



Original Articles

The magnetic touch illusion: A perceptual correlate of visuo-tactile integration in peripersonal space



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ABSTRACT

To accurately localize our limbs and guide movements toward external objects, the brain must represent the body and its surrounding (peripersonal) visual space. Specific multisensory neurons encode peripersonal space in the monkey brain, and neurobehavioral studies have suggested the existence of a similar representation in humans. However, because peripersonal space lacks a distinct perceptual correlate, its involvement in spatial and bodily perception remains unclear. Here, we show that applying brushstrokes in mid-air at some distance above a rubber hand—without touching it—in synchrony with brushstrokes applied to a participant's hidden real hand results in the illusory sensation of a “magnetic force” between the brush and the rubber hand, which strongly correlates with the perception of the rubber hand as one's own. In eight experiments, we characterized this “magnetic touch illusion” by using quantitative subjective reports, motion tracking, and behavioral data consisting of pointing errors toward the rubber hand in an intermanual pointing task. We found that the illusion depends on visuo-tactile synchrony and exhibits similarities with the visuo-tactile receptive field properties of peripersonal space neurons, featuring a non-linear decay at 40 cm that is independent of gaze direction and follows changes in the rubber hand position. Moreover, the “magnetic force” does not penetrate physical barriers, thus further linking this phenomenon to body-specific visuo-tactile integration processes. These findings provide strong support for the notion that multisensory integration within peripersonal space underlies bodily self-attribution. Furthermore, we propose that the magnetic touch illusion constitutes a perceptual correlate of visuo-tactile integration in peripersonal space.

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1. Introduction

The space close to our hands does not “feel” different than the space outside our reach. Nevertheless, a wealth of research has demonstrated that the space surrounding the body has a special representation in the brain. Single-unit recordings in monkeys have identified neurons in specific areas in the frontal and parietal association cortices that integrate visual, tactile, and proprioceptive signals (Hyvärinen & Poranen, 1974; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). These neurons feature visual receptive fields (RFs) that extend up to 40 cm from the skin surface (Fogassi et al., 1996), that are spatially anchored to the limb (and follow changes in limb position) (Graziano, Hu, & Gross, 1997) and that are independent of the direction of gaze (Graziano & Gross, 1998). Collectively, these populations of neurons build and maintain a multisensory representation of the body and its surrounding (peripersonal) space that is considered to be important for

sensory-guided movements and limb localization (Graziano & Botvinick, 2002). In humans, neuroimaging studies have found evidence for the existence of a similar representation of the space around the hand (Brozzoli, Gentile, & Ehrsson, 2012; Brozzoli, Gentile, Petkova, & Ehrsson, 2011; Makin, Holmes, & Zohary, 2007), and research on stroke patients has demonstrated that fronto-parietal lesions may result in specific deficits in multisensory integration within peripersonal space (Làdavas & Farnè, 2004). Furthermore, studies on the rubber hand illusion (Botvinick & Cohen, 1998), in which a sense of ownership of an artificial limb is elicited through synchronous touching of a participant's hidden hand and a rubber hand in view, have indicated that the feeling of limb ownership is related to multisensory integration in peripersonal space (Makin, Holmes, & Ehrsson, 2008). Three main observations support this notion: (i) the rubber hand must be placed within the theoretical limits of peripersonal space for ownership sensations to be induced (Lloyd, 2007); (ii) the illusion experience is associated with increased activity in a set of multisensory areas similar to those in which peripersonal space neurons have been identified in monkeys (Ehrsson, Spence, & Passingham,

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2004); and (iii) repeated presentation of an object close to an owned rubber hand is coupled with increased fMRI-adaptation in these cortical regions, suggesting that the object is encoded within peripersonal space when the rubber hand is perceived as part of the self (Brozzoli et al., 2012). However, a major challenge in the study of peripersonal space in humans—particularly with respect to its precise spatial extension and its involvement in the emergence of body ownership—is the lack of an experimental paradigm that allows individuals to directly “feel” multisensory integration within peripersonal space.

In this study, we report a perceptual illusion in which healthy participants perceive a “magnetic force” or “force field” between a rubber hand and an object moving in mid-air close to the hand. This “magnetic touch illusion” is elicited by synchronous brushstrokes applied to a participant's hidden real hand and brushstrokes delivered at some distance above the rubber hand but never actually touching it. In a series of eight experiments, we show that the magnetic touch sensation correlates strongly with the sense of rubber hand ownership and that it exhibits striking similarities to the known neuronal properties of perihand neurons, in terms of extension in space (Experiment 1a–1c and 4), independence of gaze direction (Experiment 1c and 4), and hand-centered spatial reference frames (Experiment 4). We also demonstrate that “tactile expectations” (Ferri, Chiarelli, Merla, Gallese, & Costantini, 2013) elicited by merely observing an object moving near the hand do not contribute to the illusion experience (Experiment 2a and 2b) and that the magnetic force cannot penetrate physical barriers (Experiment 3a and 3b), thus further linking this phenomenon to the multisensory body representation and providing valuable predictions for future neurophysiological studies. In Experiment 4, we combined motion tracking with a continuous real-time illusion strength assessment to map out the extension of the magnetic touch illusion in 3-D space and demonstrate that the illusion is anchored to the position of the rubber hand. Together, these findings led us to propose that the sense of magnetic touch constitutes a perceptual correlate of visuo-tactile integration in peripersonal space. Furthermore, the results provide strong support for the notion that multisensory integration within peripersonal space is key for the emergence of body ownership.

2. Methods

2.1. Participant information

We recruited a total of 101 healthy adult volunteers (60 female, and 89 right-handed) for the eight experiments. All subjects gave written informed consent prior to participation, and the Regional Ethical Review Board of Stockholm approved all of the experimental procedures.

2.2. Overview of the experimental design

Experiments 1–3 followed the same general structure and consisted of a 1-min period in which brushstrokes were delivered at some distance above the rubber hand and to the unseen real right hand. After each stimulation period, we quantified the illusion by using questionnaire reports in the form of visual analog scale ratings of different statements (Experiments 1a, 1b, 2a, and 3a; see Table 1) or the degree of pointing error toward the rubber hand (proprioceptive drift), using an intermanual pointing task in which participants were asked to close their eyes and indicate the position of their right index finger by using their left index finger (Experiments 1c, 2b, and 3b; see Section 2.5 below). In Experiment 4, the participants continuously reported the subjective strength of the illusion by using a sliding bar placed in their left hand. In the

questionnaire experiments (Experiments 1a, 1b, 2a, and 3a), each condition was repeated once. In the proprioceptive drift experiments (Experiments 1c, 2b, and 3b), each condition was repeated three times, in line with previously published protocols (Guterstam, Gentile, & Ehrsson, 2013).

2.3. Experimental setup and illusion induction procedure

The experiments took place in a soundproof testing room (40-decibel noise reduction). The participants sat on a comfortable chair and rested their arms on a table in front of them. The participants' right arm was placed behind a screen (for all experiments except Experiment 4, in which the arm was placed below a small table) and was thus hidden from view in every experiment. A rubber hand was placed on the table in full view of the participant. The experimenter sat opposite the participant. The illusion was elicited by applying brushstrokes to the participant's hidden right hand while simultaneously moving another brush at a predefined distance above rubber hand. A trained experimenter (AG or VM) moved the brush in mid-air in a manner that reflected the curvature of the rubber hand located below. A small sensor that continuously recorded three-dimensional spatial coordinates at a frequency of 60 Hz (see Section 2.6 below for details) was attached to the tip of brush. The brushstrokes were applied to all five fingers of the participant's right hand and the corresponding locations above the rubber hand, and they consisted of ‘long strokes’ (along the entire length of the finger) and occasional short tapping movements. In Experiments 2a–2b and 4, only tapping movements were delivered. In the illusion condition, we used an irregular but synchronous brushing rhythm. In the asynchronous condition, the pattern of brushing was irregular and alternated between the real hand and the empty space above the rubber hand. Approximately 30 strokes were applied per minute. The distance between the index finger of the participant's right hand and the index finger of the rubber hand was 15 cm.

2.4. Questionnaires

In an open-ended pilot experiment, participants spontaneously described the illusory sensation as a “repelling magnetic force”, “force field”, or “invisible rays of touch”, descriptions similar to those reported in a previous relevant study (Hohwy & Paton, 2010). In the main experiments presented here, we used questionnaires (Botvinick & Cohen, 1998; Hohwy & Paton, 2010) that were presented at the end of each condition to quantify the subjective experiences associated with the illusion. The participants were asked to confirm or deny different statements reflecting potential perceptual effects by using a seven-point visual analog scale that ranged from –3 to +3. The participants were informed that –3 indicated “I completely disagree”; +3 indicated “I agree completely”; and 0 indicated “I do not know, I can neither agree nor disagree”. Statements 1 and 2 (S1–S2) were designed to examine the sensation of magnetic touch, whereas statements 3 and 4 (S3–S4) served as controls for suggestibility and task compliance. Statements 5 and 6 (S5–S6) were designed to examine the feeling of rubber hand ownership; statements 7 and 8 (S7–S8) served as controls. Table 1 summarizes the statements used in the experiments.

2.5. Proprioceptive drift

The degree of pointing error toward an owned rubber hand—the so called proprioceptive drift—is an indirect behavioral proxy of the feeling of limb ownership (Botvinick & Cohen, 1998; Brozzoli et al., 2012; Guterstam et al., 2013; Tsakiris & Haggard, 2005; but see Rohde, Di Luca, & Ernst, 2011 for a critical view). To provide

Table 1
Questionnaire statements.

Magnetic touch sensation - illusion statements

- S1. It felt as if the brush I saw caused a sensation of touch, even though there was a visible gap between the brush and the rubber hand
S2. It seemed as though there was a “magnetic force” or “force field” between the brush and the rubber hand

Magnetic touch sensation - control statements

- S3. I felt a painful touch
S4. It seemed as though there was a “magnetic force” or “force field” directly connecting the rubber hand to my real hand behind the screen

Rubber hand ownership - illusion statements

- S5. I felt touch on the rubber hand
S6. It felt as if the rubber hand were my hand

Rubber hand ownership - control statements

- S7. It felt as if I had two right hands
S8. It appeared as if the rubber hand was drifting to the right (toward my real hand)

objective behavioral evidence for the illusion of magnetic touch, we registered the proprioceptive drift in Experiments 1c, 2b, and 3b. Immediately before and after each period of brushing, the participants were asked to close their eyes and indicate the position of their right index finger by pointing with their left index finger. Prior to obtaining this response, the experimenter placed the participant's left index finger at one of three fixed starting points (the starting points were different for each repetition of a given condition, and the order was balanced across subjects) on a 1-m metal ruler (the ruler's markings were visible only to the experimenter) positioned 1 cm above the rubber hand and the real hand. The ruler penetrated the screen that separated the real hand and the rubber hand (Fig. 2, left panel). While the participant's eyes were closed, the experimenter silently removed a large portion of the screen, allowing the participant to slide freely with his or her left index finger on the metal ruler, without colliding with the screen. Next, the experimenter asked the participant to move his or her left index finger briskly along the ruler (which contained a shallow groove) and to stop when the finger was immediately above the perceived location of the right index finger. We computed the differences in the pointing error (toward the rubber hand) between the measurements obtained before and after each stimulation period and averaged the responses from the three repetitions for each experimental condition.

2.6. Motion tracking

A methodological challenge of the study was to objectively quantify the accuracy of the experimenter in maintaining the appropriate distance between the brush moving in mid-air and the rubber hand. To this end, we used motion tracking based on electromagnetic technology (Polhemus FASTRAK, Vermont, USA). We attached a small motion sensor to the tip of the brush moving in mid-air (Fig. 1A) and recorded its three-dimensional coordinates at a rate of 60 Hz throughout Experiments 1a, 1b, 2a, and 4 (the presence of large metal objects near the sensor prevented us from using accurate motion tracking in Experiments 1c, 3a, and 3b). The experimenter controlled the recording of motion tracking data by pressing a foot pedal. A data file containing the X, Y, and Z coordinates for the brush sensor was created for each repetition in every condition and for all the participants. In the experiments that featured mid-air brushstrokes (Experiments 1a and 1b) and for purposes of visualization, we displayed only the data points in mid-air that represented the actual touch (i.e., the data points that correspond to the brush movements between the touches are not shown) (Fig. 1B). In the experiments that featured continuous ‘tapping movements’ rather than brushstrokes (Experiments 2a and 4), the data points corresponding to the entire paintbrush trajectory through 3-D space were included (Figs. 3B and 5).

2.7. Eye tracking

A CCTV camera (Protos IV, Vista, Wokingham, Berkshire, UK) mounted on a small tripod placed on the table to the left of the participant's face was used to track the movements of the left eye. We used the ViewPoint EyeTracker software (Arrington Research, Arizona, USA) to record videos of eye movements throughout the experimental sessions. The recordings were examined offline to evaluate each participant's fixation and overall alertness. No participants had to be excluded because of an inability to fixate or to keep their eyes open.

2.8. Experiments 1a, 1b, and 1c—The spatial extension of the magnetic touch illusion

There were four main goals of Experiment 1a: (i) to examine whether the previously described “magnetic touch illusion” (Hohwy & Paton, 2010) could be elicited without virtual reality technology, i.e., using the ecological rubber hand illusion setup featuring a visuo-proprioceptive conflict between the real and rubber hand; (ii) to test whether rubber hand ownership could be elicited using magnetic touch stimuli alone, i.e., without prior induction of the normal rubber hand illusion (Hohwy & Paton, 2010); (iii) to examine whether the magnetic touch illusion depends on synchronous visual and tactile stimulation; and (iv) to investigate whether increasing the distance between the rubber hand and the brush in mid-air affects the strength of the illusion. To this end, we included eight experimental conditions: synchronous brushstrokes delivered to the real hand and in mid-air at the level of 5 cm, 15 cm, 25 cm, 35 cm, 45 cm, or 55 cm above the rubber hand and two conditions featuring asynchronous brushstrokes at 5 cm or 55 cm. A fixation point that consisted of a red LED was located at the level of the rubber hand (“0 cm”, see Fig. 1A). We hypothesized that the magnetic touch illusion would be contingent on synchronous visuo-tactile stimulation (Botvinick & Cohen, 1998) and that the illusion strength would have a non-linear relationship with increased distance, with a significant decay between 35 and 45 cm, reflecting the typical extension of the visual RF for peripersonal space neurons in primates (≤ 40 cm) (Fogassi et al., 1996) and the spatial limits of the rubber hand illusion (Kalckert & Ehrsson, 2014; Lloyd, 2007). We analyzed the average ratings of the statements reflecting the magnetic touch sensation (S1–S2) and rubber hand ownership (S5–S6) separately. To examine the basic illusion experience, we computed the three-way interaction for visuo-tactile temporal congruence (synchronous, asynchronous) \times distance (5 cm, 55 cm) \times statement type (illusion, control) in a $2 \times 2 \times 2$ ANOVA. We tested for non-linearity in the illusion strength decline with distance by fitting three different curves to the data—one linear, $f(x) = a * x + b$, one logarithmic, $f(x) = a * \log(x) + b$, and one sigmoid, $f(x) = a / (1 + e^{-(x-b)/c})$ —under

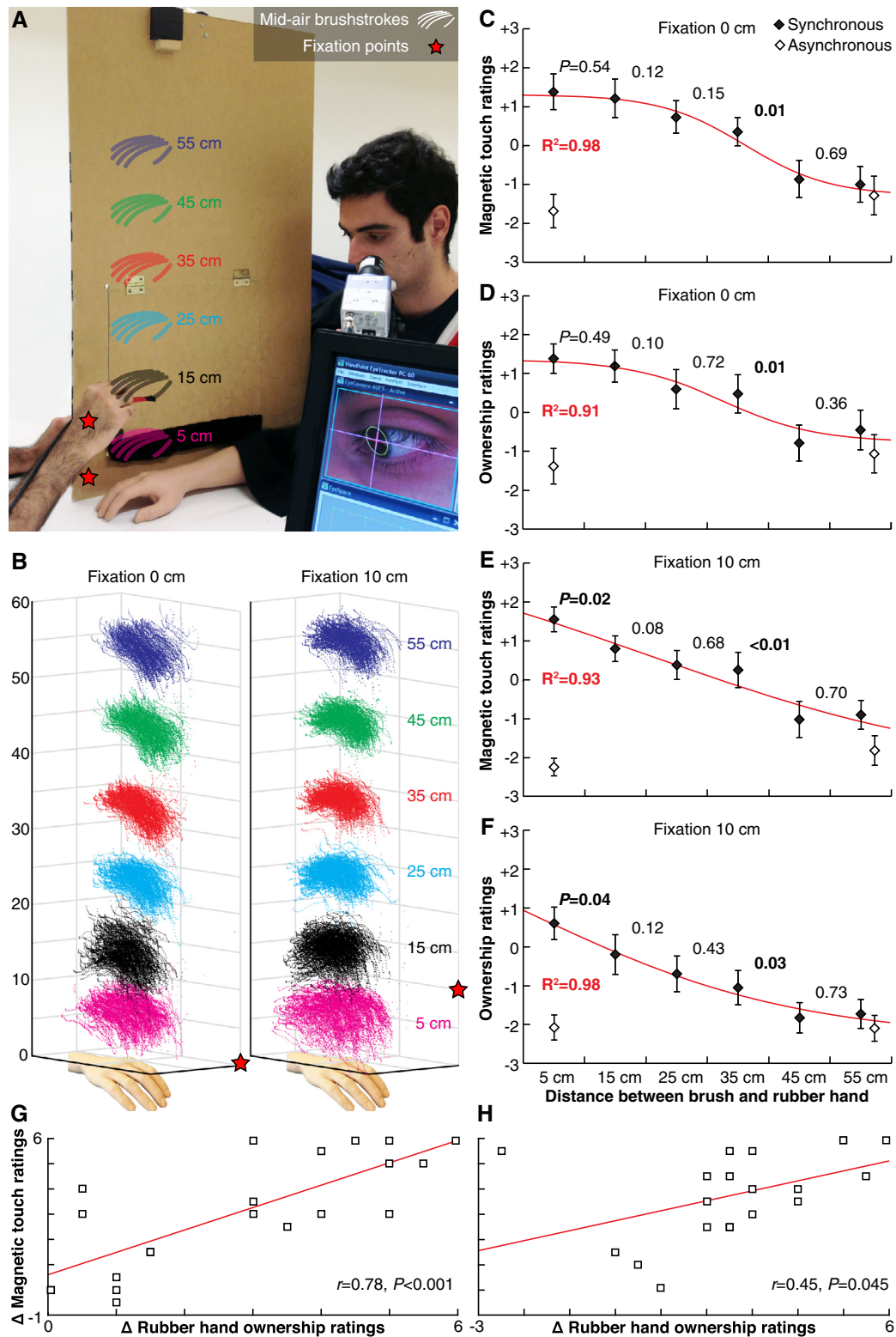


Fig. 1. The spatial extension of the magnetic touch illusion (Experiment 1a and 1b). (A) Experimental setup. The experimenter applied synchronous brushstrokes to the participant's right hand (hidden behind the screen) and in mid-air at six different distances above the rubber hand. Asynchronous brushstrokes were applied only at the lowest (5 cm) and highest (55 cm) levels. Experiment 1a featured a lower fixation point (0 cm) and Experiment 1b a higher fixation point (10 cm). (B) The motion tracking results of the brush moving in mid-air. The data points represent the 3-D spatial coordinates (at 60 Hz) of each brushstroke applied throughout Experiment 1a and 1b and demonstrate a high degree of experimenter precision and consistency. (C–F) Results. The average rating of the magnetic touch and the rubber hand ownership statements are displayed as a function of the distance between the brush in mid-air and the rubber hand for the lower (C, D) and higher fixation point (E, F), respectively. In all four cases (C–F), the decline in illusion strength was non-linear, and a sigmoid function was always a better curve fit than a linear or a logarithmic fit (see Table 2). Pairwise *t*-tests between neighboring levels in the synchronous condition showed a significant and consistent drop in the illusion strength between the distances of 35 cm and 45 cm, which was independent of fixation. The *P*-values for the pairwise contrasts are shown in the graphs between the corresponding data points. The error bars represent SEM. (G, H) In both Experiment 1a (G) and 1b (H), we observed a significant correlation between the ratings of magnetic touch and rubber hand ownership, suggesting that these two perceptual phenomena are closely related. Δ = Synchronous versus asynchronous difference.

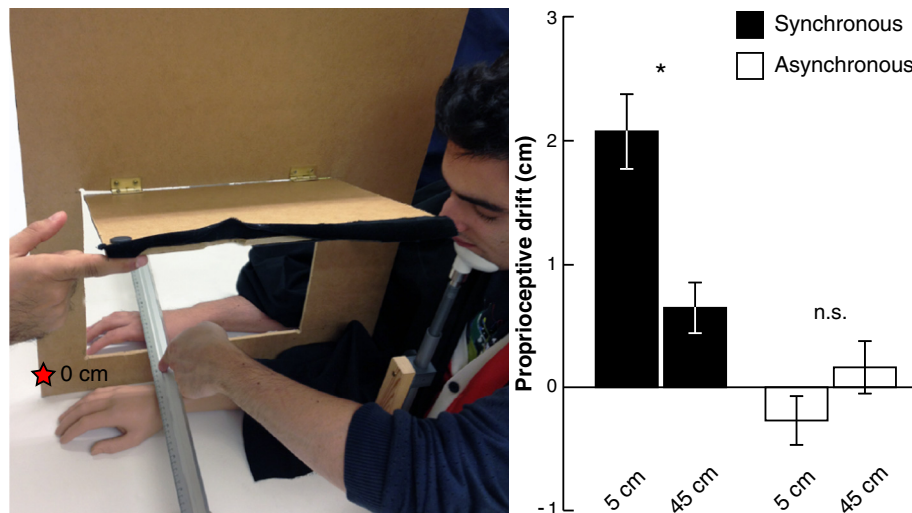


Fig. 2. Proprioceptive drift (Experiment 1c). (A) Experimental setup. Immediately before and after each trial, the participants were asked to close their eyes while their left index finger were placed in a shallow groove on a metal ruler that penetrated the screen. The experimenter then opened a large hatch in the screen and asked the participants to point to the perceived location of their right index finger. The relative difference between the 'before' and 'after' measurement constituted the proprioceptive drift of a given trial. (B) Consistently with the questionnaire results (Fig. 1), the proprioceptive drift toward the rubber hand was significantly greater in the synchronous condition when the brushstrokes were applied in mid-air 5 cm above the hand compared with 45 cm, and when asynchronous visuo-tactile stimulation was applied at either distance. * $P < 0.05$.

the hypothesis that the sigmoid function would be the best fit. For this analysis, the input consisted of the average rating of the illusion statements for each of the six levels in the synchronous condition. We applied a winner-take-all approach based on the R -squared curve fit in accordance with a previous relevant study (Lloyd, 2007). We also performed pairwise t -tests between each succeeding level and predicted a significant drop in illusion strength between 35 and 45 cm. Twenty-one participants (age 27 ± 5.1 years, 12 females) took part in Experiment 1a.

Conceivably, the non-linear illusion decline between 35 and 45 cm observed in Experiment 1a might be explained by the brush entering the far peripheral visual field rather than reflecting the spatial boundaries of the visual RF for perihand neurons. To exclude this possibility, we conducted Experiment 1b, which was identical to Experiment 1a, except that the fixation point was located 10 cm higher, i.e., 10 cm above the level of the rubber hand (see Fig. 1A). If the retinal distance between the fovea and the brush moving in mid-air fully explains the non-linear illusion decline at approximately 40 cm, elevating the fixation point by 10 cm should be accompanied by a 10 cm elevation of the upper limit of the magnetic touch illusion. However, if the spatial limits of the magnetic touch illusion are contingent on the distance between the (rubber) hand and the paintbrush in a hand-centered spatial reference frame that is akin to the RF properties of visuo-tactile neurons coding for perihand space (Fogassi et al., 1996; Graziano et al., 1997), then the level at which the illusion abruptly declines should be independent of fixation. Consistently with the latter notion and the observation of a sharp decline in the illusion between 35 and 45 cm in Experiment 1a (see Fig. 1C, upper two plots), we predicted that there would be no significant interaction between fixation (0 cm, 10 cm) and distance (35 cm, 45 cm) in a mixed 2×2 ANOVA for both the magnetic touch sensation and rubber hand ownership ratings. Twenty participants (age 27 ± 6.7 years, 15 females) took part in Experiment 1b.

To further investigate the relationship between the senses magnetic touch and rubber hand ownership, we examined the correlation between the subjective magnitudes of the two perceptual effects. To control for factors unrelated to the illusion, we compared the synchronous versus asynchronous difference in the average ratings (at the five cm level, because the other

illusion-associated levels, 15–35 cm, did not feature an asynchronous control condition) of the magnetic touch statements (S1–S2) and the rubber hand ownership statements (S5–S6). The degree of linear dependence between the two resulting variables was estimated using the Pearson product-moment correlation coefficient.

To corroborate the questionnaire results from Experiments 1a and 1b with an objective behavioral proxy of limb ownership, we quantified the proprioceptive drift associated with the illusion (for details, see Section 2.5 above). On the basis of our own empirical questionnaire data (Experiments 1a and 1b) and the theoretical arguments outlined above (Fogassi et al., 1996; Kalckert & Ehrsson, 2014; Lloyd, 2007), we expected the distance of 45 cm to fall just outside perihand space and thus to constitute the spatial constraint of the illusion. We therefore used a full factorial design with the factors visuo-tactile temporal congruence (synchronous, asynchronous) and distance (5 cm, 45 cm). In line with this hypothesis, we predicted a significant interaction between visuo-tactile temporal congruence and distance in a 2×2 ANOVA that was driven mainly by an increased proprioceptive drift in the illusion condition (synchronous 5 cm). Twenty participants (age 30 ± 8.5 years, 12 females) were included in Experiment 1c.

2.9. Experiments 2a and 2b—Excluding a contribution of tactile expectation

A previous study has claimed that the rubber hand illusion can be elicited through the mere expectation of a tactile event on the rubber hand (Ferri et al., 2013). In that study, the participants observed an object slowly approaching (2 cm/s)—without touching—a rubber hand, while no touches were delivered to the hidden real hand. If this claim that the mere expectation of tactile stimulation is sufficient to induce a sense of limb ownership were true, then the illusion under investigation should be independent of tactile stimulation of the real hand and the observed reduction in illusion strength associated with the asynchronous visuo-tactile stimulation would be caused by violations of such tactile expectations. To address this issue and to examine the reproducibility of the previous study (Ferri et al., 2013), we included three conditions in Experiments 2a and 2b: (i) visual stimulation in the form of a

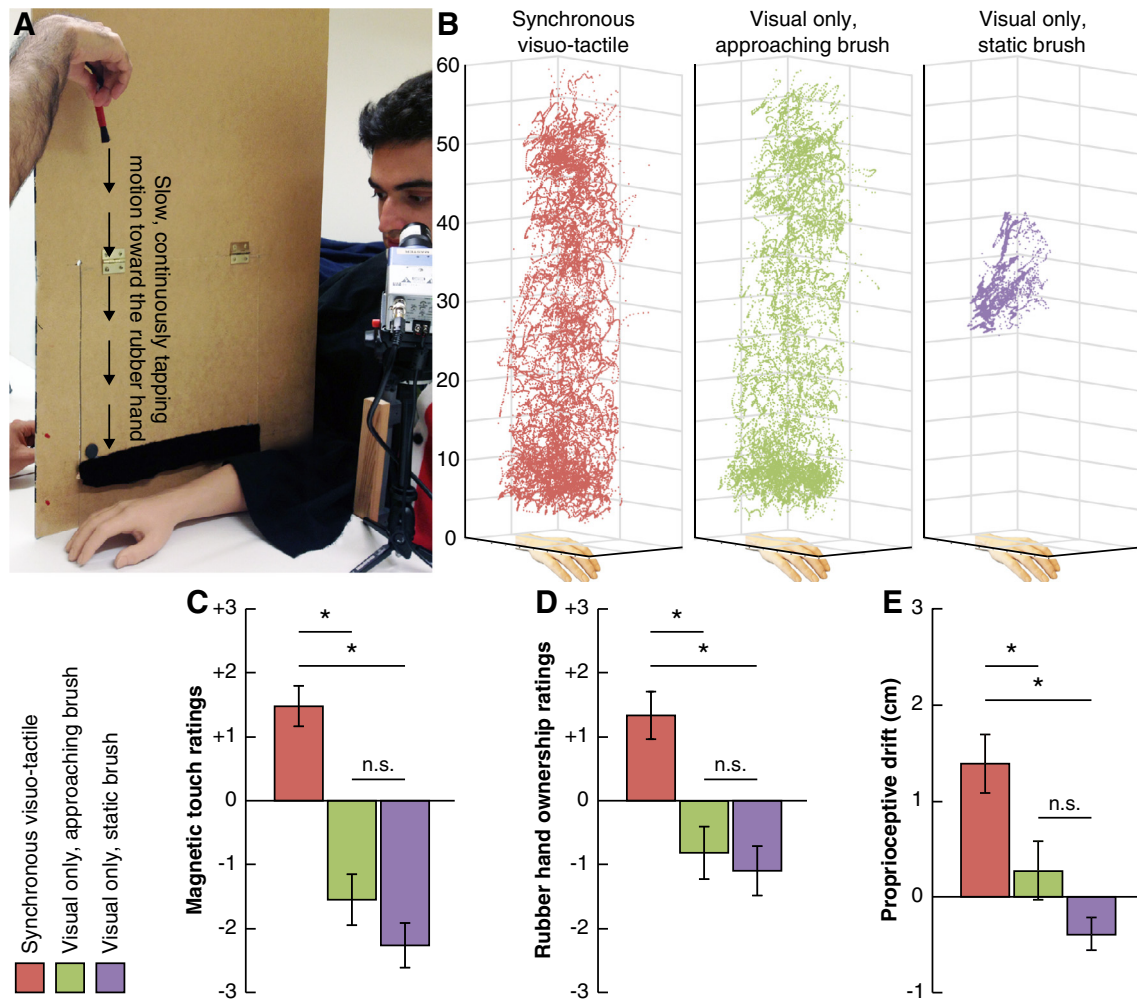


Fig. 3. Excluding the possible contribution of visually induced expectation of tactile stimulation (Experiment 2a and 2b). (A) Experimental setup. In this version of the magnetic touch illusion, the participant observed the brush slowly approaching the rubber hand in a continuous, ‘tapping’ motion while synchronous tapping occurred on the real hand (*synchronous visuo-tactile*). In the control conditions, no tactile stimulation was delivered to the real hand, but the participants viewed either the same approaching ‘tapping’ motion (*visual only, approaching brush*) or a brush held at a fixed position above the rubber hand (*visual only, static brush*). (B) The motion tracking results of the three experimental conditions. (C–E) Results. The reported strength of the sensations of magnetic touch and rubber hand ownership, as well as the proprioceptive drift magnitude, was significantly higher in the *synchronous visuo-tactile* condition than in the *visual only, approaching brush* condition, suggesting that concurrent tactile stimulation is essential to the illusion. Furthermore, there were no significant differences between the *visual only, approaching brush* versus the *visual only, static brush* conditions for magnetic touch, rubber hand ownership ratings, or proprioceptive drift. These results show that tactile expectations putatively elicited by merely viewing an object approaching in the perihand space did not contribute to the emergence of limb ownership or magnetic touch sensations in the present paradigm (see Section 4).

brush slowly approaching (2 cm/s) the rubber hand in a continuous, ‘tapping’ motion in combination with synchronous tapping on the real hand (*synchronous visuo-tactile*); (ii) only visual stimulation featuring the same approaching ‘tapping’ motion toward the rubber hand, presumably eliciting “tactile expectations” (Ferri et al., 2013) (*visual only, approaching brush*); and (iii) only visual stimulation featuring a brush held at a fixed position approximately 35 cm above the rubber hand, which should not induce tactile expectations (Ferri et al., 2013) (*visual only, static brush*) (Fig. 3A and B). The participants had no fixation point but were instructed to attentively look at the brush moving toward the rubber hand. We hypothesized that synchronous visual and tactile stimulation is critical to eliciting the illusion and that the mere sight of an object moving toward the rubber hand within its peripersonal space would not be sufficient to elicit the perceptual effects under investigation. Thus, we expected to find a significant difference between *synchronous visuo-tactile* versus the *visual only, approaching brush* condition with respect to the magnetic touch sensation, as well as rubber hand ownership (two planned paired

t-tests). Furthermore, to investigate the reproducibility of the previously observed ‘tactile expectation effect’ (Ferri et al., 2013), we contrasted *visual only, approaching brush* versus *visual only, static brush* conditions (paired *t*-test) and examined the hypothesis of significantly stronger rubber hand ownership ratings in the *visual only, approaching brush* condition. Twenty-one participants (age 27 ± 5.1 years, 12 females) were included in Experiment 2a. The same set of participants had previously taken part in Experiment 1a.

To corroborate the questionnaire results, we recruited a separate group of participants ($n = 20$, age 24 ± 4.0 years, 12 females) and measured the proprioceptive drift. The experimental procedures were identical to those in Experiment 2a. In line with the rationale described above, we expected to find a significantly greater drift in the *synchronous visuo-tactile* compared with the *visual only, approaching brush* condition. We also examined the hypothesis of Ferri et al. (2013) for a significant difference between the *visual only, approaching brush* versus *visual only, static brush*.

2.10. Experiments 3a and 3b—The effect of a physical barrier on magnetic touch

The aim of Experiment 3a was to investigate whether the magnetic touch illusion could penetrate a physical barrier. Consistently with the notions that the representation of peripersonal is influenced by an individual's ability to directly act upon or reach to a given portion of space (Maravita, Spence, & Driver, 2003) and that solid non-corporal objects disrupt the visuo-tactile integration processes associated with the rubber hand illusion (Guterstam et al., 2013; Tsakiris, Carpenter, James, & Fotopoulou, 2010), we hypothesized that a physical barrier would impose a spatial restriction on the perihand space. Under the assumption that the magnetic touch illusion is a perceptual correlate of visuo-tactile integration in perihand space, we predicted that the illusion strength would be significantly reduced by a physical barrier obstructing the illusory rays of magnetic force between the brush and the rubber hand. We tested this hypothesis by introducing a 3-cm-thick metal table between the brush moving in mid-air and the rubber hand (Fig. 4A). We included four conditions in a 2×2 factorial design: synchronous or asynchronous visuo-tactile stimulation with or without a 'barrier' between the rubber hand and the brush in mid-air. Notably, the participant's viewing angle ensured that the rubber hand and the fixation point were in full view in the two barrier conditions. The general experimental procedures were identical to those in Experiment 1a, and the brushstrokes were always delivered 15 cm above the rubber hand. We predicted a significant interaction between the factors visuo-tactile temporal congruence (synchronous, asynchronous) and barrier (free empty space, barrier) in a 2×2 ANOVA. However, because the data were not normally distributed, we performed the non-parametric Friedman

test in combination with Wilcoxon signed-rank tests between the conditions of interest. Twenty participants (age 24 ± 4.0 years, 12 females) were included in Experiment 3a. The same set of participants had previously taken part in Experiment 2b.

To complement the questionnaire results of Experiment 3a with an objective behavioral proxy of the illusion, we measured the proprioceptive drift according to the procedures described above for Experiments 1c and 2b in a separate group of twenty participants (age 27 ± 6.9 years, nine females). The experimental design and planned statistical comparisons were identical to those in Experiment 3a.

2.11. Experiment 4—The three-dimensional extension of the illusion

The aim of Experiment 4 was to map out the spatial extension of the magnetic touch illusion in three dimensions. The results of Experiments 1–3 support the notion that the illusory sensation of a magnetic force or force field between the brush moving in mid-air and the rubber hand reflects a perceptual correlate of visuo-tactile integration in peripersonal space. On the basis of neurophysiological evidence showing that the visual RF of peripersonal space neurons typically extends ≤ 40 cm from the tactile RF (Fogassi et al., 1996) and follows changes in hand position (Graziano et al., 1997; Obayashi, Tanaka, & Iriki, 2000), we hypothesized the magnetic touch illusion would display similar spatial characteristics. To map out the 3-D extension of the illusion, we constructed a setup in which the participant's right hand was hidden in a fixed position below a small 15-cm-high table. The rubber hand was placed directly on top of the small table in one of two different positions, which were displaced by eight cm laterally or medially with respect to the real hand below (Fig. 5A). A fixation

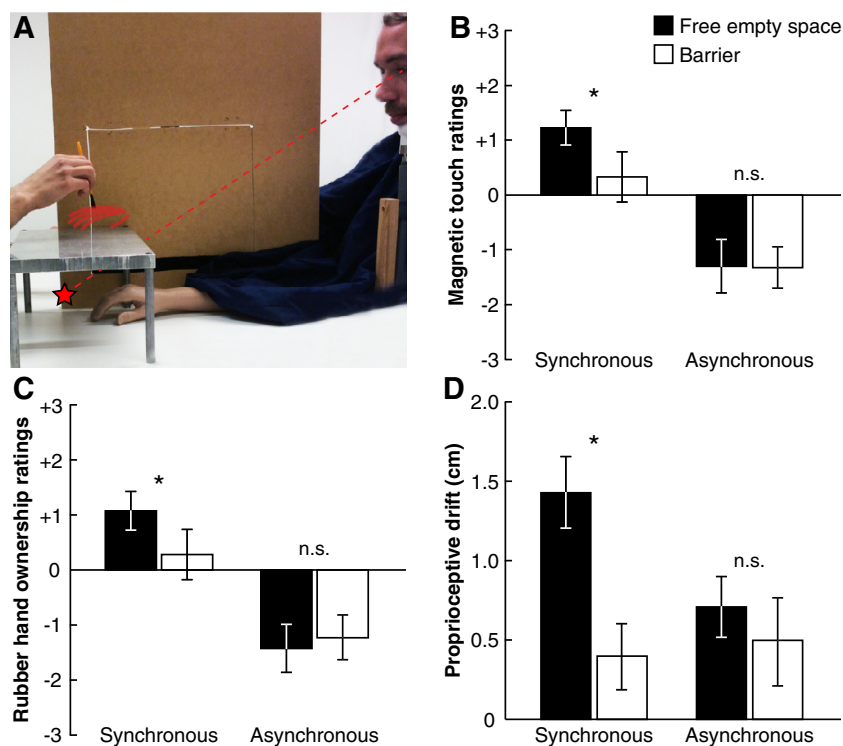


Fig. 4. The effect of a physical barrier on magnetic touch (Experiment 3a and 3b). (A) Experimental setup. Synchronous or asynchronous brushstrokes were delivered to the participant's hidden right hand and in mid-air 15 cm above the rubber hand in either the absence ("free empty space") or presence ("barrier" as shown in the figure) of a 3-cm-thick metal barrier between the rubber hand and the brush. Crucially, the fixation point, rubber hand, and brush were in the participant's line of sight in all conditions. (B–D) Results. In the absence of a barrier, the synchronous condition was associated with significantly stronger magnetic touch and rubber hand ownership ratings and a greater proprioceptive drift toward the rubber hand than was the asynchronous condition. No such significant differences were observed in the barrier conditions, suggesting that the introduction of a physical barrier between the rubber hand and the brush disrupts the magnetic touch illusion.

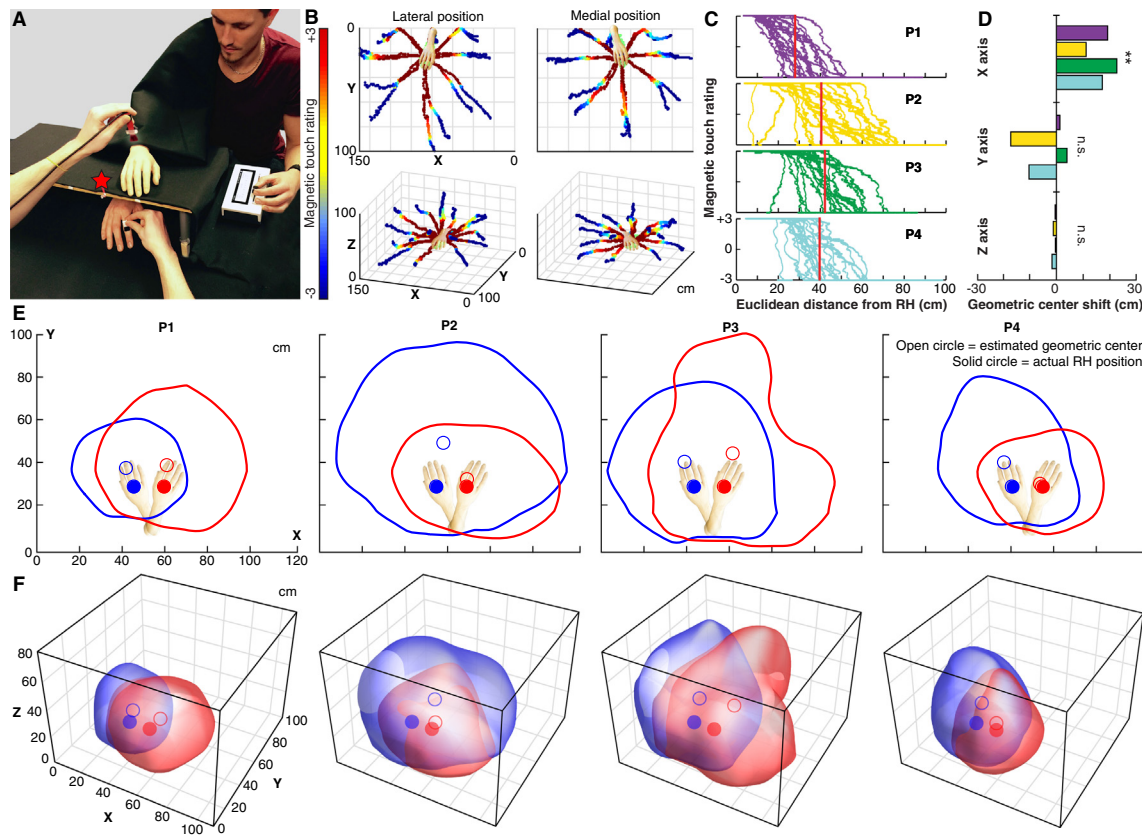


Fig. 5. The three-dimensional spatial extension of the illusion. (A) Setup. The experimenter used two small brushes to elicit the magnetic touch illusion by synchronously tapping the participant's hidden real hand and in mid-air above the rubber hand placed in full view in one of two positions (here, the medial position is shown). Once the illusion had been established, the experimenter slowly increased the distance between the brush in mid-air and the rubber hand in one out of 17 predefined directions (panel B). The participants were instructed to maintain their gaze at a fixation point (indicated by the red star) placed between the two rubber hand positions and to continuously rate the strength of the illusion by using a sliding bar. By synchronizing the real-time illusion vividness rating with the motion tracking data from the brush moving in mid-air, we mapped out the 3-D spatial extension of the illusion in four individuals. (B) The raw data for the two rubber hand positions, consisting of the spatial coordinates for the 17 'tapping trajectories', color-coded according to the illusion vividness rating, are shown for one representative participant (P1). (C) The rated illusion strength is plotted as a function of the Euclidean distance from the rubber hand (positioned medially) for each participant. Each line represents one of the 17 directions, and the red vertical line shows the median illusion break point. The illusion showed a non-linear sharp decline at approximately 20–80 cm (depending on the direction) that was consistent across participants (mean illusion break point \pm SD: 37.6 ± 6.5 cm), which is in line with the results of Experiment 1. (D) To investigate whether the illusion followed changes in the rubber hand position, we examined the difference in spatial coordinates of the geometric center for the lateral versus medial positions along the X-axis (the Y- and Z-axes served as controls). All the participants showed a large and consistent shift in the estimated geometric center along the X-axis (mean shift: 17.5 ± 4.8 cm; $P = 0.0054$) that reflected the change in rubber hand position (16 cm). The shifts along the Y- and Z-axes were non-significant (both $P > 0.05$). These results suggest that the multisensory integrative processes underlying the magnetic touch illusion operate in hand-centered spatial reference frames. (E and F) The 3-D extension of the illusion, extrapolated from the raw data displayed in panel B (see Section 2.11 for details), is shown here in 2D at a slice along the X-Y-plane at the height of the rubber hand knuckles (panel E) and in 3-D (panel F). The solid circles represent the actual rubber hand positions, and the open circles represent the estimated geometric center (blue = medial position; red = lateral position). (A–F) P1–P4 = Participant 1–4. RH = rubber hand. ** $P < 0.01$. n.s. = non-significant ($P > 0.05$).

point was placed between the positions of the rubber hand. The experimenter induced the illusion by applying synchronous tapping movements to the hidden real hand and in mid-air five cm above the rubber hand. Once the participant reported the onset of the illusion, the experimenter began to slowly increase the distance (approximately 2 cm/s) between the brush tapping in mid-air and the rubber hand. To systematically map out the 3-D extension of the illusion, the tapping brush moved away from the rubber hand in one out of 17 predefined directions: eight directions in 45° steps in-plane with the rubber hand, eight directions in 45° steps projected at an angle of 45° vertical to the plane of the rubber hand, and one direction straight upward from the rubber hand (Fig. 5B). The participants were instructed to continuously rate the subjective strength of the magnetic touch sensation (statement S2 in Table 1) by using a sliding bar (TSD115 Variable assessment transducer, BIOPAC, Goleta, California, USA) placed in their left hand. We used in-house software (developed by author HZ) to synchronize the motion tracking data from the sensor attached to the brush moving in mid-air with the input from the

sliding bar representing the participant's experience of the illusion's vividness in real time. As such, a given data point in 3-D space was assigned an illusion vividness value between -3 and $+3$, which is denoted by the color code in Fig. 5B. Finally, the location of the rubber hand within the coordinate system was determined by systematically moving the motion sensor across the entire rubbery skin surface.

We mapped the spatial extension of the illusion for the two rubber hand positions in four participants (age 30 ± 2.9 years, 1 female), all of whom had displayed a robust illusion experience (at least $+2$ rating of statement S2) in one of the previous experiments. For each participant, the data were extrapolated to a discrete 3-D volume through the following method. We first defined a $180 \times 180 \times 180$ cm³ cube with the spatial resolution of $1 \times 1 \times 1$ cm³. The fixed location of the motion tracking base station represented the origin coordinate [$X = 1, Y = 1, Z = 1$]. To each voxel, we assigned an illusion vividness value to the nearest (in terms of Euclidean distance) experimentally tested data point. Because of the sparseness of the data points further away from

the rubber hand (approximately 30 cm at the illusion ‘break point’; see Fig. 5B), the data were then smoothed with a moving average technique in which the value of each voxel was replaced with the mean value of a $30 \times 30 \times 30 \text{ cm}^3$ cube centered on that voxel. The smoothing procedure ensured a relatively homogenous surface among the experimentally tested directions. In accordance with the results of Experiment 1, we defined the illusion break point as the spatial coordinates where the rated illusion strength dropped below zero, i.e., when the participants began to deny experiencing the illusion. The 3-D surface of the illusion extension was drawn using linear interpolation (Fig. 5E and F). For display purposes, Fig. 5E shows the illusion extension for each rubber hand position in the X-Y plane at the height of the knuckles of the rubber hand, whereas Fig. 5F shows their entire 3-D surface.

To assess whether the illusion was anchored to the rubber hand, we calculated the geometric center of the illusion volume for each rubber hand position. We then tested for significant shifts along the X, Y and Z directions by using paired *t*-tests. Because the rubber hand position was changed only in the horizontal plane, we predicted that the geometric center would significantly shift only along the X-axis. We would like to emphasize that even though our sample size is “extremely low” ($n = 4$), it is possible to make group-level statistical inferences using the *t*-test, given that the effect size is large and that the shift direction is consistent across all participants (de Winter, 2013).

2.12. Statistical approach

The Kolmogorov-Smirnov test was used to assess the normality of the data. For normally distributed data sets, we used *t*-tests to analyze differences between two conditions and repeated measures ANOVAs to analyze the differences among more than two conditions. For data sets that were not normally distributed, we used the non-parametric Wilcoxon signed-rank test to analyze differences between two conditions and the Friedman test to analyze differences among more than two conditions. For simplicity, two-tailed tests were used for all analyses, and the alpha was set at 5%. The goodness of fit analyses in Experiments 1a and 1b were carried out using the Curve Fitting Toolbox for MatLab version R2015a (MathWorks, Massachusetts, USA). The other statistical analyses were carried out in SPSS version 21 (IBM, New York, USA). The 3-D extension of the illusion was estimated using Mathematica version 10 (Wolfram, Illinois, USA), and the statistical procedures are described above (see Section 2.11).

3. Results

3.1. Experiments 1a, 1b, and 1c—The spatial extension of the magnetic touch illusion

The first aim was to test the prediction that the magnetic touch illusion is dependent on synchronous visuo-tactile stimulation within the space close to the body. To this end, we first compared synchronous and asynchronous brushstrokes delivered to the real hand and in mid-air near (5 cm) or far (55 cm) above the rubber hand. In support of our hypothesis, the results showed that the synchronous 5 cm condition was associated with significantly higher ratings in the questionnaire statements that reflected the illusory experiences of magnetic touch and rubber hand ownership (three-way interaction visuo-tactile temporal congruence \times distance \times statement type, for both gaze positions, all $P < 0.001$; Fig. 1C–F), as well as a significantly greater proprioceptive drift toward the rubber hand (interaction visuo-tactile temporal congruence \times distance, $P < 0.001$; Fig. 2). In a *post hoc* control analysis, we found that the differences in mean coordinates and standard deviations of the brushstroke trajectories in the synchronous and

asynchronous conditions (Fig. 1B) were negligible—on the order of 1 cm—in all spatial dimensions and thus could not explain the observed differences in the strength of the illusion. The questionnaire ratings of magnetic touch sensation and rubber hand ownership were strongly correlated in both Experiment 1a ($r = 0.78$, $P < 0.001$; Fig. 1G) and Experiment 1b ($r = 0.45$, $P = 0.045$; Fig. 1H), suggesting an intimate relationship between tactile referral in peripersonal space and the feeling of limb ownership.

Second, we examined the prediction that the illusion strength would display a non-linear decay featuring a significant drop at an approximate distance of 40 cm between the rubber hand and the brush in mid-air, reflecting the visual RF properties of peripersonal space neurons (Fogassi et al., 1996; Kalckert & Ehrsson, 2014; Lloyd, 2007). The results showed that a sigmoid function—in comparison with a linear and a logarithmic function—was the best *R*-squared curve fit for the questionnaire data regardless of statement category (magnetic touch sensation or rubber hand ownership) and gaze (0 cm or 10 cm), as shown in Fig. 1C–F and Table 2. For the lower fixation point (0 cm; Experiment 1a), the only significant reduction in the illusion strength between neighboring levels of mid-air brushing occurred between 35 and 45 cm (Fig. 1C and D), which is compatible with our *a priori* hypothesis. The higher fixation point (10 cm; Experiment 1b) was also associated with a reduction (albeit less significant), in illusion strength between 5 and 15 cm (Figure E and F), which supposedly reflected that the 5-cm level in that experiment was the only level at which the brush in mid-air and the rubber hand were on the same side of the fixation point.

Finally, we sought to exclude the possibility that the non-linear illusion decline between 35 and 45 cm might merely be due to the visual impression of the brush falling in the far peripheral field of vision and that the spatial constraints of the illusion might consequently be defined in a purely retinotopic spatial reference frame. To this end, we tested whether elevating the level of the gaze by ten cm would be accompanied by a similar upward shift in the spatial extension of the illusion, by using a mixed 2×2 ANOVA featuring the between-subject factor gaze (0 cm, 10 cm) and the within-subject factor distance (35 cm, 45 cm). The interaction gaze \times distance was non-significant in terms of both magnetic touch ($F = 0.01$, $P = 0.92$) and rubber hand ownership ($F = 0.71$; $P = 0.40$). Importantly, the magnetic touch sensation was not significantly affected by gaze (main effect: $F = 0.07$; $P = 0.80$), although the participants rated rubber hand ownership lower when the fixation point was placed farther from the rubber hand (main effect of gaze: $F = 5.09$, $P = 0.03$). In conjunction with the observed similarities in the curve shape and a significant reduction in the illusion strength between 35 and 45 cm (Fig. 1C and D versus 1E and F), these results suggest that the spatial extension of the illusion could not be explained by mechanisms operating in retinocentric coordinates but that such a mechanism must involve

Table 2

Non-linear decay in illusion strength. A sigmoid curve best described the decline in illusion strength as a function of the distance between the rubber hand and the brush moving in mid-air. The results are displayed separately for the two gaze positions and questionnaire statement categories.

		Goodness of fit (R^2)		
		Sigmoid	Logarithmic	Linear
Fixation 0 cm	Magnetic touch sensation	0.98 ^a	0.74	0.93
	Rubber hand ownership	0.91 ^a	0.75	0.88
Fixation 10 cm	Magnetic touch sensation	0.93 ^a	0.86	0.92
	Rubber hand ownership	0.98 ^a	0.95	0.94

^a Best *R*-square fit.

spatial reference frames that are independent of gaze, such as body- or body part-centered reference frames.

3.2. Experiments 2a and 2b—Visuo-tactile integration versus visually induced tactile expectation

The aim of Experiments 2a and 2b was to disambiguate the hypothesized contribution of visuo-tactile integration in the magnetic touch illusion from the possible effect of tactile expectations automatically triggered by viewing an object moving toward the hand in peripersonal space. This investigation was motivated by a previous study claiming that the expectation of tactile stimulation alone—in the form of an object slowly approaching the rubber hand without touching it—is sufficient to induce a vivid illusion of rubber hand ownership (Ferri et al., 2013). To address this issue, we adapted our illusion setup to mimic the setup developed by Ferri and colleagues as closely as possible (see Section 2). Here, the brush moving in mid-air approached the rubber hand in a slow, continuous, tapping motion that occurred in combination with synchronous tapping on the real hand (*synchronous visuo-tactile*), without tapping on the real hand (*visual only, approaching brush*), or with just the vision of the rubber hand with the brush in mid-air held in a static position (*visual only, static brush*). Consistently with our hypothesis, the results showed that the *synchronous visuo-tactile* condition compared to the *visual only, approaching brush* condition was associated with significantly higher questionnaire ratings of magnetic touch ($t = 6.79$, $P < 0.001$; Fig. 3C) and rubber hand ownership ($t = 5.67$, $P < 0.001$; Fig. 3D), as well as greater proprioceptive drift toward the rubber hand ($t = 3.09$, $P = 0.006$; Fig. 3E). These results show that the magnetic touch illusion is dependent on congruent tactile and visual stimulation in peripersonal space, in addition to any expectation effect resulting from merely viewing a moving object near the hand. Moreover, the *visual only, approaching brush* condition was associated with negative questionnaire ratings (i.e., on average, the participants denied the illusory experiences) and did not significantly differ from the *visual only, static brush* control condition for the magnetic touch sensation ($t = 1.98$, $P = 0.062$; Fig. 3C) or rubber hand ownership ($t = 0.98$, $P = 0.339$; Fig. 3D). In line with these negative questionnaire results, we observed no significant differences in proprioceptive drift between the *visual only, approaching brush* and the *visual only, static brush* conditions ($t = 1.76$, $P = 0.095$; Fig. 3E). Thus, the visually induced tactile expectation effect reported by Ferri and colleagues was not replicated in the present study.

3.3. Experiments 3a and 3b—The effect of a physical barrier on magnetic touch

The goal of Experiments 3a and 3b was to examine whether the illusory sensation of magnetic touch would be maintained even when a solid barrier was introduced between the rubber hand and the brush moving in mid-air. To address this question, we compared *synchronous* and *asynchronous* brushstrokes on the real hand and in mid-air 15 cm above the rubber hand, with (*barrier*) or without (*free*) a 3-cm-thick metal plate positioned between the rubber hand and the brush (Fig. 4A). Compared with the *synchronous barrier* condition and the two asynchronous conditions, the participants in the *synchronous free* condition reported significantly stronger sensations of magnetic touch ($\chi^2 = 26.15$, $P < 0.001$; pairwise contrasts versus each control condition, all $P < 0.05$; Fig. 4B) and rubber hand ownership ($\chi^2 = 32.59$, $P < 0.001$; pairwise contrasts versus each of the three control conditions, all $P < 0.05$; Fig. 4C) and displayed a greater proprioceptive drift toward the rubber hand (although the interaction visuo-tactile temporal congruence \times barrier interaction was

non-significant, $F = 2.89$, $P = 0.105$, all of the pairwise contrasts versus the control conditions, were $P < 0.05$; Fig. 4D). These results suggest that solid barriers in the space close to the body restrict the spatial extension of the magnetic touch illusion, which we hypothesize is reflected in the restriction of the visual RFs of perihand neurons.

3.4. Experiment 4—The three-dimensional extension of the illusion

The aim of Experiment 4 was to map out the spatial limits of the magnetic touch illusion in 3-D. To this end, we synchronized 3-D motion tracking of the brush in mid-air with real-time illusion vividness ratings and used this setup to systematically map out the illusion decline with distance in 17 directions for two different rubber hand positions with four participants (Fig. 4A and B). The results showed that the magnetic touch illusion extended fairly homogeneously around the rubber hand (Fig. 4E and F) and displayed a non-linear abrupt decline (a sigmoid function was a better fit than a linear function for all four participants; Fig. 5C) at the mean distance of 38.7 ± 5.7 cm (\pm SD) (39.8 ± 5.5 cm and 37.6 ± 6.5 cm for the lateral and medial rubber hand position, respectively; Fig. 5C), results consistent with those from Experiment 1. Crucially, the geometric center of the “illusion volume” followed changes in the rubber hand position for all four participants (Fig. 5D and E). The estimated geometric center shifted 17.5 ± 4.8 cm along the X-axis, on average, which mirrored the 16-cm difference between the rubber hand positions in the horizontal plane. Because the shift was large and consistent across all four participants, it was statistically significant at the group-level ($t = 7.27$, $P = 0.0054$, paired t -test) despite our small sample size (de Winter, 2013). In two control analyses, we estimated the shifts along the Y- and Z-axes, which were both non-significant ($P > 0.05$; Fig. 5D). In addition to providing a qualitative validation of the results of Experiment 1, these results suggest that the illusion is anchored to the rubber hand and that the processes underpinning the magnetic touch illusion thus operates in hand-centered spatial reference frames. Finally, visual inspection of the “illusion volumes” seemed to suggest that the spatial extension of the illusion might change with the rubber hand position (see P1, P2, and P4 in Fig. 5E and F). However, the results across participants and medial-lateral rubber hand positions were inconsistent and should be systematically investigated in future studies with larger sample sizes and multiple rubber hand positions.

4. Discussion

In summary, we used motion tracking and multiple behavioral measurements to characterize a perceptual illusion that allows healthy participants to experience a “magnetic force” radiating from a brush moving in mid-air to the surface of a rubber hand. This magnetic touch illusion is induced by applying synchronous brushstrokes on the participant’s hidden hand and in mid-air at some distance above a fully visible rubber hand. Three main conclusions can be drawn from the data. First, the magnetic touch illusion exhibited a non-linear decay at a distance of approximately 40 cm from the rubber hand that was independent of gaze direction. In addition, the illusion was spatially anchored to the rubber hand, i.e., the portion of space in which the illusion could be elicited followed changes in rubber hand position, an observation bearing close similarities to the neurophysiological properties of peripersonal space neurons. Second, the integration of visual and tactile stimuli was crucial, and the mere expectation of touch—which is likely to be triggered when seeing a brush moving toward the hand in peripersonal space—contributed neither to the magnetic touch sensation nor to the feeling of rubber hand ownership,

which challenges the findings of a previous study (Ferri et al., 2013). Finally, the illusory magnetic force field could not be induced when a physical barrier was introduced between the rubber hand and the brush in mid-air, suggesting that the underlying visuo-tactile integrative mechanisms are restricted by solid barriers within the visual perihand space. Together, our findings provide converging evidence for the notion that the magnetic touch illusion reflects the visuo-tactile RF properties of hand-centered perihand neurons, potentially constituting a perceptual correlate of visuo-tactile integration in peripersonal space.

The present illusion setup was inspired by a previous study using a virtual reality (VR) version of the rubber hand illusion (Hohwy & Paton, 2010). In that study, the experimenter first induced a sense of ownership of a virtual hand that was spatially co-aligned with the real hand and then elevated the brush and continued applying brushstrokes five cm above the hand, resulting in the experience of magnetic touch. In the present study, we show that the magnetic touch illusion can be elicited outside of VR, with no prior induction of ownership of the artificial limb and despite a visuo-proprioceptive conflict between the seen and felt hands. These results suggest that visual stimulation within an artificial hand's perihand space in conjunction with spatio-temporally congruent tactile stimulation can drive the remapping of the position sense and the emergence of ownership sensations. Furthermore, our findings suggest that the magnetic touch phenomenon and rubber hand ownership are correlated and concurrent, which argues against the interpretation that the brain integrates the visual signals from the brush moving in mid-air with tactile input (resulting in the perception of magnetic touch) only if ownership of the rubber hand has previously been established by inducing the normal rubber hand illusion (Hohwy & Paton, 2010). Instead, our results suggest that the magnetic touch illusion is a perceptual correlate of the integration of spatio-temporally congruent visual stimuli in perihand space and tactile signals—a mechanism considered to be key to the emergence of body ownership (Ehrsson, 2012; Guterstam et al., 2013; Makin et al., 2008; Moseley, Gallace, & Spence, 2012; Samad, Chung, & Shams, 2015). Although there is a visible gap, the brain interprets the visual information from the brush in mid-air and the rubber hand below as causing the tactile and proprioceptive sensations from the real hidden hand, resulting in the coherent multisensory perception of a single hand (the rubber hand) being touched by an invisible magnetic force “radiating” from the tip of the brush onto the portion of the rubber hand skin surface corresponding to the location where the real hand is touched. Why is this “physically impossible” visuo-tactile integration permitted? We speculate that the answer lies in the fact that we are used to objects close to our bodies causing sensations on the skin surface without direct physical contact (e.g., air flow or radiating heat) and that unlike objects far from our bodies, an object moving within peripersonal space represents a potential impending tactile sensation (Graziano & Cooke, 2006), which thereby facilitates the integration of vision and touch. Thus, our findings suggest that the multisensory integrative processes involved in the magnetic touch illusion are similar to those underpinning the classical rubber hand illusion (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Samad et al., 2015; Tsakiris & Haggard, 2005) and that these processes are capable of “filling the gap” between the brush in mid-air and the rubber hand, as long as the brush remains within the rubber hand's peripersonal space.

The phenomenology of the magnetic touch illusion bears a close resemblance to the RF properties of peripersonal space neurons, which have been identified in the putamen (Graziano & Gross, 1993) and the premotor (Graziano et al., 1997; Rizzolatti et al., 1981) and posterior parietal cortices (Avillac, Hamed, & Duhamel, 2007; Graziano, 2000). This set of anatomically interconnected regions receives convergent visual, tactile, and proprioceptive

inputs and contains neuronal populations that build representations of the body and its surrounding peripersonal space (Graziano & Botvinick, 2002). Single-unit recordings in macaques have identified trimodal neurons featuring visual RFs that (i) extend up to 40 cm from a tactile RF (Fogassi et al., 1996), (ii) follow changes in limb position (Graziano, 1999), and (iii) are independent of gaze direction (Graziano & Gross, 1998). In line with our *a priori* hypothesis, the results from Experiments 1a–1c and 4 show that the magnetic touch illusion is dependent on temporally congruent visuo-tactile stimulation and that its spatial boundaries mimic RF properties (i)–(iii), suggesting that the magnetic touch illusion is closely related to visuo-tactile integration within perihand space. Furthermore, the vividness of the magnetic touch illusion was strongly correlated with perceived rubber hand ownership, suggesting that these two perceptual effects depend on similar underlying processes. These results not only extend beyond previous studies (Brozzoli et al., 2011; Guterstam et al., 2013; Lloyd, 2007; Pavani, Spence, & Driver, 2000; Preston, 2013) in showing an intimate relationship between multisensory integration in peripersonal space and limb ownership, but also reveal a perceptual correlate of the visuo-tactile integration in peripersonal space in the form of an illusory magnetic force between the brush moving in mid-air and the owned artificial hand.

The behavioral evidence for the existence of a functional representation of peripersonal space in humans draws primarily from neuropsychological studies of patients with deficits that manifest after brain lesions (Brozzoli, Ehrsson, & Farnè, 2014; Lådavas & Farnè, 2004). For instance, it has been shown that spatial neglect can selectively affect the space near or far from the body (Cowe, Small, & Ellis, 1994; Halligan & Marshall, 1991) and that cross-modal extinction, i.e., the failure to perceive a sensory stimulus in the contralesional space when a stimulus in another sensory modality is presented in the ipsilesional space, can be specific to the space near the patient's body (di Pellegrino, Lådavas, & Farnè, 1997). Similar cross-modal interference effects specific to the near-personal space have been observed in healthy participants performing a visuo-tactile congruency task (Holmes, Calvert, & Spence, 2004; Serino, Canzoneri, & Avenanti, 2011; Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, & Holmes, 2004). As discussed above, the behavioral properties of the rubber hand illusion in terms of the maximal distance between the real hand and the rubber hand (Kalckert & Ehrsson, 2014; Lloyd, 2007) and the anatomical spatial congruence (Ehrsson et al., 2004; Farnè, Pavani, Meneghello, & Lådavas, 2000; Pavani et al., 2000; Tsakiris & Haggard, 2005) imply the involvement of a hand-centered representation of peripersonal space. Notably, however, none of the above-mentioned experimental paradigms allow the patient or participant to consciously perceive a specific extended perceptual “object” (i.e., the force field) that corresponds to visuo-tactile integration in peripersonal space. Instead, they show that the integration of signals from different sensory modalities is facilitated within near-personal space, which is quantifiable through indirect measures, such as differences in reaction time (Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, et al., 2004). The magnetic touch illusion probably reflects a similar facilitation of multisensory integration within peripersonal space; namely, the integration of visual signals from the brush moving in mid-air and spatio-temporally congruent tactile signals but with the important addition that it is a conscious perceptual effect and thus is introspectively accessible to the participant, even allowing an individual to readily report the spatial limits of the illusory force-fields on a single-trial basis (see the results of Experiment 4). This feature constitutes a major practical advantage compared with previous paradigms, such as the cross-modal congruency task, in which the near-specific effect on reaction times is (most probably) subconscious and is usually presented at the

group-level (Farnè, Demattè, & Làdavas, 2003; Spence, Pavani, Maravita, et al., 2004). In light of the above, we propose that the magnetic touch illusion constitutes a powerful new experimental tool for investigating the representation of peripersonal space in humans, possibly constituting a perceptual correlate of activity in populations of perihand neurons with visuo-tactile RFs. However, it should be noted that the present work is limited to the context of illusory ownership of an artificial limb, and whether the illusion can also occur for the real hand remains unexplored. On the basis of the notion that multisensory peripersonal space mechanisms are involved in self-attributing not only artificial limbs but also one's real body parts (Brozzoli et al., 2011; Gentile, Guterstam, Brozzoli, & Ehrsson, 2013), we hypothesize that the magnetic touch illusion will be inducible for the real hand as well. Furthermore, in line with previous behavioral studies, we predict that the strength of the magnetic touch sensation in patients with extinction will be reduced in their contralesional space when competing visual or tactile stimuli are presented in their ipsilesional space.

The results of Experiments 3a and 3b showed that the magnetic touch sensation is disrupted by the introduction of a metal block between the brush and the rubber hand; these results have implications for understanding of the effects of physical barriers on the spatial extension of peripersonal space. The literature surrounding this issue is ambiguous. Previous studies have shown that the perihand space is dynamically updated after active tool use (Farnè & Làdavas, 2000; Iriki, Tanaka, & Iwamura, 1996; Maravita, Spence, Kennett, & Driver, 2002; but see Holmes, 2012 for a critical view) and that the responses of mirror neurons with multisensory peripersonal space properties are affected by the introduction of a transparent barrier close to the hand (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009), thus supporting a restricting effect of barriers on peripersonal space. In contrast, neuropsychological studies in brain-damaged and healthy participants using cross-modal interaction tasks have found no effect of transparent barriers on near-far-dependent visuo-tactile facilitation or extinction (Farnè et al., 2003; Kitagawa & Spence, 2004). We speculate that the restrictive barrier effect observed in the present study might be related to our use of a thick barrier made out of metal. Whereas both metal and transparent Plexiglas barriers (Farnè et al., 2003; Kitagawa & Spence, 2004) affect the participants' top-down knowledge of the possibility for the visual stimulus to reach the seen hand, a metal barrier also constitutes a salient bottom-up cue for the physical impossibility of the visual stimulus coming into contact with the hand. We speculate that this property is key for the modulating effect of physical barriers on peripersonal space to occur and predict that the magnetic touch illusion will be able to penetrate transparent barriers.

In light of a previous study claiming that ownership of an artificial limb can be induced by merely moving a brush toward the rubber hand in perihand space without touching the participant's real hand (Ferri et al., 2013), we undertook Experiments 2a and 2b to exclude the possibility that our results might be explained by such "expectation effects". In the study by Ferri and colleagues, the participants viewed the experimenter's hand slowly approaching a fully visible rubber hand from above while their real hand was hidden from view. This setup led to a strong sense of rubber hand ownership as judged from the reported questionnaire data, but no apparent sense of magnetic touch (Ferri et al., 2013). Our results clearly demonstrate that the magnetic touch illusion cannot be induced by "tactile expectation" alone and that it is indeed dependent on concurrent tactile stimulation. Moreover, we were unable to replicate the basic effect described by Ferri and colleagues, because neither the rubber hand ownership ratings nor the proprioceptive drift in the tactile expectation condition (*visual only, approaching brush*) differed significantly from the control condition in which the participants simply looked at the rubber hand

(*visual only, static brush*; Experiments 2a and 2b). We matched the key aspects of the previous study and consider it to be unlikely that the rubber hand in our study being displaced horizontally and not vertically with respect to the real hand (Ferri et al., 2013) could explain the absence of any expectation effects, because previous studies have demonstrated that the rubber hand illusion can be robustly elicited using either spatial arrangement (Botvinick & Cohen, 1998; Ehrsson et al., 2004). It also appears improbable that our use of a slightly different visual stimulus, namely the experimenter's hand holding a paintbrush and making small tapping movements while approaching the rubber hand, as compared with Ferri et al. (2013), in which the experimenter's hand made a continuous movement toward the rubber hand without holding a brush, could explain the differences in the results because of two main reasons. First, both visual stimuli represent objects approaching the rubber hand and should thus, in theory, induce "tactile expectations" (Ferri et al., 2013). Second, earlier work has shown that the rubber hand illusion can be elicited using a wide range of visual stimuli, including taps and strokes of varying lengths and trajectories using paintbrushes (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Ehrsson et al., 2004), fingers (Hohwy & Paton, 2010), balls (Brozzoli et al., 2012), ice cubes (Kanaya, Matsushima, & Yokosawa, 2012), or even laser pointer light beams (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007), thus implying that the ownership-illusion is relatively insensitive to the precise visual stimuli used. These results suggest that congruent signals from at least two sensory modalities are necessary to elicit the rubber hand illusion, and the presentation of a visual stimulus in the space near an artificial hand alone is insufficient for ownership sensations to arise. Future studies are needed to exclude cognitive bias, suggestibility and task compliance as explanations of the tactile expectation results presented by Ferri and colleagues.

In conclusion, this study characterized a perceptual illusion in which healthy individuals experience a magnetic force between an artificial hand and an object moving in its surrounding visual space. The results suggest that the illusion is confined to the space close to the hand and is dependent on visuo-tactile integration mechanisms operating in hand-centered spatial reference frames. The present findings offer an important advancement in understanding of the relationship between the representation of peripersonal space and the sense of body ownership—two processes related to the construction of a multisensory boundary separating the body from the external environment.

Conflicts of interest

None.

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