

Sensorimotor signals underlying space perception: an investigation based on self-touch

Antonio Cataldo*^{a, b, c}, Lucile Dupin^{a, d, e}, Hiroaki Gomi^f, & Patrick Haggard^{a, e}

^a Institute of Cognitive Neuroscience, University College London, Alexandra House 17 Queen Square, London WC1N 3AZ, UK

^b Institute of Philosophy, University of London, Senate House, Malet Street, London WC1E 7HU, UK

^c Cognition, Values and Behaviour, Ludwig Maximilian University, Gabelsbergerstraße 62, 80333 München, Germany

^d Institut de Psychiatrie et Neurosciences de Paris, INSERM U1266 – Université de Paris, Paris, France

^e Chaire Blaise Pascal de la Région Ile de France, Laboratoire de Neurosciences Cognitives et Computationnelles, Département d'Etudes Cognitives, Ecole Normale Supérieure, Paris.

^f NTT Communication Science Laboratories, Nippon Telegraph and Telephone Corporation, Atsugi, Japan.

*** Corresponding Author**

Address for Correspondence: Institute of Philosophy, University of London, Senate House, Malet Street, London WC1E 7HU, United Kingdom. Tel.: +44 (0)20 7664 4865. Email address: antonio.cataldo@sas.ac.uk

Abstract

Perception of space has puzzled scientists since antiquity, and is among the foundational questions of scientific psychology. Classical “local sign” theories assert that perception of spatial extent ultimately derives from efferent signals specifying the intensity of motor commands. Everyday cases of self-touch, such as stroking the left forearm with the right index fingertip, provide an important platform for studying spatial perception, because of the tight correlation between motor and tactile extents. Nevertheless, if the motor and sensory information in self-touch were artificially decoupled, these classical theories would clearly predict that motor signals – especially if self-generated rather than passive – should influence spatial perceptual judgements, but not *vice versa*. We tested this hypothesis by quantifying the contribution of tactile, kinaesthetic, and motor information to judgements of spatial extent. In a self-touch paradigm involving two coupled robots in master-slave configuration, voluntary movements of the right-hand produced simultaneous tactile stroking on the left forearm. Crucially, the coupling between robots was manipulated so that tactile stimulation could be shorter, equal, or longer in extent than the movement that caused it. Participants judged either the extent of the movement, or the extent of the tactile stroke. By controlling sensorimotor gains in this way, we quantified how motor signals influence tactile spatial perception, and vice versa. Perception of tactile extent was strongly biased by the amplitude of the movement performed. Importantly, touch also affected the perceived extent of movement. Finally, the effect of movement on touch was significantly stronger when movements were actively-generated compared to when the participant’s right hand was passively moved by the experimenter. Overall, these results suggest that motor signals indeed dominate the construction of spatial percepts, at least when the normal tight correlation between motor and sensory signals is broken. Importantly, however, this dominance is not total, as classical theory might suggest.

Keywords

Sensorimotor interaction; space perception; self-touch; motor dominance; voluntary action.

Highlights

- Many theories of space perception give motor signals an underpinning role
- We directly tested this hypothesis using a novel, robot-mediated self-touch paradigm
- Movement, especially if self-generated rather than passive, strongly affected touch
- Crucially, touch input also affected judgements of movement
- Our results warrant a revision of strong motor-based theories of space perception

1. Introduction

Many experiences are spatial in nature. Yet, philosophers, psychologists and neuroscientists have long argued how the spatial nature of experience arises. Lotze's theory of "Local Signs" proposed that the perceived location, or "thereness", of visual and tactile objects directly originates from the motor commands that produce eye- and hand-movements, respectively (Hatfield, 1990; Lotze, 1852; Melmoth et al., 2009; for a review see Rose, 1999). This account contrasts with classical textbook explanations of position perception, which traditionally refer to cortical topographic projections. Indeed, accounts of space perception in terms of spatial projection seem circular. For example, many textbook explanations point to the somatotopic homunculus in the somatosensory cortex as an 'explanation' of spatial perception on the skin. However, this amounts to explaining space in terms of something that is itself spatial, so counts as a circular definition of space, rather than a usefully reductive definition (Ribot, 1879). Instead, some nonspatial, *intensive* signal should underlie perception of spatial *extent* (i.e. based on intensity, as opposed to "extensive", or based on extent) (Lotze and Hamilton, 1885; Lotze, 1852). The intensive parameter of motor commands required to orient to a stimulus would provide a "kinaesthetic signature" (or "*local sign*") of the corresponding stimulus location. The subjective experience that a stimulus is "just *there*" thus reduces to the muscular contraction required to orient to the stimulus and explore it, either visually or haptically (Hatfield, 1990; Lotze, 1884). The brain would then estimate the spatial distance between two visual, or two tactile stimuli based on the intensity of muscular contraction necessary to – respectively – saccade or reach from one stimulus to the another. Moving between closer objects would require less "intensive motor effort" than moving between objects farther apart. Action thus makes a constitutive, rather than a merely causal contribution to perception (Hurley, 2001). Motor dominance over perception is also supported by studies on sensory attenuation showing that motor signals reduce the perceived intensity of sensory feedback (Bays et al., 2005; Blakemore et al., 1999; Kilteni et al., 2019). This early insight may have inspired many later theories of 'active vision' (Findlay and Gilchrist, 2003; O'Regan and Noë, 2001).

Interestingly, the opposite prediction, that tactile input affects movement, has rarely been directly tested (but see Blanchard et al., 2011; Edin and Abbs, 1991; Moscatelli et al., 2019, 2016). However, the strictly reciprocal relation between motor command and sensory input (von Holst and Mittelstaedt, 1950; Wolpert and Ghahramani, 2000) clearly raises the question about why motor signals should be foundational for perception of tactile input, rather than *vice versa*. In fact, there are some clear suggestions that somatosensory information may contribute to calibration of motor signals, rather than the other way around. For example, Moscatelli and colleagues (2019) have recently shown that touch provides an important online feedback during movement, that could be used to guide motor control. In particular, sliding a finger against a ridged surface produces a robust deviation of movement, depending on the orientation of the ridges (Moscatelli et al., 2019). This result is consistent with the idea that tactile signals are actively used for kinaesthesia, motor control, and adaptation (Cluff et al., 2015; Scott, 2012; Witney et al., 2004). For example, studies on visuomotor adaptation (i.e. adaptation to spatial deviations due to altered visuomotor gains) show how visual (or other) signals can affect the spatial extent of a voluntary movement (Cohen et al., 2019; Krakauer et al., 2000; Prager and Contreras-Vidal, 2003; Tong et al., 2007; Vindras and Viviani, 2002). However, to the best of our knowledge, no study has yet directly investigated to what extent perception of spatial extent of voluntary movement is reciprocally affected by tactile and kinaesthetic signals.

We developed a novel self-touch paradigm to systematically investigate the respective contributions of tactile, kinaesthetic, and motor cues to perception of spatial extent. In ecological conditions, self-touch is characterized by spatial congruency: if we slide our right-hand finger along our left forearm, we feel that the movement sensation and the tactile sensation are linked, proportionate, and equal in extent. This recalls the *touchant-touché* situation (Bolanowski et al., 2004; Merleau-Ponty, 1976; Schütz-Bosbach et al., 2009; White and Davies, 2011). Importantly, regardless of the focus of attention, we both *know* and experience that motor and tactile experiences during self-touch have the same spatial extent. This situation offers an ideal opportunity to investigate the relative contributions of motor and tactile signals to spatial perception, if only the correlation between them could be disentangled. We have therefore

developed a master-slave robot configuration to break the normal spatial correlation between movement and somatosensory feedback (see Figure S1 in the Supplementary Material). This novel arrangement allowed us to 1) quantify the contribution of motor signals to tactile spatial perception, 2) equally, quantify the contribution of tactile signals to the perception of motor extent, and 3) disentangle the respective contributions to spatial perception of afferent kinaesthetic information , and of efferent motor command underlying voluntary movements.

2. Materials and Methods

2.1 Participants

The sample size ($n = 24$) was decided *a priori* on the basis of the results of two previous similar experiments (see <https://osf.io/eybdh>).

Twenty-seven right-handed healthy participants (20 female) took part in the experiment (mean age \pm SD: 22 ± 3.6). Based on exclusion criteria established *a priori* (see <https://osf.io/eybdh>), three participants were excluded during the training phase, because they proved unable to use the robotic device to produce smooth self-stimulation movements. Thus, the final sample size was 24.

The experimental protocol was approved by the research ethics committee of University College London. Recruitment of participants and experimental procedures were conducted in accordance with the Declaration of Helsinki. All participants were naïve regarding the hypotheses underlying the experiment. All participants provided their written informed consent before the beginning of the testing, after receiving written and verbal explanations of the purpose of the study.

2.2 Apparatus

Figure 1 shows a schematic representation of the setup. Participants sat in front of a computer screen with their left arm on a fixed moulded support, and their right arm on an articulated armrest support (Ergorest, series 330 011, Finland). Both the participants' arms, and the robotic setup were covered by a horizontal screen and remained unseen throughout the experiment. The sensorimotor stimulation was implemented using two six-degrees-of-freedom robotic arms (3D Systems, Geomagic Touch X, South Carolina, USA) linked as a computer-controlled master-slave system. In this system, any 3D-movement of the right-hand master robot is reproduced by the slave robot, which carries a paintbrush that strokes the participant's left forearm. To estimate the lag between master and slave, we measured the time taken for the slave device to reach successively sampled positions along the forward movement axis of the master device, in each

trial of the experimental dataset. The mean lag was 2.47 ms (SD across participants 0.62 ms). Participants held the handle of the master robot with their right hand and performed repeated, proximo-distal movements with the right hand. A soft flat paint brush (12.7 mm) attached to the handle of the slave robot stroked the dorsum of the participants' left forearm providing a gentle tactile stimulation proportional to the movements of the master robot. Thus, moving the master handle back and forth with the right hand produced the percept of stroking one's own left forearm with a brush (see https://osf.io/gcvbm/?view_only=b530e560d121479db7156b4be2a27451 for a video demo of the setup). Importantly, manipulating the gain between the master and slave robot allowed us to decouple the spatial relationship between movement and touch, without affecting the temporal sensorimotor association typical of self-touch. In particular, changing the gain lead to changes in the speed, so that the master and slave movements started synchronously and ended synchronously in all cases (see Supplementary Figures S2 and S3 for details on the kinematics of the robots across conditions).

Participants chose for themselves the onset time and speed of the right-hand movements. However, the extension of each movement was controlled as an experimental factor. Two “virtual walls” were created using the force-feedback system of the robots. Participants then made a voluntary movement from the front wall to the back wall, then returning again to the front wall. The position of the front walls was fixed throughout the entire experiment, while the position of the back walls changed from trial to trial according to the specific motor and tactile extents intended for each trial. We thus produced all possible combinations of 3 movement extents for the right hand (6, 8, or 10cm) and three extents of stroking applied to the left hand (6, 8, or 10cm). We sampled randomly and equiprobably from these 9 possible conditions. The master-slave arrangement guaranteed that movement and stroking always began and ended at the same time, even when their spatial extents differed. All movements were confined to the anteroposterior axis of the forearm.

Because the master-slave robot system gave us experimental control of the relation between the extent of movement and the extent of stroking, we could break the strict spatial

congruence between movement and tactile input that characterises normal self-touch. Specifically, the movement participants made and the stroking sensation that they felt could be spatially decorrelated under experimental control.

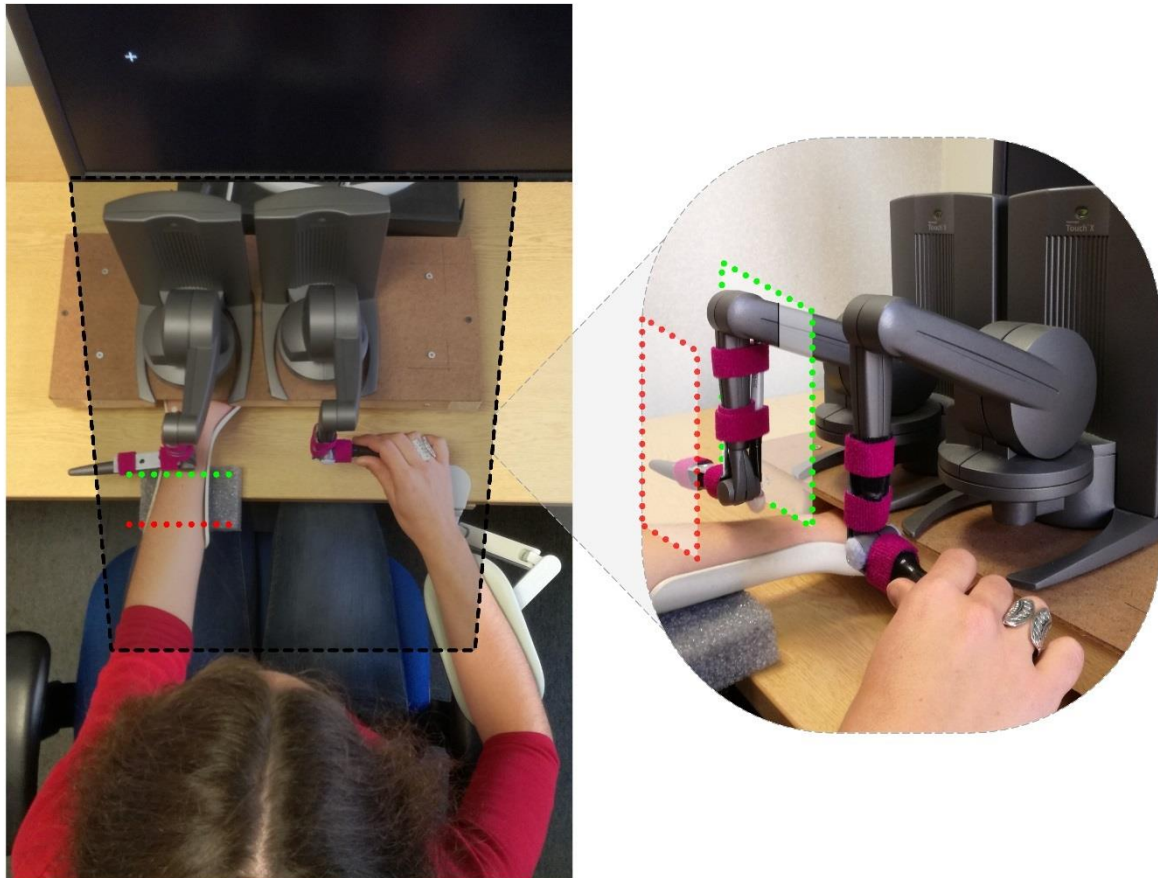


Figure 1. Experimental setup for self-touch stimulation.

Participants moved the handle of the master robot with their right hand and simultaneously felt a corresponding stroke on the left forearm from a brush attached to the slave robot. A horizontal screen (black dashed line) covered both the participants' arms and the robotic setup throughout the experiment. The physical lengths of movement and tactile feedback were independently modulated via two "virtual walls" (red and green dotted lines/planes; planes are only shown for the tactile sensation for clarity reasons). In the active movement condition, participants produced straight back-and-forth movements between the front wall (green dotted line/plane) and the back wall (red dotted line/plane). In the passive movement condition participants maintained their arm as relaxed as possible, while the experimenter held the vertical arm of the master robot and moved back-and-forth between the walls, thus passively displacing the participant's right hand, which continued to grip the tip of the robot with the fingers of the right hand. After sensorimotor

stimulation, participants reported the perceived length of either their own movement (judge movement block) or the tactile sensation (judge touch block) by adjusting the length of a line presented on a computer screen using foot pedals. See https://osf.io/gcvbm/?view_only=b530e560d121479db7156b4be2a27451 for a video demo of the setup.

Participants were instructed to judge in separate blocks either the spatial extent of the right hand's movement, or the spatial extent of the stroke felt on the left forearm. Participants reported judgements of extent using a foot pedal to adjust the length of a line presented on a screen, in order to match the length of either the right-hand movement or the tactile sensation on their left forearm. An additional important factor in our design was the mode of right-hand movement. In the *active* movement condition, participants made voluntary movements to move the master robot between the nearer and farther wall. In the *passive* condition, the participant again held the end-effector of the master robot, but did not actively move it. Instead, the experimenter also gripped another part of the slave robot, and then applied the force required to move it smoothly between the front and back wall, matching as closely as possible the movements that participants had been trained to make in the active condition. This factor was blocked, with active and passive movements being tested in separate conditions.

2.3 Experimental design and procedure

The factors of judgement (judge movement/judge touch) and movement type (active/passive) were blocked and counterbalanced across participants. The spatial extent of the to-be-judged events (movement, or stroke) was randomised. Thus, each participant performed all the 36 different conditions derived from our 2 (Judgement type: judge touch, judge movement) x 2 (Movement type: active, passive) x 3 (Length of the to-be-judged stimulus: 6, 8, 10cm) x 3 (Length of the task-irrelevant stimulus: 6, 8, 10cm) within-subjects design. Each of the 36 cells of this design was experienced six times, for a total of 216 trials per participant, corresponding to a testing session lasting approximately one hour. The testing was divided into 8 blocks of 27 trials each, and breaks were allowed between blocks.

At the beginning of the experiment, participants were familiarised with the experimental setup by performing a few free movements with their right hand, and feeling the simultaneous tactile feedback from the slave robot on the left forearm. Next, a training phase took place for either movement condition (active or passive), depending on the starting condition of each participant. In the active movement condition, participants were instructed to perform a back-and-forth movement of the right hand from the distal wall to the proximal wall, then returning to the starting position. Participants knew the position of the virtual walls because of the haptic feel of touching the wall, which was augmented by a beep. In the passive movement condition, instead, the master handle was moved by the experimenter in the same back-and-forth trajectory described for the active condition. Participants were asked to hold the master handle with their right hand and to follow completely passively the movements produced by the experimenter. In particular, they were asked to relax the muscles of their right arm and to rest their arm completely on the articulated armrest support. This allowed the experimenter to smoothly move the participant's right arm along with the robot handle, providing the same kinaesthetic information as in the active condition, but in absence of any motor command. In both conditions, both participants' arms and robots were occluded by a horizontal baffle, and participants fixated a cross presented on a computer screen throughout.

The training phase was actively supervised by the experimenter, and participants practiced the movement until they were able to reliably produce a smooth, straight line from wall to wall in the active condition. To make sure that participants remained as passive as possible in the passive condition, "catch movements" were introduced during training. In these trials, the experimenter unpredictably changed the speed or the direction of the movements, so as to feel if the participant was actively contributing to the movement. If that was the case, the experimenter produced a series of movements in random directions, to encourage the participant to remain as passive as possible. The number of catch movements varied for each participant, depending on their capacity to relax their muscles and allow the experimenter to move their arm without any active muscle contraction.

Each training phase ended with a practice block (10 trials) of the spatial extent judgement task. Participants were asked to focus only on the “to-be-judged” experience of the block – either the extent of the right hand’s movement, or the extent of the stroke on the left forearm, as appropriate - and to ignore the other sensation. For example, in the “judge touch” block, participants attended to the length of the tactile sensation on the left forearm and neglected the right-hand movements. After each active or passive movement, the fixation cross on the screen was replaced by a line of a random length (between 4 and 10 cm). Participants then used two foot-pedals to adjust the length of the line on the screen in order to match the length of either the movement or the tactile sensation, according to condition. Fixation cross and matching line were aligned with the participants’ left arm in the case of the “judge touch” task, and with the participants’ right hand in the case of the “judge movement” task, to control for spatial attention. After adjusting the length of the line, participants clicked a button on the handle of the master robot to confirm their response and start a new trial. In all trials of the practice block, movements and tactile feedback were 8 cm in length, so the spatial correlation of natural self-touch was continuously present.

The main testing phase was identical to the training phase, except that the master and slave robots had one of the nine possible combinations of movement (6, 8, 10 cm) and tactile extent (6, 8, 10 cm). This allowed us to investigate the perceived extent of the to-be-judged sensation (e.g. touch in the “judge touch” task), as a function of the task-irrelevant spatial extent of the other, task-irrelevant event (e.g. movement in the “judge touch” task).

2.4 Statistical analysis

For our main analyses, we fitted the following model to quantify the effect of the task-irrelevant length information on the to-be-judged length.

$$\mathbf{JudgedLength} \sim \mathbf{Scale}_{\text{Indiv}} ((1 - \omega) \mathbf{ToBeJudgedLength} + \omega \mathbf{TaskIrrelevantLength}) \quad (1)$$

Where $Scale_{Indiv}$ is an individual scaling factor to capture participant's cross-modal mapping from motor/tactile stimulation extent to visual line response, ω is the weight of the task-irrelevant length ($TaskIrrelevantLength$) on the judged length of $ToBeJudgedLength$ information. We did not fit any intercept in this model, since we assumed a judged distance of zero in the absence of any actual spatial stimulation (Eisenhauer, 2003; for a similar approach in perceptual judgement tasks, see Leib et al., 2016). In this model, $\omega = 0$ would correspond to the situation where the participant would report the target length independently from the task-irrelevant information (e.g. no effect of movement on touch in the “judge touch” task). Conversely, $\omega = 1$ would mean that the participants' to-be-judged length perception is entirely based on the task-irrelevant information (and, since to-be-judged and task-irrelevant lengths were uncorrelated, not at all on the to-be-judged information). Finally, a weight between 0 and 1 would indicate the partial integration of task-irrelevant information in judged length. Fitting this model allowed us to calculate a single summary numerical value from all the raw judgement data, capturing the influence of movement on touch, and another value capturing the influence of touch and movement¹.

To investigate the effect of movement on tactile perception, and vice versa, we then analysed these weights using a 2 x 2 repeated measures ANOVA with factors of Judgement type (“judge touch”, “judge movement”) and Movement type (active, passive). All data used in the ANOVA followed normal distribution (Kolmogorov-Smirnov test, all $p > 0.13$). The ANOVA was computed using IBM SPSS Statistics 23 while other statistical analyses including model fitting were computed using Wolfram Mathematica 10.1. Data normality was verified using Pearson's Chi² test prior to performing t-test comparisons.

In addition, a full ANOVA model was fitted with the pre-registered design (see <https://osf.io/gcvbm/>). The analysis of raw data (Figure 2A-D and table S1 in the Supplementary

¹ This approach constrains the influences of $TaskIrrelevantLength$ and $ToBeJudgedLength$ to sum to 1. For transparency, we mention that this constraint was not explicitly declared in the pre-registration. The pre-registration referred to 2x2 ANOVA on the summary measure expressing the influence of the not-judged event.

Material) and of model weights (Figure 2E) are essentially similar, with model weights giving a clearer focus on the mutual influences between movement and touch.

Finally, we calculated the precision of judgements in each condition of our 2 x 2 design. Precision was defined as the inverse sample variance of the six replicates of each combination of distance, judgement type and movement type. We used the precision data to test whether the weightings of tactile and movement signals in self-touch were related to precision in each condition.

3. Results

3.1 Effect of the task-irrelevant information on perception of the judged/target length

First, we quantified the weights of the task-irrelevant information (i.e. weight of movement length when the task was to judge tactile length and vice-versa) in the four experimental conditions (judge touch/movement x active/passive) using the model (1). Results of ω for each participant are detailed in Table S2 in the Supplementary Material.

A strong motor-based theory of space perception makes two key predictions about this situation. First, it predicts a strong influence of movement on tactile length (i.e. a weight $\omega > 0$ for movement in the “judge touch” task), but much less, or zero, influence of tactile stroking on perception of movement (i.e. a weight $\omega = 0$ for touch in the “judge movement” task). To test these predictions, we ran one-sample, one-tailed t-tests on the weight of the task-irrelevant information in the four conditions (task x movement type).

Effect of movement on tactile extent judgement - “Judge Touch” tasks

In the case of the effect of movement on touch (“judge touch”) weights ω were significantly greater than 0 (active: 0.56 ± 0.16 , $t_{23} = 17.1$, $p < 0.0001$; passive: 0.46 ± 0.15 , $t_{23} = 15.1$, $p < 0.0001$). That is, when participants are instructed to judge the spatial extent of tactile stroking, they are nevertheless influenced by the extent of the movement that caused the stroking, even though this is task-irrelevant. This result is predicted by theories of the motor basis of spatial perception. However, the effect of movement information was partial since ω s were also significantly lower than 1 (active $t_{23} = 13.6$, $p < 0.0001$; passive: $t_{23} = 17.7$, $p < 0.0001$,). Thus, judgements of tactile extent are not entirely based on motor information.

Effect of touch on movement extent judgement - “Judge Movement” tasks

When participants had to judge the length of their movement, weights were also significantly greater than 0 (active: 0.36 ± 0.13 , $t_{23} = 13.1$, $p < 0.0001$; passive: 0.43 ± 0.16 , $t_{23} = 13.1$, $p < 0.0001$), indicating that judgements of movement extent were significantly influenced by task-

irrelevant information about the extent of self-induced tactile stroking. The effect of movement information was again partial since ω s were significantly lower than 1 (active $t_{23} = 23.5$, $p < 0.0001$ passive: $t_{23} = 17.5$, $p < 0.0001$).

Thus, significant integration of tactile and movement information took place in all the four experimental conditions. Participants were unable to judge extent based only on the right-hand motor or left arm tactile input to which they were asked to attend, but were consistently and automatically affected by the other signal.

We next ran a 2 x 2 repeated measures ANOVA on the weights of task-irrelevant information ω to investigate the effect of movement on tactile perception (and vice versa) in both active and passive movement conditions. The analysis showed a significant main effect of Judgement type ($F_{1,23} = 6.60$, $p = 0.017$, $\eta_p^2 = 0.22$): the interfering effect of movement length when judging touch was (mean \pm SD: 0.51 ± 0.15) was significantly higher than the effect of tactile information on judgements of movement (0.39 ± 0.15). There was no significant main effect of Movement type ($F_{1,23} = 0.32$, $p = 0.58$). Interestingly, the interaction between the two factors was significant ($F_{1,23} = 17.45$, $p < 0.001$, $\eta_p^2 = 0.43$). This interaction was further explored by post hoc “simple effects” testing. First, we compared active and passive conditions within each level of the judgement factor. When judging touch, we found significantly higher weights (indicating stronger interfering effects of movement) for active than for passive movements (0.56 ± 0.16 ; 0.46 ± 0.15 ; $p = 0.002$). In contrast, when judging movement, we found significantly *lower* weights for active than for passive movements (0.36 ± 0.13 ; 0.43 ± 0.16 , $p = 0.045$). Next, we investigated the effect of judgement task for active and passive movements separately. For active movements, we found significantly higher weights (indicating stronger influence) when judging touch than when judging movement (0.56 ± 0.16 ; 0.37 ± 0.13 ; $p = 0.001$). For passive movements, we found no difference between weights when judging touch and when judging movement (0.46 ± 0.15 ; 0.43 ± 0.16 ; $p = 0.49$).

We also analysed the precision of extent judgements, using the same 2x2 design. We found no significant effect of judgement type ($F_{1,23} = 0.03$, $p = 0.864$), or of movement type ($F_{1,23}$

= 0.89, $p = 0.769$), but a significant interaction between these factors ($F_{1,23} = 7.379$, $p = 0.012$, $\eta_p^2 = 0.243$). The interaction arose because making active vs. passive movements increased the precision of tactile extent judgements, but decreased the precision of movement extent judgements. The lack of main effects indicates absence of evidence for a general difference in the difficulty of the two judgement types, and of the two movement conditions. On the assumption that attention enhances perceptual judgements, the pattern of interaction cannot readily be explained by the idea that participants' attention is drawn to the limb that they actively move.

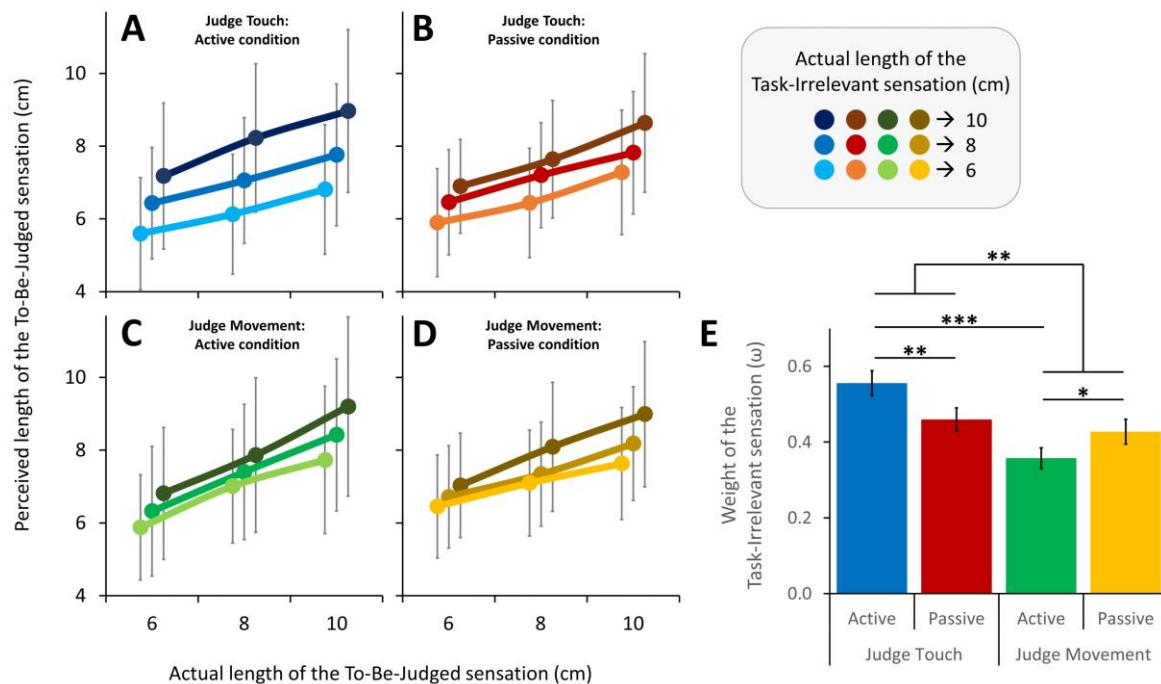


Figure 2. Results.

A-D: Perceived length of the to-be-judged sensation as a function of its actual length and of the actual length of the task-irrelevant sensation. The spread between the coloured lines in each panel (A-D) represents the effect of the task-irrelevant sensation on spatial perception. That is, if the task-irrelevant sensation had no effect on participants' spatial judgements, the three coloured lines in each panel should superimpose. In the "judge touch" task (A-B), the physical length of the movement significantly affected the perceived length of tactile stroking, as

predicted by the Local Sign theories. The effect of movement on touch was significantly stronger when participants' movements were self-generated (**A**) compared to when they were passively produced by the experimenter (**B**). Importantly, in the "judge movement" task (**C-D**), the perceived length of the participant's movement was also significantly affected by the physical length of the task-irrelevant tactile sensation, although to a lesser extent than in **A-B**. **E**: The weighting of the task-irrelevant sensation in spatial perception was calculated in each condition. Error bars represent the standard error of the mean.

3.2 Correlation between judgements of movement and judgements of touch

We additionally explored correlations that might reveal trait factors underlying automatic integration of touchant and touché. First, we reasoned that a negative correlation between the weights of the unjudged signal in the judge touch and judge movement conditions would be consistent with a trait factor that biased each individual either towards movement or towards touch. For example, a strongly motor-dominant individual would have a high weighting of motor information when judging touch, but a low weighting of tactile information when judging movement. A positive correlation would be interpreted rather differently, since it implies a trait factor common to both modalities, perhaps reflecting a general strength of automatic integration, or an inability to selectively attend to just one of the two components self-touch. Thus, a participant who had high weightings both when judging movement, and when judging touch, would be effectively unable to select just the task-relevant source of information while excluding the other source, thus showing strong automatic integration. Conversely, a person with generally excellent selectivity would have low weightings both when judging action and when judging touch. Put another way, positive correlation would be consistent with individual differences in the extent to which distinct touchant and touché components were merged into an irreducible perceptual experience. In fact, we found a negative correlation between judge movement and judge touch conditions, for active movements ($r = -0.53$, $p = 0.015$, see Figure 3), but no correlation for passive movements ($r = -0.03$, *NS*, not shown, Bonferroni-corrected for two

comparisons). A clear individual difference factor thus appears to be the extent to which active motor signals dominate over tactile feedback, or vice versa.

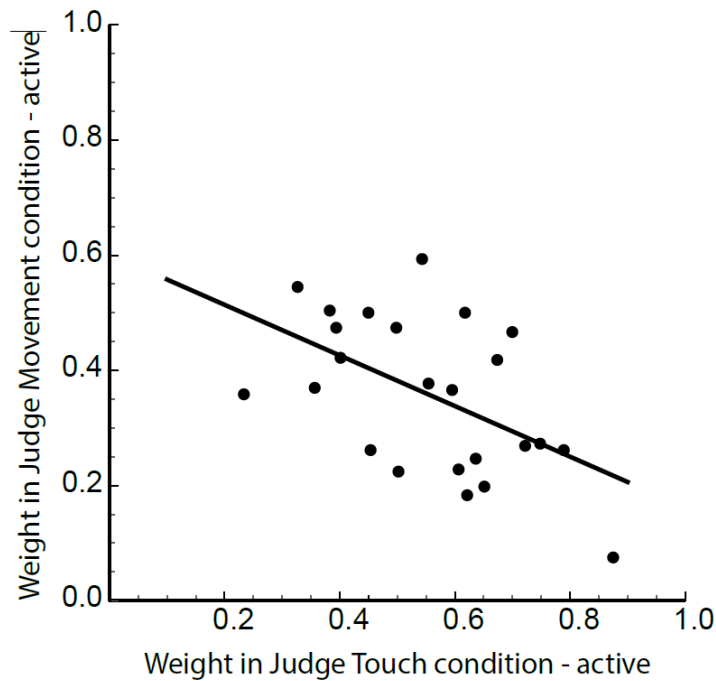


Figure 3. Correlation between judgements of movement and judgements of touch.

The weights of the TaskIrrelevantLength in the active condition of the judge movement and judge touch tasks were inversely correlated ($r = -0.53$, $p = 0.015$), consistent with individual differences in some factor determining whether motor signals dominate over tactile feedback, or vice versa.

	Active Movement	Passive Movement
Judge Movement	1.23 (SD 0.62)	1.53 (SD 0.67)
Judge Touch	1.52 (SD 0.89)	1.29 (SD 0.64)

Table 1. Precision (in $1/\text{cm}^2$) of spatial extent judgements for each cell of the 2 x 2 factorial design.

4. Discussion

The present study examined two important issues concerning the nature of human space perception: (1) whether the interaction between tactile and motor information is unidirectional, as postulated by action-based theories of space, and (2) whether afferent kinaesthesia and efferent motor signals differ in the way they combine with tactile spatial information. To investigate these questions, we measured perception of spatial extent in a novel self-touch paradigm where the normal overlap between sensorimotor signals was artificially disrupted. The lack of correlation between the tactile feedback and the movement that caused it provided a unique opportunity for a baseline test of how motor, kinaesthetic, and tactile signals contribute to space perception. While these signals are perfectly correlated in normal life, our experiment abolished this correlation, allowing us to see if one signal would ‘naturally’ influence perception of the other. A positive result would provide a new way of investigating dominance and priority among sensory signals. Specifically, it would provide a direct test of the classical view that perception of spatial extent depends on information about amplitude of motor commands (Lotze, 1852). This idea has dominated psychological accounts of space for over 150 years. For example, current accounts of spatial perception are based on integrating locomotor signals (Hartley et al., 2014). Active motor exploration is commonly used to build up perceptual representations of the spatial world (Canzoneri et al., 2013; O’Keefe and Nadel, 1978; Serino et al., 2007). However, the stronger claim that all spatial percepts depend ultimately on motor signals, while often assumed, has rarely been tested directly.

We manipulated participants’ attentional focus in a self-touch situation, by asking them to report either the extent of their movement, or the extent of the tactile stroke that the movement produced. We measured the degree of influence of the task-irrelevant event on the to-be-judged event, as a proxy for automatic integration between touchant and touché signals. We also manipulated whether the right hand’s movement was actively or passively produced. We found that judgements of spatial extent of movement, or of spatial extent of touch, were never purely driven by one of these inputs, but were always influenced by transfer of spatial information from

the other modality, that is, from the other hand. Participants' judgments of spatial extent of touch on the left forearm were influenced by the amplitude of the right-hand movement that caused the tactile stimulation. Equally, their judgements of right-hand movement extent were influenced by the extent of the resulting tactile stimulation of the left forearm. This result carries three important implications for spatial perception. First, it implies an integration between the two components of the touchant-touché situation. Perception of tactile and motor space were substantially interdependent, even though our unusual experimental situation had completely abolished the normally perfect statistical correlation between movement and sensation. Second, it implies a strong inter-hemispheric cross-talk between the left hemisphere handling movement information and the right hemisphere handling tactile information. Third, our result implies an automatic mutual influence between spatial information from motor and sensory sources – even though information from the to-be-judged modality was irrelevant and unhelpful for the perceptual task, it still contributed strongly to participants' experience of spatial extent. In this sense, our experimental results confirm the philosophical intuition that self-touch generates a synthetic percept that involves an indissoluble interaction between movement and touch, rather than a mere superposition of two signals (Merleau-Ponty, 1976). Analyses of the precision of repeated judgements suggested that the two judgement conditions were comparable in difficulty, as were the two movement conditions. The same analyses suggested that any attentional demands of movement could not readily account for differences in mean perceptual judgements.

4.1 Implications for spatial perception

We noted that action-based theories of space perception, such as Local Sign theories, would predict a strong influence of movement extent when judging touch, but no influence of tactile extent when judging movements. Moreover, this asymmetric influence might be stronger for an active than a passive movement condition, reflecting the priority of efferent signals for space perception according to “outflow” theories (Mach, 1897; Southall, 1962; von Helmholtz, 2013).

We confirm the strong influence of movement on tactile perception, as local sign theories predict. However, we also found a strong effect of tactile extent on movement perception, contrary to local sign theories. Interestingly, the former effect was statistically stronger than the latter, providing some *relative* support to local sign theories. Most importantly, we found that the asymmetric influence between judging movement and judging touch was strong for active movement, but was small and statistically non-significant for passive movement, leading to the 2-way interaction of Figure 2E. This interaction supports the particular subset of local sign theories that emphasise the foundational role of *effluent command* signals for spatial perception. In particular, local sign theories argue that perception of spatial extent is based on an *intensive*, non-spatial motor signal. In principle, proprioceptive feedback from the moving arm could also contribute to founding spatial perception. However, the contribution of right-hand movement extent to judgements of tactile extent on the left arm should then be comparable in active and passive conditions, since proprioceptive information is comparable in both cases. In fact, we found much stronger effects for active than for passive movement. This difference could be interpreted in one of two ways. Either proprioception is incapable of providing a foundation for spatial perception, or, alternatively, proprioception is a more reliable signal during active than during passive movement. Interestingly, studies of kinaesthetic perception offer important support for the latter interpretation (Azuma and Haggard, 1999; Gandevia et al., 2006; Paillard and Brouchon, 1968; Proske and Gandevia, 2012; Smith et al., 2009).

Our results thus offer some support for a foundational role of movement in space perception. Nevertheless, we found that effects of tactile extent on movement perception were always well above zero. This is not predicted by local sign theories. Clearly, everyday experience shows that people may have percepts of spatial extent in the absence of any overt movement. Local sign theory could still insist on a foundational role of motoric information for spatial perception, arguing that the sensory stimulation in such cases has *previously* been associated with a corresponding movement (e.g., stimulation of a retinal location may have been associated with the saccade to fixate that location) (Wundt, 1862). By association, sensory stimulation alone will therefore evoke the previously-associated motor command or motor

representation, even when actual movement is absent. Any actual movement should presumably provide a much stronger motor signal than a mere motor memory, or unexecuted motor representation. Yet, we nevertheless found that tactile extent influences judgements of a concurrent active movement. If percepts of tactile extent are derived from motor commands, as local sign theory implies, it is hard to see how this tactile-to-motor influence could arise.

Importantly, we used a robotic environment to break the correlation between motor and tactile extent that normally exists in self-touch, and that underpins local sign theories more generally. Although our experimental situation differs from everyday skin-to-skin self-touch in some respects – notably the mediation by a master-slave robot device – it is analogous to it in important ways. First, tool-mediated self-touch is an extremely familiar action in everyday life (e.g. brushing make-up powder on our cheeks, shaving our face, combing our hair, scratching our arm with a pen, etc). Second, numerous studies of tool use suggest a neural plasticity by which the brain processes indirect tool-mediated touch in ways that overlap substantially with direct touch processing (Canzoneri et al., 2013; Farnè and Làdavas, 2000; Miller et al., 2018; Serino et al., 2007). Similarly, several studies show that indirect or transformed spatial-motor relations are readily learned and relearned (e.g. Stratton’s (1896) famous inverting spectacles; see also (Imamizu et al., 2000). Finally, our setup has clear similarities with the classical (Botvinick and Cohen, 1998) and the motor (Hara et al., 2015) rubber hand illusions. In these situations, proprioception readily adapts so that the difference in spatial location is effectively nulled by a recalibration procedure. Hence, we believe that the spatial discrepancy between the moving hand and the tactile sensation on the arm in our setup did not play any major role for the key research question of our study.

4.2 Automatic integration of motor and tactile signals

In our experiment, tactile and motor extent were randomly and independently chosen on each trial. This design has three important consequences. First, it means that any influence of touch on movement perception or vice versa represents automatic integration, rather than functional perception of relevant additional information. For example, our design prevents people using

movement extent as a convenient proxy for tactile extent, or vice versa. Second, in such conditions, the brain cannot build the consistent association between spatial perception and motor command on which some versions of local sign theory depend (Wundt, 1862). Third, while in most naturalistic self-touch conditions people can decide the extent of their movement *before* moving (i.e. people might perceive a touch on the arm to be about 8 cm in extent *because* they have *decided* to perform an 8 cm movement in the first place), our participants did not have this possibility. Rather, the extent of their own movements was always constrained by the virtual walls of the robotic setup and was completely unpredictable

Nevertheless, we do find evidence for a strong effect of voluntary movement on tactile spatial perception in our data. Clearly, this cannot reflect consistent association between motor and tactile extent learned during the course of the experiment, since there was no statistically reliable relation between movement and tactile extents. Alternatively, it might reflect a residual effect of previous experience of correlations between movement and touch, obtained prior to the experiment – though the specific combination of hand movement and forearm stroking that we have used is rare in everyday life. Thus, our results would favour a hard-wired, rather than an acquired, dominance of motor information over sensory spatial information, in line with a nativist rather associationist version of local sign theory. However, the support for local sign theories is incomplete. We also found effects of touch on movement perception that are difficult to explain according to classical theories, since these theories reduce spatial perception to movement signals. Our results suggest that sensory representation alone may be sufficient to ground some intrinsic spatial perceptual qualities, independent of motor information.

We performed additional correlations to explore the basis of automatic integration. We found that participants who showed strong influence of active movement on tactile judgement tended to show weak influence of tactile judgement on active movement, and vice versa. This suggests a factor of modality-dominance in automatic integration. For some individuals, motor signals would dominate the automatic integration of the synthetic percept underlying judgements of spatial extent, while tactile signals would dominate for other individuals. Interestingly, this negative correlation was absent in passive movement conditions, suggesting it may reflect

individual variability in the strength or accessibility of an efferent motor signal. Importantly, we did find evidence for strong individual differences in the extent of automatic integration itself, with some individuals integrating strongly and others maintaining more distinct representations of movement and touch. Strong variation in the degree of integration would imply a positive correlation between the influence of movement on touch, and of touch on movement – yet a negative correlation was found. Thus, the main source of variation across our participants appeared to be in *which signal* dominated the integration process, with the degree of integration itself being less variable. These exploratory analyses should be confirmed in future studies.

4.3 Relation to optimal integration frameworks

Current theories of multisensory perception are based on optimal integration of multiple sources of information. Each source of information is weighted according to its reliability or precision (Ernst and Banks, 2002). Self-touch has some features in common with classic multisensory perception scenarios. For example, many theories emphasise the integration between motor and tactile signals (Merleau-Ponty, 1976) – a finding supported by our quantitative analyses. However, our results cannot simply be reduced to another instance of optimal integration in perception, for two reasons. First, optimal integration studies involve perceptual judgements about a *single source object*, which gives rise to two or more sensory signals (Cao et al., 2019). That is not the case here: participants are explicitly told to select one event for judgement, and ignore the other. There is no single source object that the participants aim to perceive. As a result, any cue integration necessarily reduces task performance, making an important contrast with optimal integration frameworks. Our results may be better explained by interference in judgement of one sensory event, due to automatic (and unhelpful) integration of another task-irrelevant event.

Second, optimal integration is based on the idea of weighting cues according to their precision. However, the differences in precision across the conditions of our 2 x 2 design cannot explain the pattern of weightings shown in Figure 2E. Optimal integration theory predicts that high precision should lead to high weighting in any integration stage. Traditionally, this involves

using the precision of each unisensory signal as a weighting when estimating the mean of multisensory judgements (Ernst and Banks, 2002). We could not perform this traditional test, since we did not obtain touch-only or movement-only judgements. However, we found that tactile extent judgements were more strongly influenced by active than by passive movements. Optimal integration theory might seek to explain finding in terms of lower precision of tactile information and/or higher precision of movement information in active vs passive conditions. In fact, however, tactile judgements showed higher precision for active vs passive conditions, while movement judgements showed lower precision for active vs passive conditions. That is, contrary to optimal integration theory, more precise signals did not appear dominate in the (automatic) integration processes that gave rise to our results.

Thus, while self-touch clearly involves a strong element of integration between signals, conventional optimal integration frameworks cannot straightforwardly explain our results. This may be because of the selective perceptual task that we gave our participants. Since we instructed them to separate tactile and motor signals, rather integrate them. The core assumption of optimal integration, namely that of a single common source object, may therefore not apply here. In future studies, it would be interesting to compare judgements of the same motor and tactile events, in matched perceptual tasks requiring either separation or integration.

Self-touch provides an interesting situation where the sensorimotor system is both the agent, and the sentient recipient of action. Agency is based on the integration of efferent and afferent sensorimotor information (Blakemore and Frith, 2003; David et al., 2008; Haggard, 2005; Jeannerod, 2009). In our experiment, efference copy of participants' movements would provide an extra signal, parallel to kinaesthesia, carrying additional information about the spatial property of the movement (Wolpert and Ghahramani, 2004). Thus, in the active condition of our "judge touch" task, there are potentially two signals that might influence perception of tactile extent: kinaesthetic afference and motor efference copy. The greater influence of motor information in active compared to passive conditions when judging touch may reflect this additional information from the right hand. This result is in line with reports that the interaction between active movements and touch can strongly affect body representations (Dummer et al.,

2009; Hara et al., 2015; Kalckert and Ehrsson, 2012; Kammers et al., 2009; Suzuki et al., 2013). For example, using a setup similar to ours, Hara et al. (2015) have shown that voluntary self-touch increases body ownership. Similarly, our effect of motor dominance over tactile space perception recalls studies on tactile attenuation showing that motor signals affect the perceived tactile intensity (Bays et al., 2005; Blakemore et al., 1999; Kilteni et al., 2019). However, although the attenuation theory, in its most extreme form, would suggest no tactile perception on the touched hand at all, early studies recognised that spatial perception appears unaffected (Williams et al., 1998).

4.4 Relevance for sense of self

Finally, our results shed new light on the touchant-touché self-touch situation itself. Touchant-touché is a key example in the philosophical literature on phenomenology of bodily awareness. However, experimental studies of the perception of self-touch are surprisingly rare (but see Bolanowski et al., 2004; Schütz-Bosbach et al., 2009; White and Davies, 2011). The philosophical literature emphasises integration of the two components of the self-touch situation into a single synthetic percept. Our findings broadly agree with this finding. In particular, we show that the integration involves an automatic integration between the touchant and the touché components leading to an unavoidable influence of one component on the other: participants in our task were required to judge just one of the two components, yet were always strongly influenced by the other, irrelevant component, even though this in fact interfered with their performance on the perceptual task. This automatic integration during self-touch contrasts strikingly with the normal ability to selectively orient to tactile information on just one hand (Farne et al., 2000). Thus, our results are consistent with the idea that the synchronized experiences generated by self-touch provide a powerful integration of multiple sensory and motor signals. This integration may underpin the distinctive experience of the body as a coherent, unified self.

CRedit author statement

Antonio Cataldo: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Visualization, Funding Acquisition. **Lucile Dupin:** Conceptualization, Methodology, Software, Formal Analysis, Writing – Review & Editing. **Hiroaki Gomi:** Resources, Writing – Review & Editing, Supervision. **Patrick Haggard:** Conceptualization, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition.

Funding

AC was supported by an award of the 2017 Summer Seminars in Neuroscience and Philosophy (SSNAP - Duke University), funded by the John Templeton Foundation. The project was additionally supported by a research contract between NTT and UCL. LD was supported by FRM MADOCS, and by a Post-doctoral bursary of the Fondation Fyssen. PH was additionally supported by a Chaire Blaise Pascal of the Région Ile de France.

Declarations of interest

None

References

- Azuma, R., Haggard, P., 1999. Effects of response type on coordinated responses during arm movement. *Percept. Psychophys.* 61, 579–590.
- Bays, P.M., Wolpert, D.M., Flanagan, J.R., 2005. Perception of the consequences of self-action is temporally tuned and event driven. *Curr. Biol.* 15, 1125–1128.
- Blakemore, S.-J., Frith, C., 2003. Self-awareness and action. *Curr. Opin. Neurobiol.* 13, 219–224.
- Blakemore, S.J., Frith, C.D., Wolpert, D.M., 1999. Spatio-temporal prediction modulates the perception of self-produced stimuli. *J. Cogn. Neurosci.* 11, 551–559. <https://doi.org/10.1162/089892999563607>
- Blanchard, C., Roll, R., Roll, J.-P., Kavounoudias, A., 2011. Combined contribution of tactile and proprioceptive feedback to hand movement perception. *Brain Res.* 1382, 219–229.
- Bolanowski, S., Verrillo, R., McGlone, F., 2004. Passive, active and intra-active (self) touch. *Behav. Brain Res.* 148, 41–45.
- Botvinick, M., Cohen, J., 1998. Rubber hands ‘feel’ touch that eyes see. *Nature* 391, 756–756. <https://doi.org/10.1038/35784>
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A., 2013. Tool-use reshapes the boundaries of body and peripersonal space representations. *Exp. Brain Res.* 228, 25–42.
- Cao, Y., Summerfield, C., Park, H., Giordano, B.L., Kayser, C., 2019. Causal inference in the multisensory brain. *Neuron* 102, 1076–1087.
- Cluff, T., Crevecoeur, F., Scott, S.H., 2015. A perspective on multisensory integration and rapid perturbation responses. *Vision Res.* 110, 215–222.
- Cohen, E.J., Wei, K., Minciocchi, D., 2019. Visuomotor perturbation in a continuous circle tracing task: novel approach for quantifying motor adaptation. *Sci. Rep.* 9, 1–9.
- David, N., Newen, A., Vogeley, K., 2008. The “sense of agency” and its underlying cognitive and neural mechanisms. *Conscious. Cogn.* 17, 523–534.
- Dummer, T., Picot-Annand, A., Neal, T., Moore, C., 2009. Movement and the rubber hand illusion. *Perception* 38, 271–280.
- Edin, B.B., Abbs, J.H., 1991. Finger movement responses of cutaneous mechanoreceptors in the dorsal skin of the human hand. *J. Neurophysiol.* 65, 657–670.
- Eisenhauer, J.G., 2003. Regression through the origin. *Teach. Stat.* 25, 76–80.
- Ernst, M.O., Banks, M.S., 2002. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415, 429–433. <https://doi.org/10.1038/415429a>
- Farnè, A., Làdavas, E., 2000. Dynamic size-change of hand peripersonal space following tool use. *Neuroreport* 11, 1645–1649.
- Farne, A., Pavani, F., Meneghello, F., Ladavas, E., 2000. Left tactile extinction following visual stimulation of a rubber hand. *Brain* 123, 2350–2360.
- Findlay, J.M., Gilchrist, I.D., 2003. *Active vision: The psychology of looking and seeing.* Oxford University Press.
- Gandevia, S.C., Smith, J.L., Crawford, M., Proske, U., Taylor, J.L., 2006. Motor commands contribute to human position sense. *J. Physiol.* 571, 703–710.
- Haggard, P., 2005. Conscious intention and motor cognition. *Trends Cogn. Sci.* 9, 290–295.
- Hara, M., Pozeg, P., Rognini, G., Higuchi, Takahiro, Fukuhara, K., Yamamoto, A., Higuchi, Toshiro, Blanke, O., Salomon, R., 2015. Voluntary self-touch increases body ownership. *Front. Psychol.* 6, 1509.
- Hartley, T., Lever, C., Burgess, N., O’Keefe, J., 2014. Space in the brain: how the hippocampal formation supports spatial cognition. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 20120510.

- Hatfield, G.C., 1990. *The natural and the normative: Theories of spatial perception from Kant to Helmholtz*. MIT Press.
- Hurley, S., 2001. Perception and action: Alternative views. *Synthese* 129, 3–40.
- Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., PuÈtz, B., Yoshioka, T., Kawato, M., 2000. Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature* 403, 192–195.
- Jeannerod, M., 2009. The sense of agency and its disturbances in schizophrenia: a reappraisal. *Exp. Brain Res.* 192, 527.
- Kalckert, A., Ehrsson, H.H., 2012. Moving a rubber hand that feels like your own: a dissociation of ownership and agency. *Front. Hum. Neurosci.* 6, 40.
- Kammers, M.P., Longo, M.R., Tsakiris, M., Dijkerman, H.C., Haggard, P., 2009. Specificity and coherence of body representations. *Perception* 38, 1804–1820.
- Kilteni, K., Houborg, C., Ehrsson, H.H., 2019. Rapid learning and unlearning of predicted sensory delays in self-generated touch. *eLife* 8, e42888. <https://doi.org/10.7554/eLife.42888>
- Krakauer, J.W., Pine, Z.M., Ghilardi, M.-F., Ghez, C., 2000. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J. Neurosci.* 20, 8916–8924.
- Leib, A.Y., Kosovicheva, A., Whitney, D., 2016. Fast ensemble representations for abstract visual impressions. *Nat. Commun.* 7, 13186.
- Lotze, 1884. *Metaphysic: In Three Books, Ontology, Cosmology, and Psychology*. Clarendon Press.
- Lotze, Hamilton, 1885. *Microcosmus, an Essay Concerning Man and His Relation to the World*, Tr. By E. Hamilton and EEC Jones.
- Lotze, R.H., 1852. *Medicinische Psychologie oder Physiologie der Seele*. Von Dr. Rudolph Hermann Lotze Professor in Göttingen. Weidmann'sche Buchhandlung.
- Mach, E., 1897. *Contributions to the Analysis of the Sensations*. Open court publishing Company.
- Melmoth, D.R., Tibber, M.S., Grant, S., Morgan, M.J., 2009. The Poggendorff illusion affects manual pointing as well as perceptual judgements. *Neuropsychologia* 47, 3217–3224.
- Merleau-Ponty, M., 1976. *Phénoménologie de la perception (1945)*. Libr. Gallimard Paris.
- Miller, L.E., Montroni, L., Koun, E., Salemme, R., Hayward, V., Farnè, A., 2018. Sensing with tools extends somatosensory processing beyond the body. *Nature* 561, 239.
- Moscattelli, A., Bianchi, M., Ciotti, S., Bettelani, G., Parise, C., Lacquaniti, F., Bicchi, A., 2019. Touch as an auxiliary proprioceptive cue for movement control. *Sci. Adv.* 5, eaaw3121.
- Moscattelli, A., Bianchi, M., Serio, A., Terekhov, A., Hayward, V., Ernst, M.O., Bicchi, A., 2016. The change in fingertip contact area as a novel proprioceptive cue. *Curr. Biol.* 26, 1159–1163.
- O'Keefe, J., Nadel, L., 1978. *The hippocampus as a cognitive map*. Clarendon Press ; Oxford University Press, Oxford : New York.
- O'Regan, J.K., Noë, A., 2001. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24, 939–973.
- Paillard, J., Brouchon, M., 1968. Active and passive movements in the calibration of position sense. *Neuropsychol. Spatially Oriented Behav.* 11, 37–55.
- Prager, A.D., Contreras-Vidal, J.L., 2003. Adaptation to display rotation and display gain distortions during drawing. *Hum. Mov. Sci.* 22, 173–187.
- Proske, U., Gandevia, S.C., 2012. The proprioceptive senses: their roles in signaling body shape, body position and movement, and muscle force. *Physiol. Rev.* 92, 1651–1697.
- Ribot, T., 1879. *La psychologie allemande contemporaine (école expérimentale)*. Baillière.
- Rose, D., 1999. The historical roots of the theories of local signs and labelled lines. *Perception* 28, 675–685.

- Schütz-Bosbach, S., Musil, J.J., Haggard, P., 2009. Touchant-touché: The role of self-touch in the representation of body structure. *Conscious. Cogn.* 18, 2–11.
- Scott, S.H., 2012. The computational and neural basis of voluntary motor control and planning. *Trends Cogn. Sci.* 16, 541–549.
- Serino, A., Bassolino, M., Farne, A., Ladavas, E., 2007. Extended multisensory space in blind cane users. *Psychol. Sci.* 18, 642–648.
- Smith, A.M., Chapman, C.E., Donati, F., Fortier-Poisson, P., Hayward, V., 2009. Perception of simulated local shapes using active and passive touch. *J. Neurophysiol.* 102, 3519–3529.
- Southall, J.P.C., 1962. Helmholtz's Treatise on Physiological Optics: Translated from the Third German Edition. Dover.
- Stratton, G.M., 1896. Some preliminary experiments on vision without inversion of the retinal image. *Psychol. Rev.* 3, 611–617. <https://doi.org/10.1037/h0072918>
- Suzuki, K., Garfinkel, S.N., Critchley, H.D., Seth, A.K., 2013. Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia* 51, 2909–2917.
- Tong, J., Aydin, M., Bedell, H.E., 2007. Direction and extent of perceived motion smear during pursuit eye movement. *Vision Res.* 47, 1011–1019.
- Vindras, P., Viviani, P., 2002. Altering the visuomotor gain. *Exp. Brain Res.* 147, 280–295.
- von Helmholtz, H., 2013. Treatise on physiological optics. Courier Corporation.
- von Holst, E., Mittelstaedt, H., 1950. Das reafferenzprinzip. *Naturwissenschaften* 37, 464–476.
- White, R.C., Davies, A.M.A., 2011. Touching my left elbow: The anatomical structure of the body affects the illusion of self-touch. *Perception* 40, 95–98.
- Williams, S.R., Shenasa, J., Chapman, C.E., 1998. Time Course and Magnitude of Movement-Related Gating of Tactile Detection in Humans. I. Importance of Stimulus Location. *J. Neurophysiol.* 79, 947–963. <https://doi.org/10.1152/jn.1998.79.2.947>
- Witney, A.G., Wing, A., Thonnard, J.-L., Smith, A.M., 2004. The cutaneous contribution to adaptive precision grip. *Trends Neurosci.* 27, 637–643.
- Wolpert, D.M., Ghahramani, Z., 2004. Computational motor control. *Science* 269, 1880–1882.
- Wolpert, D.M., Ghahramani, Z., 2000. Computational principles of movement neuroscience. *Nat. Neurosci.* 3, 1212.
- Wundt, W.M., 1862. Beiträge zur Theorie der Sinneswahrnehmung. CF Winter.

Figure Captions

Figure 1. Experimental setup for self-touch stimulation.

Participants moved the handle of the master robot with their right hand and simultaneously felt a corresponding stroke on the left forearm from a brush attached to the slave robot. A horizontal screen (black dashed line) covered both the participants' arms and the robotic setup throughout the experiment. The physical lengths of movement and tactile feedback were independently modulated via two "virtual walls" (red and green dotted lines/planes; planes are only shown for the tactile sensation for clarity reasons). In the active movement condition, participants produced straight back-and-forth movements between the front wall (green dotted line/plane) and the back wall (red dotted line/plane). In the passive movement condition participants maintained their arm as relaxed as possible, while the experimenter held the vertical arm of the master robot and moved back-and-forth between the walls, thus passively displacing the participant's right hand, which continued to grip the tip of the robot with the fingers of the right hand. After sensorimotor stimulation, participants reported the perceived length of either their own movement (judge movement block) or the tactile sensation (judge touch block) by adjusting the length of a line presented on a computer screen using foot pedals. See https://osf.io/gcvbm/?view_only=b530e560d121479db7156b4be2a27451 for a video demo of the setup.

Figure 2. Results.

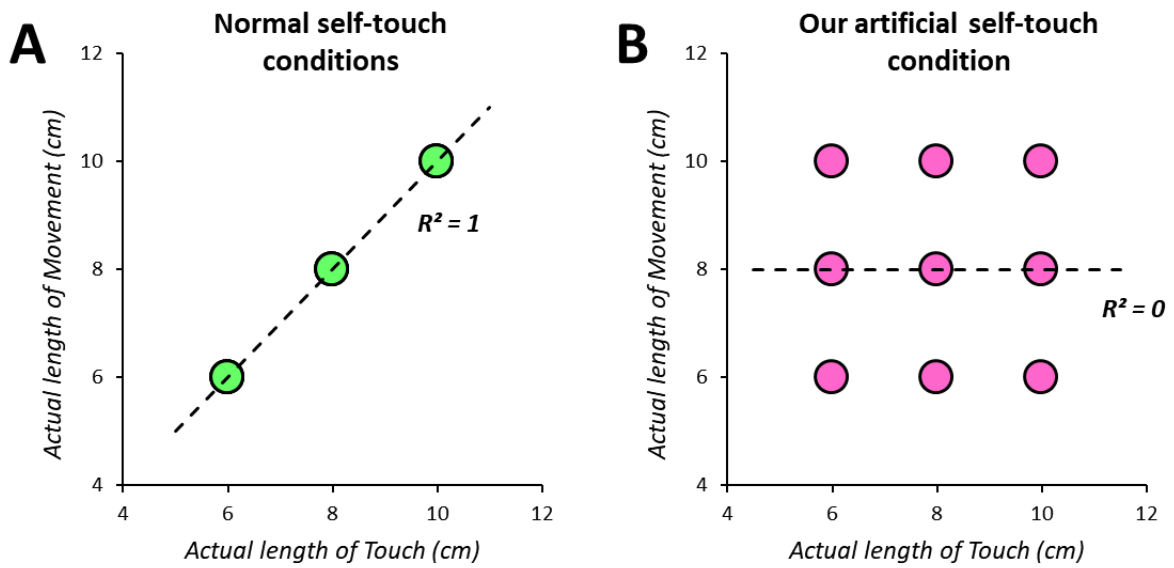
A-D: Perceived length of the to-be-judged sensation as a function of its actual length and of the actual length of the task-irrelevant sensation. The spread between the coloured lines in each panel (**A-D**) represents the effect of the task-irrelevant sensation on spatial perception. That is, if the task-irrelevant sensation had no effect on participants' spatial judgements, the three coloured lines in each panel should superimpose. In the "judge touch" task (**A-B**), the physical length of the movement significantly affected the perceived length of tactile stroking, as predicted by the Local Sign theories. The effect of movement on touch was significantly stronger when participants' movements were self-generated (**A**) compared to when they were passively produced by the experimenter (**B**). Importantly, in the "judge movement" task (**C-D**), the perceived length of the participant's movement was also significantly affected by the physical length of the task-irrelevant tactile sensation, although to a lesser extent than in **A-B**. **E:** The weighting of the task-irrelevant sensation in spatial perception was calculated in each condition. Error bars represent the standard error of the mean.

Figure 3. Correlation between judgements of movement and judgements of touch.

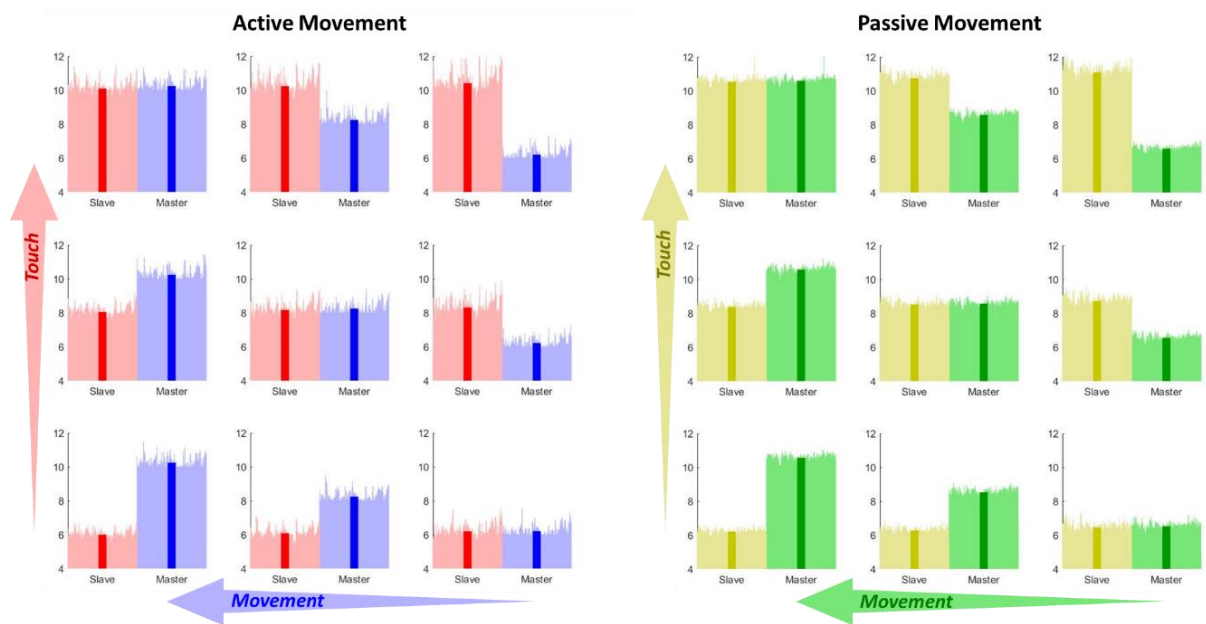
The weights of the TaskIrrelevantLength in the active condition of the judge movement and judge touch tasks were inversely correlated ($r = -0.53$, $p = 0.015$), consistent with individual differences in some factor determining whether motor signals dominate over tactile feedback, or vice versa.

Table 1. Precision ($1/\text{cm}^2$) of spatial extent judgements for each cell of the 2 x 2 factorial design.

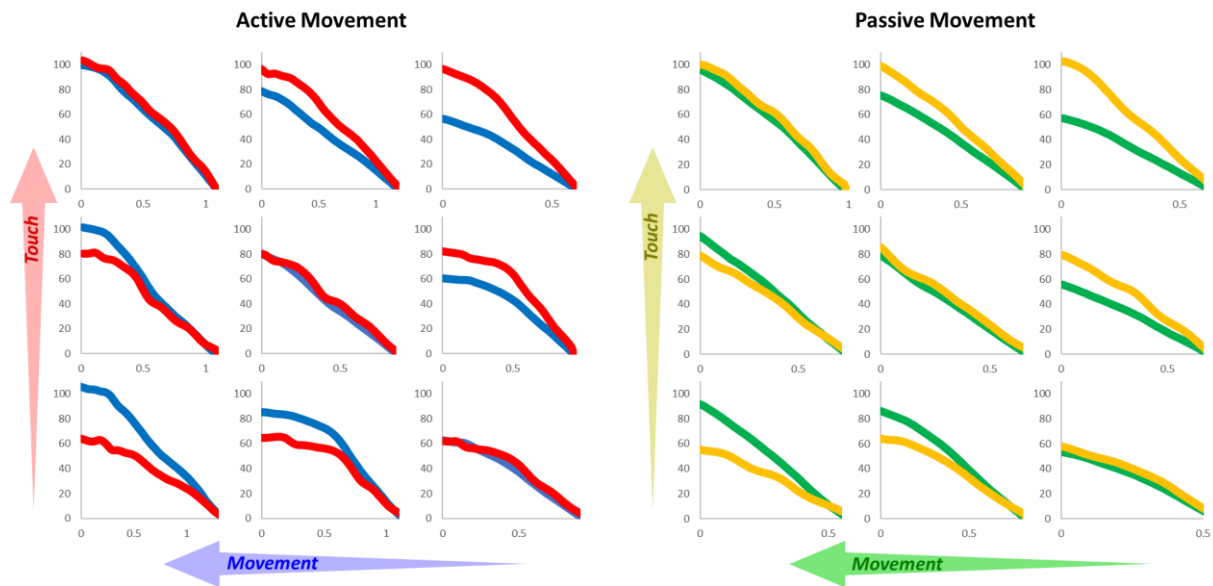
Supplementary Material



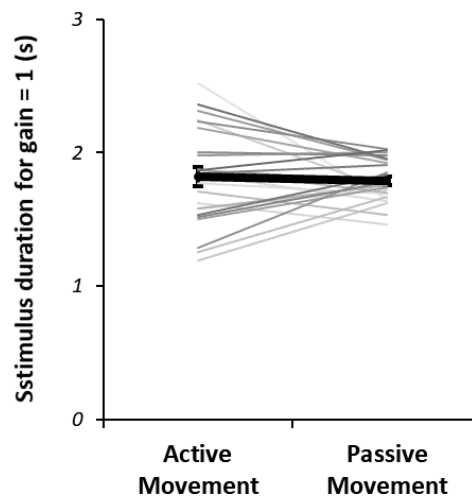
Supplementary Figure S1: *Normal self-touch conditions (left panel) provide a perfect spatial overlap between the motor and the tactile extents. Our artificial, tool-mediated self-touch paradigm, instead, created a unique situation where the brain cannot use spatial information from one sensation as a proxy for the other. This allowed us to isolate each sensation from the other and disentangle the specific contribution of tactile, kinaesthetic, and motor information to space perception.*



Supplementary Figure S2: *Z-axis kinematics of master and slave robots in all trials in all participants. Shaded lines represent single trials, dark bars represent means. The active (left) and passive (right) movement conditions were substantially identical, except for a lower variability in the passive condition.*



Supplementary Figure S3: Z-axis kinematics over time (s) of master (blue/green) and slave (red/yellow) robots in representative trials of a representative subject (Participant #1, blocks #4-5).



Supplementary Figure S3: Mean stimulus duration for trials with gain = 1 for the active and passive movement conditions. Shaded lines represent individual participants, the dark line is the mean, and the error bars represent the standard error of the mean. Stimulus duration (and speed) was substantially identical in the active and passive movements. A repeated measures ANCOVA showed that the variability in stimulus duration between conditions did not contribute to our effect, leaving the statistical inferences unchanged (i.e. significant main effect of Judgment type: $F_{1,22} = 7.296$, $p = 0.013$; $\eta^2 = 0.249$; no significant effect of Movement type: $F_{1,22} = 0.309$, $p = 0.584$; $\eta^2 = 0.014$; significant interaction between factors: $F_{1,22} = 19.783$, $p < 0.001$; $\eta^2 = 0.473$)

Supplementary Table S1: ANOVA table of effects in the 2 (Judgement type: Judge Touch, Judge Movement) \times 2 (Movement type: Active, Passive) \times 3 (To-be-judged length: 6, 8, 10 cm) \times 3 (Task-irrelevant length: 6, 8, 10 cm) within-subjects design.

Source	df	F	Sig.	η_p^2
Judgement type	1, 23	1.341	0.259	0.055
Movement type	1, 23	0.164	0.689	0.007
To-be-judged length	1.3, 29.6	183.832	< 0.0001	0.889
Task-irrelevant length	1.3, 29.8	148.707	< 0.0001	0.866
Judgement type * Movement type	1, 23	0.416	0.525	0.018
Judgement type * To-be-judged length	1.5, 34.6	3.922	0.040	0.146
Movement type * To-be-judged length	2, 46	5.969	0.005	0.206
Judgement type * Movement_type * To-be-judged length	2, 46	5.986	0.005	0.207
Judgement type * Task-irrelevant length	1.5, 33.4	7.400	0.005	0.243
Movement type * Task-irrelevant length	1.3, 30.7	6.992	0.008	0.233
Judgement type * Movement type * Task-irrelevant length	2, 46	5.727	0.006	0.199
To-be-judged length * Task-irrelevant length	2, 46	6.057	< 0.0001	0.208
Judgement type * To-be-judged length * Task-irrelevant length	4, 92	1.289	0.280	0.053
Movement type * To-be-judged length * Task-irrelevant length	3, 68	0.113	0.950	0.005
Judgement type * Movement type * To-be-judged length * Task-irrelevant length	4, 92	1.709	0.155	0.069

Results from analysing raw judgement data are essentially similar to those obtained with weights from the mutual influence model. First, the main effect of Judgement type in the weights model ($F_{1,23} = 6.60$, $p = 0.017$, $\eta_p^2 = 0.22$) is confirmed here by the significant Judgement type * Task-irrelevant length interaction ($F_{1.5,33.4} = 7.40$, $p = 0.005$, $\eta_p^2 = 0.21$). Second, the significant Judgement type * Movement type interaction in the weights model ($F_{1,23} = 17.45$, $p < 0.001$, $\eta_p^2 = 0.43$) was also present in ANOVA of raw judgement data (Judgement type * Movement type * Task-irrelevant length: $F_{2,46} = 5.73$, $p = 0.006$, $\eta_p^2 = 0.20$). Finally, the non-significant main effect of Movement type in the weights model ($F_{1,23} = 0.32$, $p = 0.58$) was instead significant here (Movement type * Task-irrelevant length: $F_{1.3,30.7} = 6.99$, $p = 0.008$, $\eta_p^2 = 0.23$). Greenhouse-Geisser correction was applied to every case that violated the sphericity assumption (these cases are shown in blue).

Supplementary *Table S2: Estimated ω for each participant (n=24) and each condition.*

Judge Touch		Judge Movement	
Active	Passive	Active	Passive
0.45	0.3	0.5	0.32
0.4	0.6	0.42	0.48
0.7	0.39	0.47	0.6
0.87	0.81	0.08	0.25
0.62	0.39	0.18	0.35
0.33	0.49	0.54	0.63
0.61	0.52	0.23	0.35
0.72	0.58	0.27	0.47
0.23	0.33	0.36	0.33
0.75	0.66	0.27	0.45
0.79	0.54	0.26	0.28
0.45	0.43	0.26	0.5
0.64	0.55	0.25	0.35
0.67	0.71	0.42	0.25
0.62	0.46	0.5	0.41
0.55	0.28	0.38	0.1
0.5	0.27	0.22	0.31
0.38	0.46	0.5	0.68
0.39	0.38	0.47	0.84
0.36	0.21	0.37	0.33
0.54	0.38	0.59	0.42
0.65	0.46	0.2	0.52
0.59	0.54	0.37	0.54
0.5	0.28	0.47	0.51

For each participant we fitted the following model to quantify the effect of the task-irrelevant length information on the to-be-judged length.

$$\mathbf{JudgedLength} \sim \mathbf{Scale}_{\text{Indiv}} ((1 - \omega) \mathbf{ToBeJudgedLength} + \omega \mathbf{TaskIrrelevantLength}) \quad (1)$$

Where $Scale_{\text{Indiv}}$ is an individual scaling factor to capture participant's cross-modal mapping from motor/tactile stimulation extent to the visual line response, ω is the weight of the task-irrelevant length ($\mathbf{TaskIrrelevantLength}$) on the judged length. In this model, $\omega = 0$ would correspond to the situation where the participant would report the target length independently from the task-irrelevant information. Conversely, $\omega = 1$ would mean that the participants' to-be-judged length perception is entirely based on

the task-irrelevant information (and, since to-be-judged and task-irrelevant lengths were uncorrelated, not at all on the to-be-judged information). Finally, a weight between 0 and 1 would indicate the partial automatic integration of task-irrelevant information in judged length. Larger weights indicate stronger automatic integration. Fitting this model allowed us to calculate a single summary numerical measure from raw judgement data in each condition of the 2x2 (MovementType*JudgementType) design.

Supplementary *Table S3: Intercept values for every condition in our 2 x 2 design.*

	Active	Passive
Judge Movement	0.97 (SD 1.98)	2.52 (SD 1.66)
Judge Touch	0.37 (SD 1.53)	1.55 (SD 1.51)

To check whether our model could have missed a bias that could change our results and interpretations, we have run the analyses on the same model with an intercept:

$$\mathbf{JudgedLength} \sim \mathbf{ScaleIndiv} ((1 - \omega) \mathbf{ToBeJudgedLength} + \omega \mathbf{TaskIrrelevantLength}) + \mathbf{Intercept} \quad (2)$$

The intercept values were not significantly different from 0 in active condition (t-test, all $p > .06$) but significantly different from 0 in passive condition (all $p < .005$, t-test)

Supplementary *Table S4: Comparison of the weights of the TaskIrrelevantLength from a model with (right) and without (left) intercept.*

	<i>JudgedLength ~ ScaleIndiv ((1 - ω) ToBeJudgedLength + ω TaskIrrelevantLength)</i>		<i>JudgedLength ~ ScaleIndiv ((1 - ω) ToBeJudgedLength + ω TaskIrrelevantLength) + Intercept</i>	
	Active	Passive	Active	Passive
Judge Movement	0.36 (SD 0.13)	0.43 (SD 0.16)	0.32 (SD 0.17)	0.52 (SD 0.88)
Judge Touch	0.56 (SD 0.16)	0.46 (SD 0.15)	0.54 (SD 0.23)	0.43 (SD 0.20)

Both models (with and without intercept) produced weights significantly different from 0 (all $p < .001$, t-tests, normality verified). Moreover, the statistical inference was not affected by the introduction of an intercept in the model. Overall, the addition of this new parameter in the model (1) go against the parsimony of the model, (2) adds variability (seen in standard deviations, some weights are outliers for some participants and it was not the case with the previous model), and (3) does not change the main results, suggesting that a model without intercept should be preferred.

