation (s) of peripersonal space. *Cognitive processing*. **5**, 94–105 (2004).
- 715
- 716 3. E. Azañón, M. R. Longo, S. Soto-Faraco, P. Haggard, The posterior parietal cortex remaps touch into external space. *Current Biology*. **20**, 1304–1309 (2010).
- 717
- 718 4. A. Kurjak, G. Azumendi, N. Vecek, S. Kupesic, M. Solak, D. Varga, F. Chervenak, Fetal hand movements and facial expression in normal pregnancy studied by four-dimensional sonography. *J Perinat Med*. **31**, 496–508 (2003).
- 719
- 720
- 721 5. S. Bolanowski, R. Verrillo, F. McGlone, Passive, active and intra-active (self) touch. *Behavioural brain research*. **148**, 41–45 (2004).
- 722
- 723 6. M. Merleau-Ponty, *Phénoménologie de la perception* (1945). *Librairie Gallimard, Paris* (1976).
- 724 7. S. Schütz-Bosbach, J. J. Musil, P. Haggard, Touchant-touché: The role of self-touch in the representation of body structure. *Consciousness and cognition*. **18**, 2–11 (2009).
- 725
- 726 8. S. Gallagher, A. N. Meltzoff, The earliest sense of self and others: Merleau-Ponty and recent developmental studies. *Philosophical psychology*. **9**, 211–233 (1996).
- 727
- 728 9. S. Dieguez, M. R. Mercier, N. Newby, O. Blanke, Feeling numbness for someone else's finger. *Current Biology*. **19**, R1108–R1109 (2009).
- 729
- 730 10. M. P. M. Kammers, F. de Vignemont, P. Haggard, Cooling the Thermal Grill Illusion through Self-Touch. *Current Biology*. **20**, 1819–1822 (2010).
- 731
- 732 11. H. E. van Stralen, M. J. E. van Zandvoort, H. C. Dijkerman, The role of self-touch in somatosensory and body representation disorders after stroke. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **366**, 3142–3152 (2011).
- 733
- 734
- 735 12. M. Hara, P. Pozeg, G. Rognini, T. Higuchi, K. Fukuwara, A. Yamamoto, T. Higuchi, O. Blanke, R. Salomon, Voluntary self-touch increases body ownership. *Frontiers in psychology*. **6**, 1509 (2015).
- 736
- 737 13. J. J. Gibson, The senses considered as perceptual systems. (1966).
- 738 14. R. Descartes, *Treatise of man* (Harvard University Press, 1972).
- 739 15. W. Penfield, T. Rasmussen, The cerebral cortex of man; a clinical study of localization of function. (1950).
- 740 16. B. Bridgeman, in *The Oxford Handbook of Eye Movements* (Oxford University Press, Oxford, 2011), pp. 511–521.
- 741
- 742 17. R. H. Lotze, *Medizinische Psychologie oder Physiologie der Seele*. Von Dr. Rudolph Hermann Lotze Professor in Göttingen (Weidmann'sche Buchhandlung, 1852).
- 743
- 744 18. W. M. Wundt, *Beiträge zur Theorie der Sinneswahrnehmung* (CF Winter, 1862).
- 745 19. N. Gangopadhyay, J. Kiverstein, Enactivism and the unity of perception and action. *Topoi*. **28**, 63–73 (2009).
- 746 20. J. K. O'Regan, A. Noë, A sensorimotor account of vision and visual consciousness. *Behavioral and brain sciences*. **24**, 939–973 (2001).
- 747
- 748 21. J. M. Findlay, I. D. Gilchrist, *Active vision: The psychology of looking and seeing* (Oxford University Press, 2003).
- 749

- 750 22. M. A. Goodale, A. D. Milner, others, Separate visual pathways for perception and action (1992).
- 751 23. H. C. Dijkerman, E. H. De Haan, Somatosensory processing subserving perception and action: Dissociations,
752 interactions, and integration. *Behavioral and brain sciences*. **30**, 224–230 (2007).
- 753 24. M. O. Ernst, M. S. Banks, Humans integrate visual and haptic information in a statistically optimal fashion.
754 *Nature*. **415**, 429–433 (2002).
- 755 25. H. Helson, S. M. King, The tau effect: an example of psychological relativity. *Journal of Experimental
756 Psychology*. **14**, 202–217 (1931).
- 757 26. W. J. Conover, *Practical nonparametric statistics* (John Wiley & Sons, 1998), vol. 350.
- 758 27. M. O. Ernst, H. H. Bülthoff, Merging the senses into a robust percept. *Trends in cognitive sciences*. **8**, 162–169
759 (2004).
- 760 28. K. P. Körding, D. M. Wolpert, Bayesian integration in sensorimotor learning. *Nature*. **427**, 244–247 (2004).
- 761 29. D. Alais, D. Burr, The Ventriloquist Effect Results from Near-Optimal Bimodal Integration. *Current Biology*.
762 **14**, 257–262 (2004).
- 763 30. H. H. Ehrsson, N. P. Holmes, R. E. Passingham, Touching a Rubber Hand: Feeling of Body Ownership Is
764 Associated with Activity in Multisensory Brain Areas. *J. Neurosci*. **25**, 10564–10573 (2005).
- 765 31. L. Dupin, P. Haggard, Dynamic Displacement Vector Interacts with Tactile Localization. *Current Biology*. **29**,
766 492–498.e3 (2019).
- 767 32. S.-J. Blakemore, D. M. Wolpert, C. D. Frith, Central cancellation of self-produced tickle sensation. *Nature
768 neuroscience*. **1**, 635 (1998).
- 769 33. S. E. Laskin, W. A. Spencer, Cutaneous masking. I. Psychophysical observations on interactions of multipoint
770 stimuli in man. *Journal of Neurophysiology*. **42**, 1048–1060 (1979).
- 771 34. J. C. Craig, Attending to two fingers: Two hands are better than one. *Perception & Psychophysics*. **38**, 496–511
772 (1985).
- 773 35. L. Tamè, C. Braun, N. P. Holmes, A. Farnè, F. Pavani, Bilateral representations of touch in the primary
774 somatosensory cortex. *Cognitive Neuropsychology*. **33**, 48–66 (2016).
- 775 36. E. B. de Condillac, *Traité des sensations* (chez les Librairies Associés, 1793).
- 776 37. A. Bicanski, N. Burgess, Neuronal vector coding in spatial cognition. *Nature Reviews Neuroscience*. **21**, 453–
777 470 (2020).
- 778 38. M. Martin, in *The Contents of Experience*, T. Crane, Ed. (New York: Cambridge University Press, 1992).
- 779 39. F. Fardo, B. Beck, T. Cheng, P. Haggard, A mechanism for spatial perception on human skin. *Cognition*. **178**,
780 236–243 (2018).
- 781 40. W. James, *The principles of psychology, Vol I.* (Henry Holt and Co, New York, NY, US, 1890), *The principles
782 of psychology, Vol I.*
- 783 41. P. Haggard, The Neurocognitive Bases of Human Volition. *Annual Review of Psychology*. **70**, 9–28 (2019).
- 784 42. B. Hommel, R. W. Wiers, Towards a Unitary Approach to Human Action Control. *Trends Cogn Sci*. **21**, 940–
785 949 (2017).
- 786 43. M. Tsakiris, G. Prabhu, P. Haggard, Having a body versus moving your body: How agency structures body-
787 ownership. *Consciousness and Cognition*. **15**, 423–432 (2006).

- 788 44. P. Haggard, S. Clark, J. Kalogeras, Voluntary action and conscious awareness. *Nat Neurosci.* **5**, 382–385
789 (2002).
- 790 45. R. Boehme, S. Hauser, G. J. Gerling, M. Heilig, H. Olausson, Distinction of self-produced touch and social
791 touch at cortical and spinal cord levels. *PNAS*. **116**, 2290–2299 (2019).
- 792 46. T. Metzinger, in *Neural Correlates of Consciousness: Empirical and Conceptual Questions*, T. Metzinger, Ed.
793 (MIT Press, 2000; <http://sammelpunkt.philo.at/267/>).
- 794 47. V. Chambon, H. Théro, M. Vidal, H. Vandendriessche, P. Haggard, S. Palminteri, Information about action
795 outcomes differentially affects learning from self-determined versus imposed choices. *Nature Human
796 Behaviour*, 1–13 (2020).
- 797 48. J. Cohen, *Statistical power analysis for the behavioral sciences 2nd edn* (Erlbaum Associates, Hillsdale, 1988).
- 798 49. F. Faul, E. Erdfelder, A. Buchner, A.-G. Lang, Statistical power analyses using G* Power 3.1: Tests for
799 correlation and regression analyses. *Behavior research methods*. **41**, 1149–1160 (2009).
- 300 50. J. G. Eisenhauer, Regression through the origin. *Teaching statistics*. **25**, 76–80 (2003).
- 301 51. A. Y. Leib, A. Kosovicheva, D. Whitney, Fast ensemble representations for abstract visual impressions. *Nature
302 communications*. **7**, 13186 (2016).
- 303

304 **Acknowledgments**

305 **Funding:** AC and PH were supported by a European Research Council Advanced
306 Grant (HUMVOL, project NO. 323943) to PH. LD and PH were supported by the
307 Chaire Blaise Pascal de la Région Ile de France. AC was additionally supported by an
308 award of the 2017 Summer Seminars in Neuroscience and Philosophy (SSNAP - Duke
309 University), funded by the John Templeton Foundation. LD was additionally
310 supported by “Fondation pour la Recherche Médicale” (FRM - DPP20151033970).
311 PH was additionally supported by a research contract between Nippon Telegraph and
312 Telephone and UCL.

313

314 **Author contributions:** AC: Conceptualization, Methodology, Software, Formal
315 Analysis, Investigation, Data Curation, Writing – Original Draft, Visualization. LD:
316 Conceptualization, Methodology, Software, Formal Analysis, Writing – Review &
317 Editing. HDJ: Data Curation, Writing – Review & Editing. HG: Resources, Writing –
318 Review & Editing. PH: Conceptualization, Resources, Writing – Review & Editing,
319 Supervision, Project Administration, Funding Acquisition.

320

321 **Competing interests:** None

322

323 **Data and materials availability:** The datasets generated during and/or analyzed
324 during the current study are available on <https://tinyurl.com/y3ssgho4>. All data needed
325 to evaluate the conclusions in the paper are present in the paper and/or the
326 Supplementary Materials.

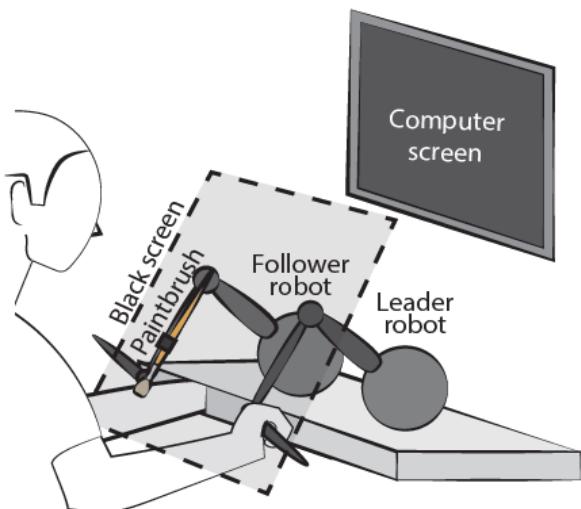
327

328 **Figures and Tables**

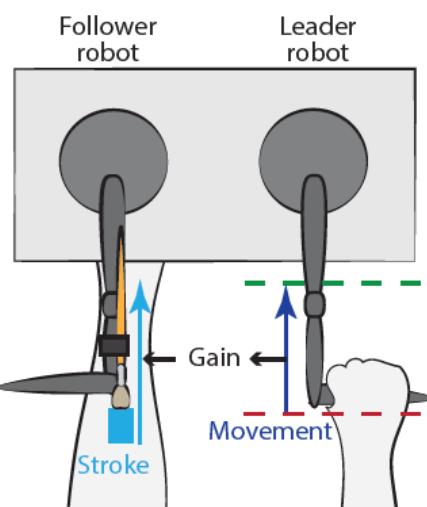
329

Figure 1

A



B



330

331 **Figure 1. Experimental setup and stimuli.** **A.** Participants moved the handle of the
332 leader robot with their right hand and simultaneously felt a corresponding stroke on
333 the left forearm from a brush attached to the follower robot. A black screen (black
334 dashed line) covered both the participants' arms and the robotic setup throughout the
335 experiment. **B.** The physical extent of movement was modulated via two “virtual
336 walls” defining start (red dashed line) and stop (green dashed line) positions, which
337 varied between trials. The relation between the extent of movement (dark blue arrow)
338 and touch (light blue arrow) depended on the gain of the leader:follower robot
339 coupling, which was randomized across trials (see <https://tinyurl.com/yxf34yna> for a
340 video of the setup).

Figure 2

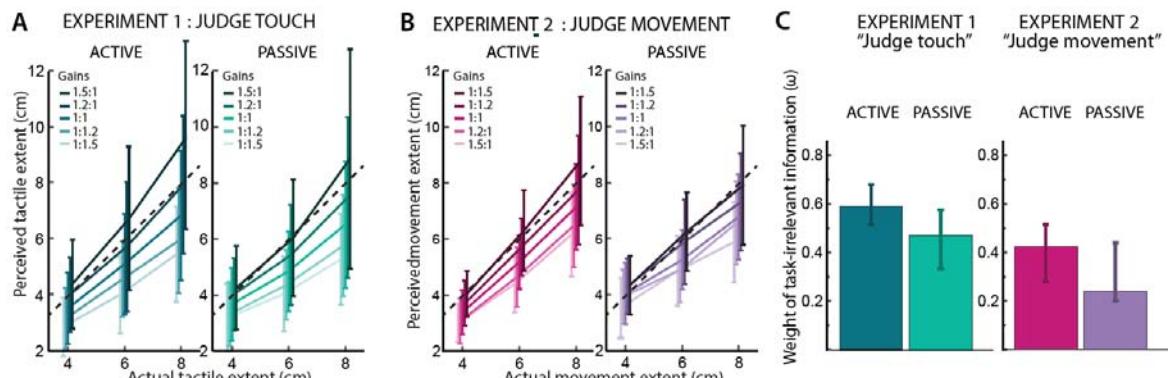


Figure 2. Results from Experiment 1 and 2. A Mean perceived tactile extent

(Experiment 1) as a function of actual stimulus extent, and gain applied to the task-irrelevant information. B Mean perceived movement extent (Experiment 2) as a

function of actual movement extent and gain applied the task irrelevant information.

Error bars in A-B represent the Standard Deviation of the Mean (SD). C Median

weights (ω) of the task-irrelevant information (median was used because weights were

not normally distributed). The positive weights in both experiments show that motor

information influences tactile judgement even when task-irrelevant, and that tactile

information similarly influences judgements about movement. Error bars represent the

95% CIs for the median (26).

341

342

343

344

345

346

347

348

349

350

351

352

Figure 3

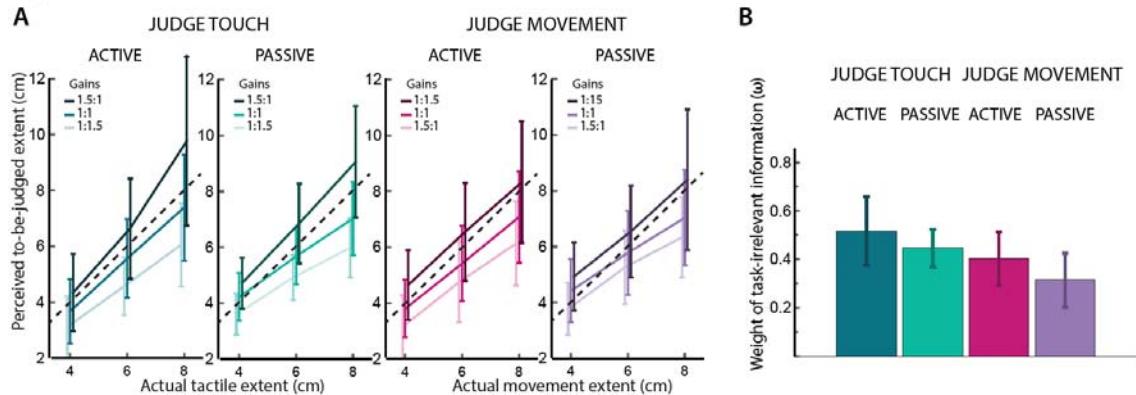
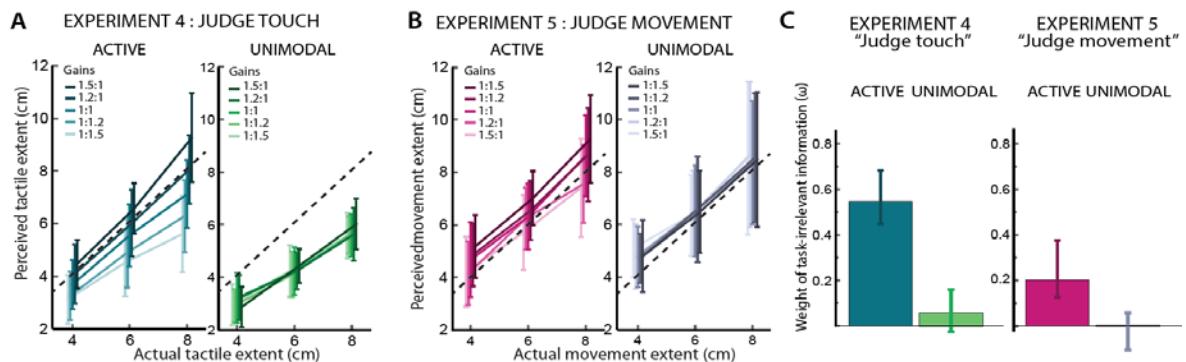


Figure 3. Results from Experiment 3. A-B Mean perceived extent of the target sensation as a function of actual stimulus extent, and gain applied to the task-irrelevant information in Experiment 3. Error bars represents the SD. **C** Mean weights (ω) of the task-irrelevant information in Experiment 3. Error bars represent the 95%CI of the mean.

Figure 4



360 **Figure 4. Results from control Experiment 4 and 5. A-B** In Experiments 4 and 5,

361 the passive conditions were replaced with unimodal versions of the task where tactile

362 sensations occurred in absence of task-irrelevant information.

363 (A) or movement (B) sensations occurred in absence of task-irrelevant information.

364 Error bars in A-B represents SD. C Weights (ω) of the task-irrelevant information.

365 Error bars represent 95% CIs of the median.

366

| | Weighting of movement on tactile extent perception | Weighting of touch on motor extent perception |
|---|---|--|
| Independent spatial coding of movement and touch | $\omega = 0$ | $\omega = 0$ |
| Motor dominance over tactile signals | $\omega = 1$ | $\omega = 0$ |
| Partial integration | $0 < \omega < 1$ | $0 < \omega < 1$ |

367

368 **Table 1.** Three alternative accounts of the relation between motor and tactile signals
369 during self-touch, and their predictions for the interference weighting between signals.

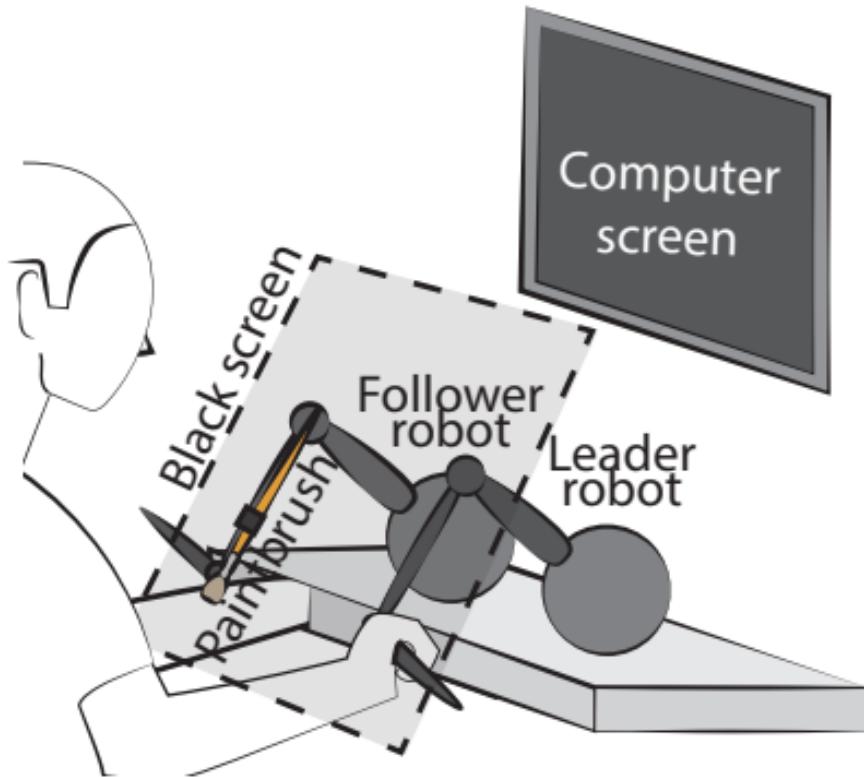
370

| Experiment | Task | Condition | | |
|-------------------|-----------------------|---|--|----------------------------------|
| | | Active movement mean \pm SD | Passive movement mean \pm SD | Unimodal mean \pm SD |
| 1 | Judge Touch | 1.78 ± 1.19 | 1.77 ± 0.90 | |
| 2 | Judge Movement | 1.53 ± 0.49 | 1.39 ± 0.64 | |
| 3 | Judge Touch | 1.37 ± 1.01 | 1.33 ± 0.84 | |
| | Judge Movement | 1.21 ± 0.97 | 1.16 ± 0.57 | |
| 4 | Judge Touch | 1.8 ± 0.94 | | 2.14 ± 1.40 |
| 5 | Judge Movement | 0.94 ± 0.48 | | 1.08 ± 0.61 |

371 **Table 2.** Precision data (cm^{-2}) for each condition of each experiment.

Figure 1

A



B

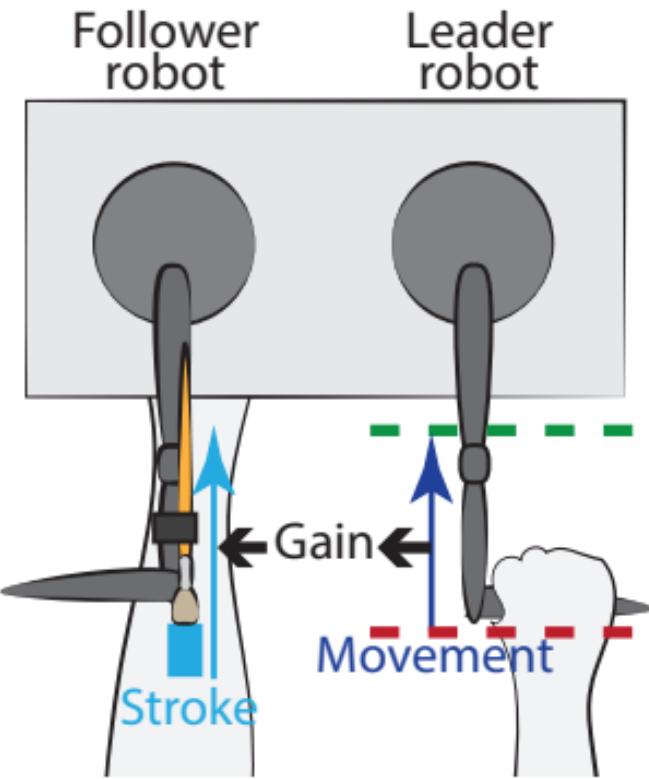


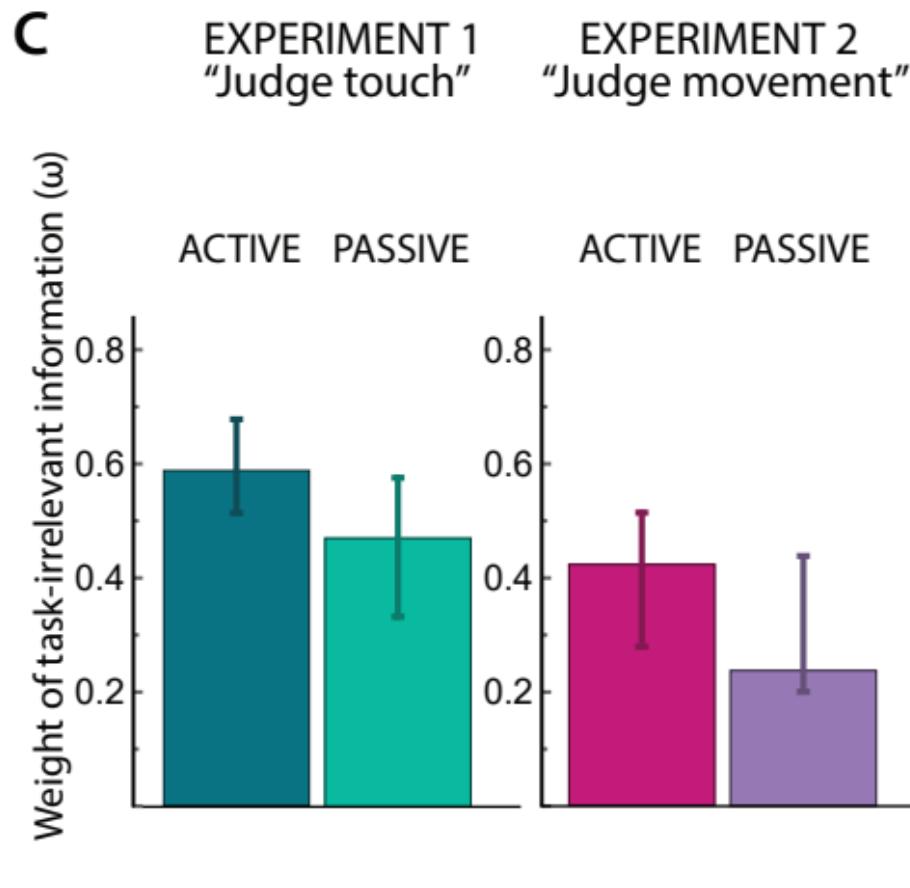
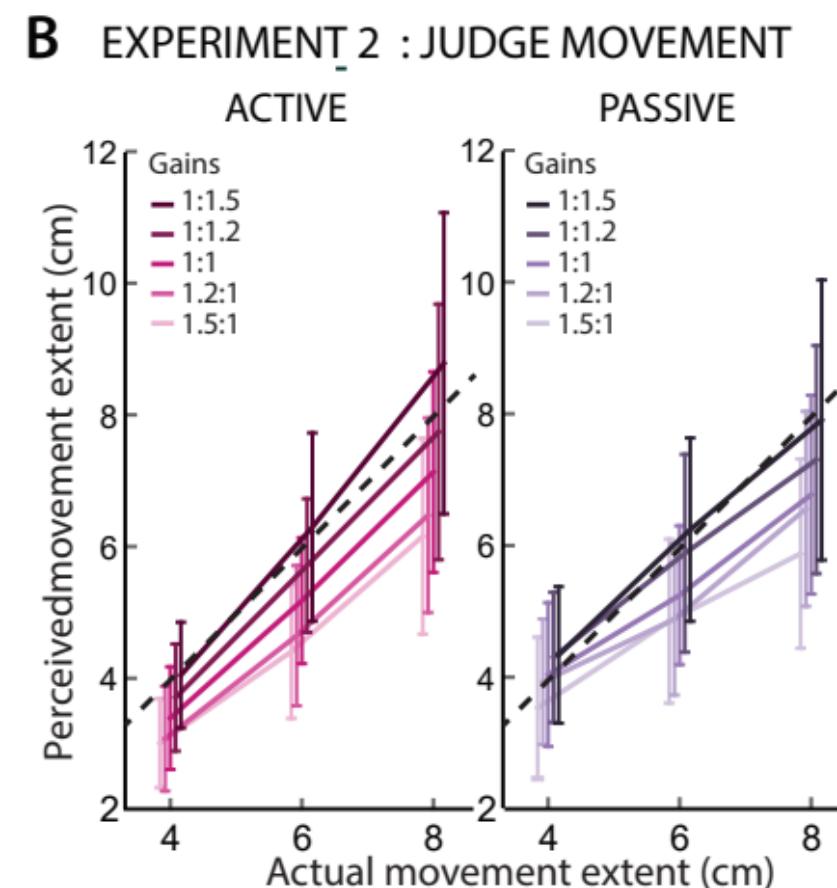
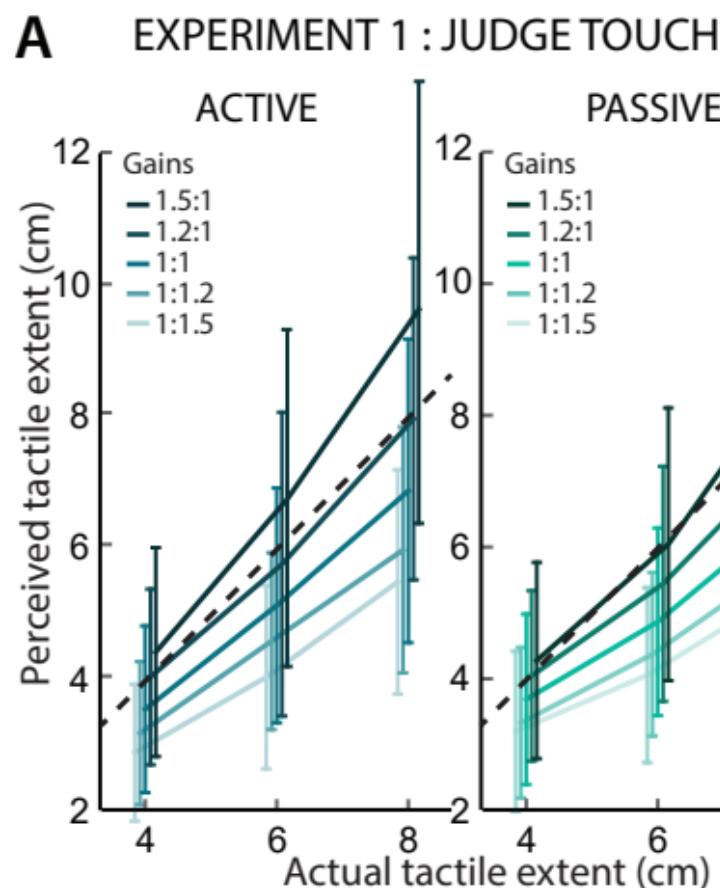
Figure 2

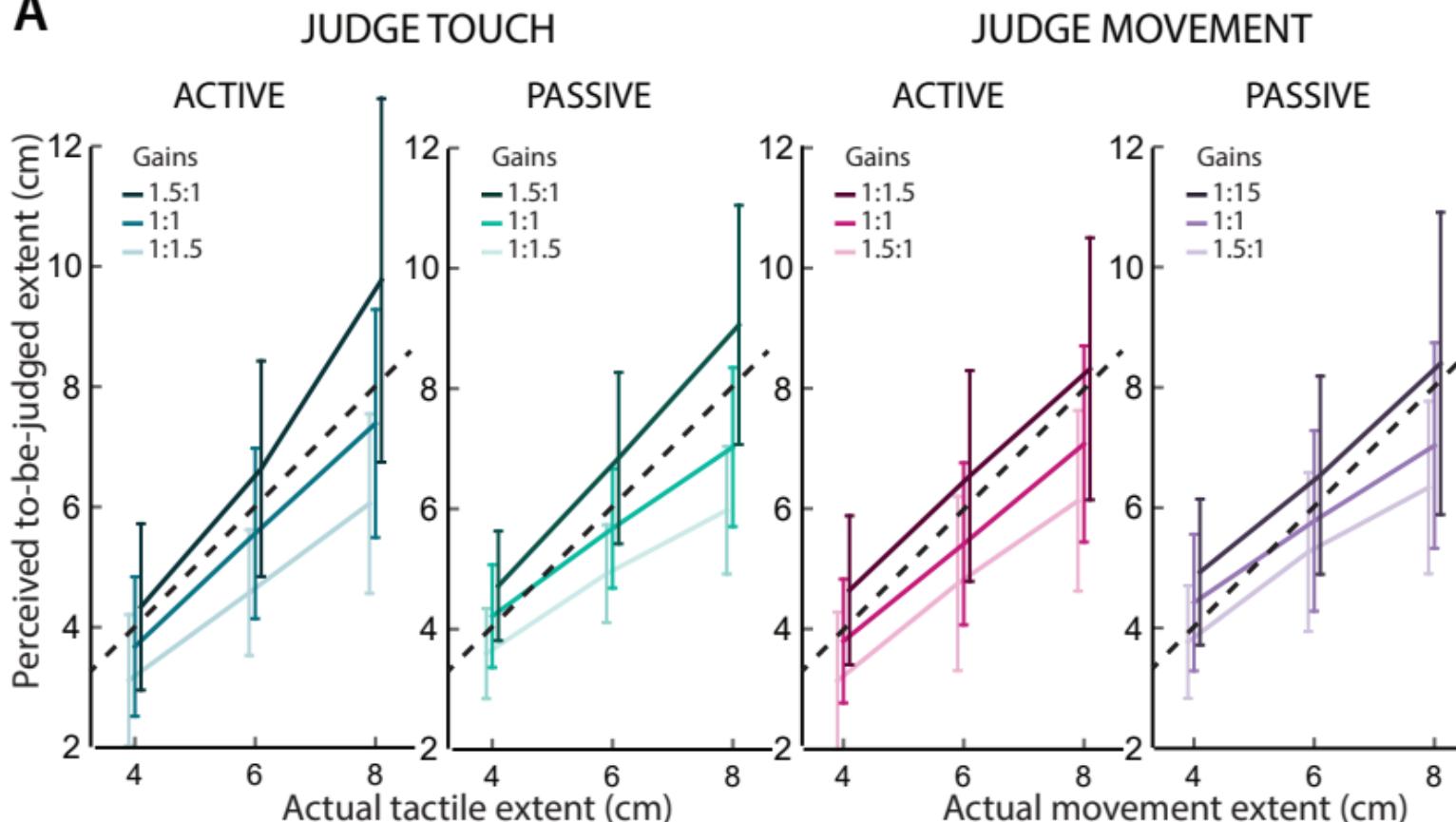
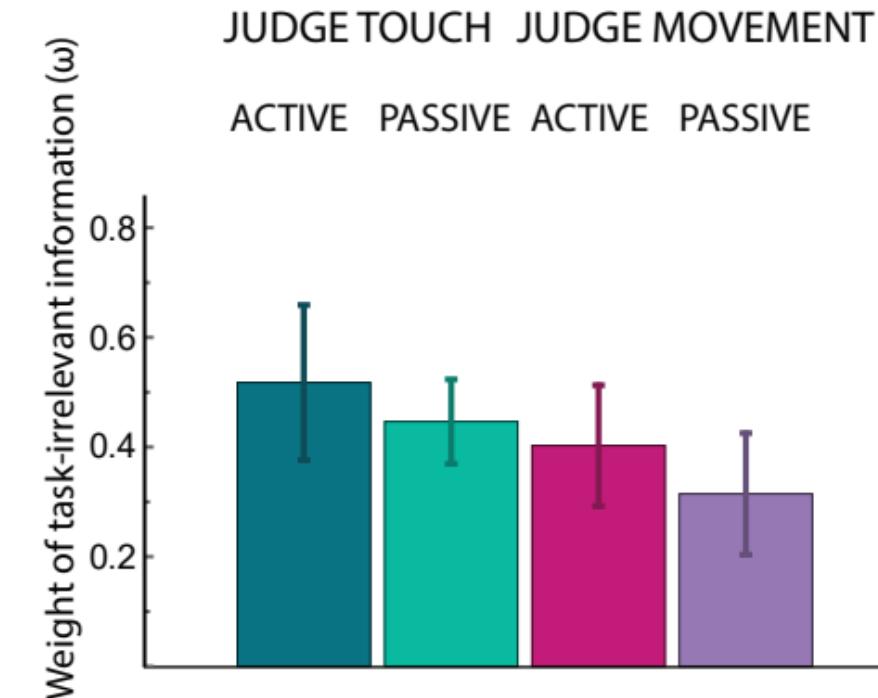
Figure 3**A****B**

Figure 4