



Sense of ownership and not the sense of agency is spatially bounded within the space reachable with the unaugmented hand

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Abstract

While reaching for a coffee cup, we are aware that the hand we see belongs to us and it moves at our will (reflecting our senses of ownership and agency, respectively), and that the cup is within our hand's reach rather than beyond it (i.e., in reachable space, RS, rather than in non-reachable space, NRS). Accepted psychological explanations of our sense of ownership, sense of agency, and our perception of space surrounding the body as RS or NRS propose a unitary dependence on Euclidean distance from the body. Here, we propose an alternate, affordance-based explanation of experienced ownership, agency, and perception of space surrounding the body as RS and NRS. Adult participants experienced the static rubber hand illusion (RHI) and its dynamic variant, while the rubber hand was either within their arm's reach (i.e., in self-identified RS) or beyond it (i.e., in self-identified NRS). We found that when the participants experienced synchronous visual and tactile signals in the static RHI, and synchronous visual and kinesthetic signals in the dynamic RHI, they felt illusory ownership when the rubber hand was in RS but not when it was in NRS. Conversely, when the participants experienced synchronous visual and kinesthetic signals in the dynamic RHI, they felt agency, regardless of the rubber hand's location. In addition, illusory ownership was accompanied by proprioceptive drift, a feeling that their hand was closer to the rubber hand than it actually was, but agency was not accompanied by proprioceptive drift. Together, these results indicate that our sense of ownership, while malleable enough to incorporate visible non-corporeal objects resembling a body part, is spatially constrained by proprioceptive signals specifying that body part's actual location. In contrast, our sense of agency can incorporate a visible non-corporeal object, independent of its location with respect to the body. We propose that the psychological processes mediating our sense of ownership are closely linked with our perception of space surrounding the body, and that the spatial independence of our sense of agency reflects the coupling between our actions and perception of the environment, such as while using handheld tools as extensions of our body.

Keywords Body ownership · Forward model · Multisensory integration · Rubber hand illusion · Self-attribution · Self-recognition

Introduction

The awareness of our body and of space surrounding our body underlies simple actions like reaching for a coffee cup—for instance, the awareness that the hand we see belongs to us and moves at our will and that the coffee cup

is within our hand's reach. Three distinct neuropsychological processes are associated with this perceptual experience: (a) the sense of ownership, (b) the sense of agency, and (c) the categorization of space surrounding the body (i.e., the space within which we can act with our hands as reachable space, RS; and the space in which we cannot act as non-reachable space, NRS). The sense of ownership refers to the subjective feeling that a body part belongs to one's body (Ehrsson et al. 2004; Tsakiris 2010; Ehrsson 2012). The sense of agency refers to the subjective feeling that a body part moves as and when we desire (David et al. 2008; Engbert et al. 2008; Haggard and Chambon 2012; Chambon et al. 2013; Haggard 2017). Typically, RS is the region of space immediately surrounding our body, and is considered to have a unitary

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dependence on Euclidean distance from the body (Làdavas 2002; Holmes and Spence 2004; di Pellegrino and Làdavas 2015).

The complexity of perceptual organization underlying our sense of ownership, sense of agency, and categorization of space surrounding our body, although typically hidden from our conscious awareness, is apparent in certain neuropathological conditions. For example, in phantom limb syndrome, patients attribute phantom sensations or pain to an amputated limb—claiming to “own” a limb that does not even exist (Flor et al. 2006; Giummarra et al. 2007). In contrast, patients with alien hand syndrome can move their hand but attribute its movement to an alien agent; they feel neither “ownership” nor “agency” over their hand (Doody and Jankovic 1992; Biran and Chatterjee 2004). The perceptual complexity is also apparent in our actions with objects that we use as extensions of our body. When using tools, for example, our sense of agency shifts to the tool (Umiltà et al. 2008; Arbib et al. 2009; Mangalam and Fragaszy 2016; Fragaszy and Mangalam 2018), and the boundary of our RS, as indexed by a variety of responses associated with the concept of peripersonal space, extends to encompass the tool (Farnè and Làdavas 2000; Berti and Frassinetti 2000; Pegna et al. 2001; Holmes et al. 2004; Longo and Lourenco 2006; Canzoneri et al. 2013b). Similarly, the boundary between RS and NRS contracts towards the body following an amputation (Makin et al. 2009; Canzoneri et al. 2013a) and extends away from the body when amputees become accustomed to wearing a prosthetic hand (Canzoneri et al. 2013a).

The above observations highlight the enormous degree of plasticity in our sense of ownership, sense of agency, and categorization of space surrounding our body. Understanding the causal relationships among these psychological phenomena would revolutionize our ability to enhance the embodiment of prosthetic limbs, teleoperated surgical devices, and other human–machine interfaces (Pazzaglia and Molinari 2016; Makin et al. 2017; Yang et al. 2018; Berger et al. 2018; Beckerle et al. 2018). While several models have been proposed to explain the three phenomena individually (Ehrsson et al. 2004; David et al. 2008; Engbert et al. 2008; Tsakiris 2010; Ehrsson 2012; Chambon et al. 2013; Moore 2016) or in pairs (Tsakiris et al. 2006, 2007, Kalckert and Ehrsson 2012, 2014a; D’Angelo et al. 2018), none of the existing models incorporates all three as components of an integrated dynamic system.

The rubber hand illusion (RHI) is a commonly used paradigm to study our senses of ownership and agency. The RHI paradigm allows for manipulation of the senses of ownership and agency in healthy individuals. In the static RHI, synchronously stroking the index fingers of the participant’s occluded hand and of a visible fake rubber hand elicits strong illusory sense of ownership over the rubber hand (e.g., Botvinick and Cohen 1998; Ehrsson

et al. 2004, 2005). The participants perceive their hand to be closer to the fake hand than it is—a phenomenon known as proprioceptive drift (Botvinick and Cohen 1998; Kalckert and Ehrsson 2014b). The illusory sense of ownership is so strong that histamine reactivity in the participant’s biological hand increases (Barnsley et al. 2011) as if their brain is rejecting their biological hand and instead, is accepting the rubber hand as their hand. In addition, threatening the rubber hand (e.g., puncturing the rubber hand during the illusion) even elicits a cortical anxiety response (Ehrsson et al. 2007). In the dynamic RHI, synchronous movements of the index finger of the rubber hand (owing to mechanical coupling with the index finger of the participant’s hand) elicits strong sense of agency over the rubber hand, in addition to strong illusory sense of ownership (e.g., Dummer et al. 2009; Kalckert and Ehrsson 2012).

Taken together, we interpret the findings from the body of studies using the RHI paradigm as indicative that our senses of ownership and agency have entirely distinct multisensory origins. Figure 1 provides a flowchart describing our view of various afferent and efferent pathways that contribute to the multisensory origins of our senses of ownership and agency. Other than the complete dissociation between the multisensory origins of our sense of ownership and agency which we propose in the present study, our model is largely consistent with existing views. Our sense of ownership is primarily grounded in the detection of statistical correlations in multisensory afferent signals, which ultimately results in an amodal neural representation of the body (Blanke 2012). Multisensory integrative processes typically privilege visual signals, as they have higher reliability and spatial acuity than tactile and proprioceptive/kinesthetic signals (Stein and Stanford 2008). Consequently, temporally synchronous visual and tactile or proprioceptive/kinesthetic signals elicit illusory sense of ownership over a visible fake rubber hand insofar as the visually specified location of the rubber hand is congruent with proprioceptively specified location of the participant’s hand (Pavani et al. 2000; Ehrsson et al. 2004; Tsakiris and Haggard 2005; Costantini and Haggard 2007; Kalckert and Ehrsson 2012; Preston 2013). Thus, the participant’s illusory sense of ownership is highly sensitive to the spatial congruence of the rubber hand and their biological hand (Ehrsson et al. 2004; Tsakiris and Haggard 2005; Costantini and Haggard 2007). The increasing lateral distance between the rubber hand and midline of the participant’s body (Preston 2013; Kalckert et al. 2019), as well as increasing vertical distance of the rubber hand from the participant’s hand (Kalckert and Ehrsson 2014b), weaken the illusory sense of ownership. Finally, the illusory sense of ownership is accompanied by proprioceptive drift but only when the rubber hand is in an anatomically congruent position.

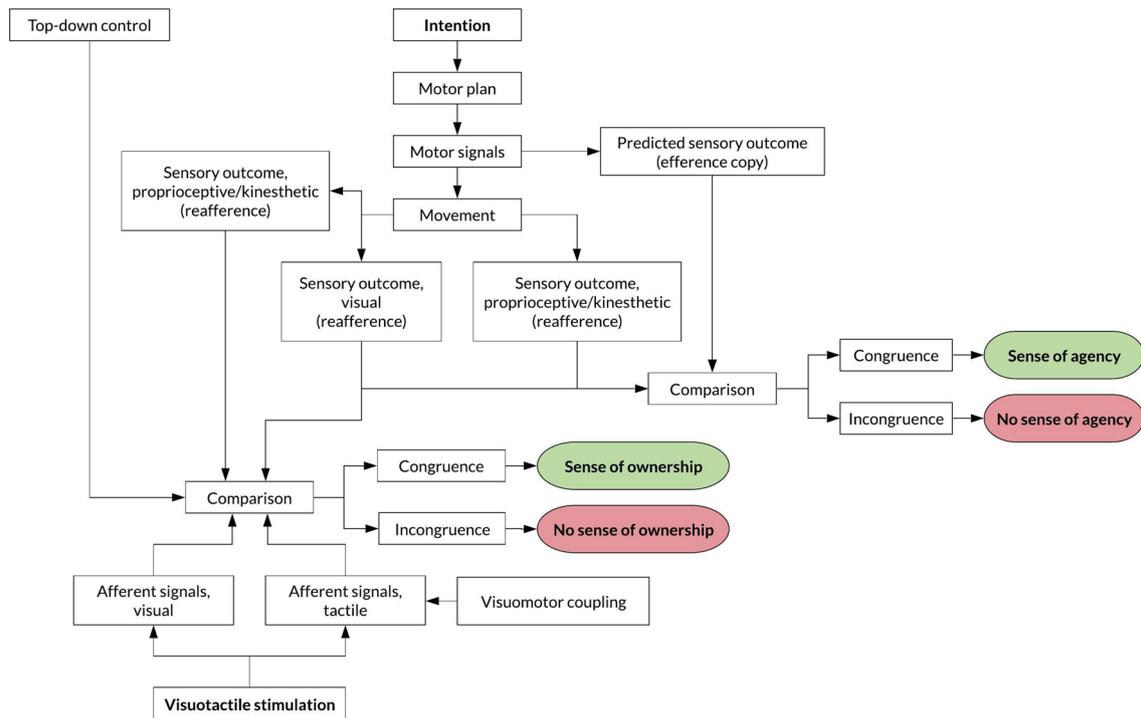


Fig. 1 A flowchart describing our view of various afferent and efferent pathways that contribute to the multisensory origins of our senses of ownership and agency

Self-produced movement primarily drives our sense of agency. Motor commands generate an “efference” copy specifying the sensory consequences of the planned movement (Wolpert et al. 1995; Miall and Wolpert 1996; Wolpert and Flanagan 2001). Temporal congruency between the sensory signals specifying the current state of the body (i.e., reafference) and the efference copy elicits the sense of agency; increasing the temporal discrepancy weakens the sense of agency (Sato and Yasuda 2005; Haggard 2017). Self-produced movement is thus necessary to the development of the sense of agency (Fig. 1), but not sufficient. For example, Kalckert and Ehrsson (2012, 2014a) systematically varied the relative timing of movements of the fingers of the participant’s hand and the rubber hand (synchronous vs. asynchronous movement), the mode of movement (active vs. passive movement), and the position of the rubber hand (anatomically congruent vs. incongruent). The authors found that asynchronous movements eliminated both illusory ownership and agency, passive synchronous movement eliminated the agency but left the illusory ownership intact, and incongruent positioning of the rubber hand diminished the illusory ownership but did not influence the agency. In addition, proprioceptive drift was correlated with the strength of illusory ownership but not the strength of illusory agency. Thus, spatial congruence of visual and proprioceptive information is not a requirement for the development of the sense of agency, but temporal synchrony is necessary.

Comparatively fewer studies have investigated whether and the extent to which the multisensory processes underlying our senses of ownership and agency overlap. The outcomes of these studies are difficult to integrate. Tsakiris et al. (2006) asked participants to watch a projection of their hand under three conditions: active finger movement, passive finger movement, and tactile stimulation. The projection was either temporally synchronous or asynchronous with respect to the stimulation of the hand. The participants felt stronger illusory ownership following synchronous than asynchronous stimulation in each condition. In the passive and tactile conditions, proprioceptive drift was localized to the stimulated finger. Conversely, during active movement, proprioceptive drift spread across the whole hand. The authors interpreted these findings as evidence that while a purely proprioceptive sense of ownership is local and fragmented, the sense of agency integrates distinct body parts into a coherent, unified sense of ownership (Tsakiris et al. 2006, 2007); the sense of agency enhances the sense of ownership. However, the fact that tapping any one finger is accompanied by simultaneous changes in the isometric forces exerted by the other fingers (Latash et al. 1998; Aoki et al. 2003) undermines the authors’ conclusion. During active movement, isometric contractions of the other fingers could have generated proprioceptive/kinesthetic signals responsible for the spread of proprioceptive drift across the whole hand; the authors did not control for this possibility.

Kalckert and Ehrsson (2014b) came to a different conclusion than Tsakiris et al. (2006) regarding the relationship between our senses of ownership and agency. Kalckert and Ehrsson (2014a) reported that the number of participants experiencing the illusory sense of ownership and sense of agency, and the strengths of illusory ownership were comparable whether the participants underwent the static or dynamic RHI procedure (cf. Riemer et al. 2013). Proprioceptive drift was also comparable across the two paradigms. Given the absence of self-produced movement in the static RHI, Kalckert and Ehrsson (2014a) concluded that self-produced movement in the dynamic RHI did not further strengthen the illusory sense of ownership; they interpreted their findings as evidence that our sense of ownership modulates our sense of agency, contradicting Tsakiris et al.'s (2006, 2007) hypothesis that self-produced movement plays a significant role in the development of the sense of ownership. In the face of these contradictory findings, the respective contributions of various afferent and efferent pathways to the multisensory origins of our senses of ownership and agency, and the relationship of the two senses with our perception of space surrounding the body remain unclear.

As a potential solution to this impasse, we propose an affordance-based model describing the relationship among our senses of ownership and agency, and our perception of space surrounding the body as reachable vs. non-reachable. While synchronized multisensory afferent signals contribute to our sense of ownership and our perception of space as reachable in the Euclidean framework, the combination of efference copy and reafference signals contributes to our sense of agency. In contrast, the spatial independence of our sense of agency reflects the coupling between our actions and perception of the environment, such as while using handheld tools as extensions of our body. Neurophysiological findings from single-unit recordings in macaque monkeys strongly support our proposition. Single neurons in the macaque premotor cortex (PMv) differentially respond to a stimulus present in RS or NRS (Fogassi et al. 1996). Caggiano et al. (2009) reported that a subgroup of neurons that responded to the sight of an object in RS stopped firing when a wire mesh was placed between the macaques and the object. Conversely, a subgroup of the neurons that responded to the sight of an object in NRS started to respond to the sight of the object behind the mesh. Consistent with the perception–action explanation of the independent psychological processes underlying our sense of agency and our perception of space as reachable in the Euclidean framework, the activity of single neurons reflected whether the object afforded to be grasped by the macaque, rather than reflecting a unitary dependence on physical distance. In summary, we propose a differential relationship between our senses of ownership and agency and our perception of space surrounding our body.

We reasoned that to identify experimentally the relationship among our sense of ownership, sense of agency, and categorization of space surrounding our body, the experimental design must provide conditions expected to produce: (a) illusory ownership in the absence of agency. (b) Agency in the absence of illusory ownership. (c) Illusory ownership and agency together. First, this design can potentially reveal if either sense can develop independently (i.e., does not impose constraints on the development of the other), confirming non-overlapping mechanisms. Second, if agency drives ownership (cf. Tsakiris et al. 2006, 2007), then illusory ownership would be stronger in the presence of agency than in the absence of agency. Conversely, if ownership drives agency (Longo et al. 2008; Kalckert and Ehrsson 2012, 2014a), then the agency should be stronger in the presence of illusory ownership than in the absence of illusory ownership. In addition, it should include a variable of space surrounding the body (i.e., by positioning the rubber hand in the participant's self-identified RS vs. NRS) to identify whether the sense of ownership, sense of agency, or both depend on self-identified RS–NRS boundary.

In two sequential studies (study 1 and 2), we exposed two different groups of participants to the static RHI and its dynamic variant, while a visible fake rubber hand was in their self-identified RS or NRS. In study 1, we exposed 36 participants to the static RHI procedure (cf. Botvinick and Cohen 1998; Ehrsson et al. 2004, 2005). We compared the number of participants who felt illusory ownership when the rubber hand was in their RS and NRS, the strength of illusory ownership, and proprioceptive drift. In study 2, we exposed 36 participants to the dynamic RHI procedure (cf. Kalckert and Ehrsson 2012, 2014a, b). We compared the number of participants who felt illusory ownership and/or agency when the rubber hand was in RS and NRS, the strengths of illusory ownership and agency, and proprioceptive drift.

Study 1: static RHI

Methods

Participants

Thirty-six undergraduate students (17 men and 19 women; mean \pm SD age = 20.3 \pm 1.6 years; right-handed) at the University of Georgia (Athens, GA) voluntarily participated in study 1 in exchange for partial course credits. Each participant signed a printed consent form describing the purposes and procedures of the study, and the potential risks and benefits of participation. The University of Georgia's Institutional Review Board (IRB) approved this study.

Procedure

Each participant wore a white latex glove on his/her right hand and sat on a chair in front of a table with the table's edge extending to the participant's abdomen at his/her waist height. We attached to the table top a custom sliding sleeve assembly consisting of a raised wooden platform—10 cm above the table top—that could be slid on two parallel rods. This setup allowed us to adjust the position of the rubber hand relative to the participant (i.e., in his/her RS or NRS) easily by sliding the wooden platform back and forth in the participant's sagittal plane. To determine the participant's RS–NRS boundary, we instructed the participant to say “stop” when he/she perceived a vertical pointer suspended from the platform as reachable with his/her right hand, while

we slowly slid the upper platform towards the participant. The pointer's position denoted the participant's RS–NRS boundary. We carried out this procedure only once at the beginning of the experiment. Since our interest was primarily in knowing the perceived RS–NRS boundary, we did not determine the participant's actual RS–NRS boundary (e.g., by asking the participant to reach and grasp an object placed at the perceived RS–NRS boundary). As the reaching distance may vary with the trunk movement, we instructed the participant to sit erect. We conducted the subsequent experiment in the same posture. We then tested the participant for an illusory sense of ownership over a visible fake rubber hand placed in his/her RS and NRS (i.e., the tip of the rubber hand's index finger 15 cm inside and outside RS–NRS boundary, respectively; Fig. 2a, b). After the participant put

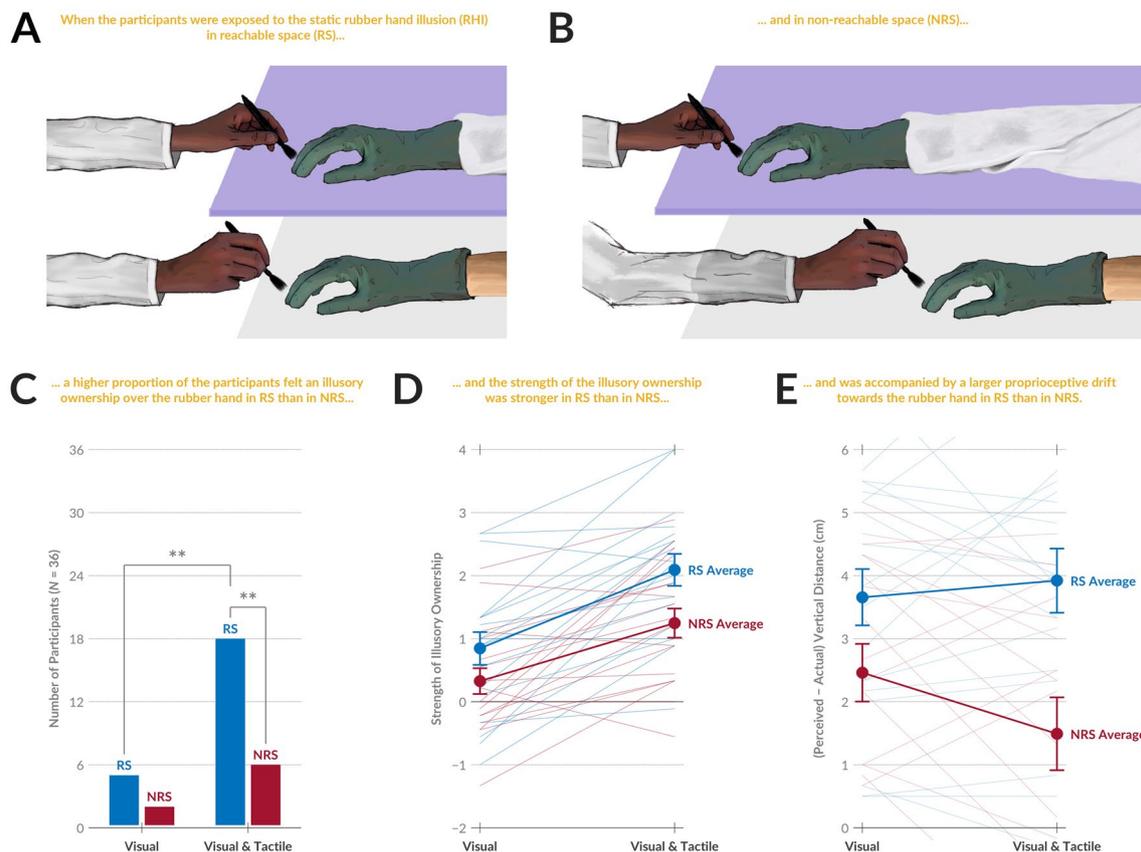


Fig. 2 The participants felt a strong illusory sense of ownership over a visible fake rubber hand in the static rubber hand illusion (RHI) when the rubber hand was in reachable space (RS), but did not feel any illusory sense of ownership when the rubber hand was in non-reachable space (NRS). **a** The static RHI procedure with the rubber hand positioned in the participant's RS. **b** The static RHI procedure with the rubber hand positioned in the participant's NRS. Source: drawings by Antonio Jose Osuna Mascaró. **c** The number of participants who felt the illusory sense of ownership. A participant felt the illusory sense of ownership when the average ratings for the ownership illusion statements (O-I1, O-I2, and O-I3) were ≥ 1 . **d** The

strength of the illusory sense of ownership for the 16 participants who felt the illusory sense of ownership when the rubber hand was in RS, calculated by subtracting the average of the ratings for the ownership control statements (O-C1, O-C2, and O-C3) from the average of the ratings of the ownership illusion statements (O-I1, O-I2, and O-I3). **e** The distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger for the participants who felt the illusory sense of ownership when the rubber hand was in RS. The actual vertical position of the tip of the participant's index finger is at 0. $**p < 0.005$. Error bars indicate SE ($N = 16$)

his/her right hand on the table top, we placed a fake rubber hand covered with an identical white latex glove on the wooden platform in an anatomically congruent posture. We draped an opaque black flannel over the participant's shoulders and arms to create the appearance that the rubber hand was the participant's outstretched hand (Fig. 2a, b).

Each participant experienced two stimulus conditions. In the “visual” condition, the experimenter applied soft, rhythmic strokes to the index finger of the visible rubber hand—beginning at the fingertip and ending at the knuckle—for 90 s using a 12 mm-wide flat paintbrush, as the participant stared at it and his/her hand remained occluded. In the “visual and tactile” condition, the experimenter applied soft, rhythmic, and synchronous strokes simultaneously to the index fingers of the participant's hand and the rubber hand for 90 s using two identical (12 mm-wide flat) paintbrushes as the participant stared at the index finger of the visible rubber hand. Because strictly regular strokes could result in perfectly regular visuotactile integration and elicit weaker illusions than irregular strokes, the experimenter applied a quick “double stroke” at frequent but irregular intervals instead of always applying a “single stroke.” We instructed the participant before each trial in the visual and tactile condition to look continually at the index finger of the rubber hand while simultaneously attending to the tactile sensations from the strokes applied to his/her index finger.

In each trial, after completing the above RHI procedure, we used a pointing task to estimate the participant's perceived vertical position of his/her [occluded] right index fingertip. To this end, we attached a graph paper to a board

mounted to the left of the RHI apparatus, laterally to the participant's midsagittal plane. After 90 s of stroking, the participant closed his/her eyes and indicated the perceived vertical position of his/her right index fingertip by rapidly touching the graph paper with his/her left index fingertip. The experimenter marked the position of the center of the participant's index fingertip. We later used this position to determine proprioceptive drift as the (signed) distance between the proprioceptively perceived and actual vertical position of the tip of the index finger to the nearest half centimeter.

Immediately after the pointing task, each participant filled in the RHI inventory of six statements examining the participant's illusory sense of ownership over the rubber hand (Table 1). Each participant responded to each statement on a seven-step visual analog scale (VAS): “— — —”, “— —”, “—”, “o”, “+”, “++”, and “+++”, wherein “— — —” corresponds to “strongly disagree,” “o” corresponds to a neutral response, and “+++” corresponds to “strongly agree”. We then transformed the responses to the numerical values of -3 , -2 , -1 , 0 , 1 , 2 , and 3 corresponding to “— — —”, “— —”, “—”, “o”, “+”, “++”, and “+++”, respectively, for analysis. In the RHI inventory (Table 1), statements O-I1, O-I2, and O-I3 tested for the illusory sense of ownership, while statements O-C1, O-C2, and O-C3 served as control statements that were expected to invoke neutral responses. We randomized the order of presentation of the six statements for each trial.

We tested each participant individually in a 60–75-min session composed of 12 RHI trials, three trials each for

Table 1 The rubber hand illusion (RHI) inventory examining the illusory sense of ownership and the sense of agency over the rubber hand in the static and dynamic RHI

	#	Ownership
Illusion	O-I1	It felt as though I was feeling the touch of the paintbrush (movement of my finger) in the location where the rubber hand was being touched (moved)
	O-I2	It felt as though I was looking at my hand when I was looking at the rubber hand
	O-I3	It felt as though the rubber hand was part of my body
Control	O-C1	It felt as though my hand was turning “rubbery”
	O-C2	It felt as though I had more than one right hand or arm
	O-C3	It felt as though the rubber hand was drifting towards my hand (i.e., downwards)
	#	Agency
Actual	A-I1	The rubber hand moved just like I wanted it to, as though it was obeying my will
	A-I2	It felt as though I was controlling the movement of the rubber hand
	A-I3	Whenever I moved my finger, I expected the finger of the rubber hand to move in the same way
Control	A-C1	It felt as though the rubber hand was controlling my movement
	A-C2	I could sense the movement from somewhere between my hand and the rubber hand
	A-C3	It appeared as though the rubber hand had a will of its own

The participants responded to each statement on a seven-step visual analog scale (VAS): “— — —”, “— —”, “—”, “o”, “+”, “++”, and “+++,” wherein “— — —” corresponds to “strongly disagree,” “o” corresponds to a neutral response and “+++” corresponds to “strongly agree;” and the scale translates to the numerical values -3 , -2 , -1 , 0 , 1 , 2 , and 3 for the analysis

each of the four combinations of stimulus (visual vs. visual and tactile) and space (RS vs. NRS). The visual condition always preceded the visual and tactile condition. However, we randomized the order of presentation of the trials for RS and NRS for each participant.

Analysis

We first identified individual participants who felt the illusory sense of ownership in the visual and tactile condition in RS. We considered that a given participant had felt the illusory sense of ownership if his/her average rating for the ownership illusion statements was ≥ 1 . For each participant who felt the illusory sense of ownership in the visual and tactile condition in RS, we calculated the strength of illusory ownership in each of the four combinations of stimulus (visual vs. visual and tactile) and space (RS vs. NRS) by subtracting the average ratings for the ownership control statements (O-C1, O-C2, and O-C3) from the average ratings for the ownership illusion statements (O-I1, O-I2, and O-I3). We used Chi-squared tests to compare the number of participants (out of 36) who felt the illusory sense of ownership (a) between the visual and visual and tactile conditions (in RS), and (b) between RS and NRS (in the visual and tactile condition). We used two (stimulus) \times 2 (space) repeated-measures analyses of variance (ANOVAs) to examine the influences of stimulus (visual vs. visual and tactile) and space (RS vs. NRS) on the strength of illusory ownership and on the distance (in cm) between perceived and actual vertical position of the tip of the participant’s right index finger in the static RHI. We performed all statistical analyses on SPSS 20 (IBM Inc., Chicago, IL) and considered the outcomes significant at the two-tailed alpha level of 0.05. We report effect sizes as partial eta-squared (η_p^2) in Tables 2 and 3.

Results and discussion

Synchronous visual and tactile signals elicited a strong illusory ownership of the rubber hand when the rubber hand was in RS but not when the rubber hand was in NRS. When the rubber hand was in RS, synchronous visual and tactile signals elicited illusory ownership in a higher proportion of the participants than did visual reference to anticipated tactile signals alone (18 out of 36 vs. 5 out of 36), $\chi^2 = 10.80$, $p = 0.001$ (Fig. 2c). In addition, in the visual and tactile condition, a higher proportion of the participants felt illusory ownership when the rubber hand was in RS than when in NRS (18 out of 36 vs. 6 out of 36), $\chi^2 = 9.00$, $p = 0.003$ (Fig. 2c).

We conducted a 2 (stimulus) \times 2 (space) repeated-measures ANOVA on the strength of illusory ownership with within-subject factors of stimulus condition and space in the 18 participants who felt illusory ownership in RS. Table 2 provides the results of the ANOVA. We found a significant main effect of stimulus, $F_{1,17} = 27.78$, $p < 0.001$. Across both spaces—RS and NRS, the participants felt stronger illusory ownership in the visual and tactile condition (mean \pm SE = 1.67 ± 0.18) than in the visual condition (0.59 ± 0.17) (Fig. 2d). In addition, we found a significant main effect of space, $F_{1,17} = 12.87$, $p = 0.002$ (Fig. 2d). Across both stimulus conditions—visual and visual and kinesthetic, the participants felt stronger illusory ownership when the rubber hand was in RS (1.47 ± 0.21) than when in NRS (0.79 ± 0.17). The interaction effect of stimulus \times space was not significant, $F_{1,17} = 3.11$, $p = 0.096$.

Next, we conducted a 2 (stimulus) \times 2 (space) repeated-measures ANOVA on the distance between the actual position and the proprioceptively perceived position of the tip of the participant’s right index finger with within-subject factors of stimulus condition and space in the 17 participants who felt illusory ownership when the rubber hand

Table 2 Overview of the results of 2 (stimulus) \times 2 (space) repeated-measures ANOVAs on the strength of illusory ownership and the distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger in the static RHI

	Factor	df	F	p	η_p^2	β
Strength of illusory ownership (among the 18 participants who felt illusory ownership)	Stimulus	1, 17	27.78	< 0.001	0.62	1.00
	Space	1, 17	12.87	0.002	0.43	0.92
	Stimulus \times space	1, 17	3.11	0.096	0.16	0.38
(Perceived–actual) vertical distance (among the 17 participants who felt illusory ownership) ^a	Stimulus	1, 16	1.54	0.233	0.09	0.21
	Space	1, 16	7.44	0.015	0.12	0.73
	Stimulus \times space	1, 16	4.54	0.049	0.22	0.52
(Perceived–actual) vertical distance (among the 18 participants who did not feel illusory ownership)	Stimulus	1, 17	3.40	0.083	0.17	0.41
	Space	1, 17	0.42	0.525	0.02	0.09
	Stimulus \times space	1, 17	3.67	0.072	0.18	0.44

Boldface values indicate statistical probability at the alpha level of 0.05

^aAfter removal of an outlier

Table 3 Overview of the results of 2 (stimulus) × 2 (space) repeated-measures ANOVAs on the strength of illusory ownership, the strength of agency, and the distance between the actual position and

proprioceptively perceived vertical position of the tip of the index finger in the dynamic RHI

	Factor	df	F	p	η_p^2	β
Strength of illusory ownership (among the 21 participants who felt illusory ownership when the rubber hand was in RS)	Stimulus	1,20	6.50	0.019	0.25	0.68
	Space	1,20	6.31	0.021	0.24	0.67
	Stimulus × space	1,20	5.51	0.029	0.22	0.61
(Perceived–actual) vertical distance (among the 21 participants who felt illusory ownership when the rubber hand was in RS)	Stimulus	1,20	4.08	0.057	0.17	0.49
	Space	1,20	5.88	0.025	0.23	0.64
	Stimulus × space	1,20	0.31	0.585	0.02	0.08
Strength of agency (among the 35 participants who felt agency when the rubber hand was in RS)	Stimulus	1,34	220.27	<0.001	0.87	1
	Space	1,34	0.58	0.450	0.02	0.12
	Stimulus × space	1,34	0.21	0.647	0.01	0.01
(Perceived–actual) vertical distance (among the 14 participants who felt agency but not illusory ownership when the rubber hand was in RS)	Stimulus	1,13	0.02	0.886	0	0.05
	Space	1,13	2.25	0.152	0.12	0.29
	Stimulus × space	1,13	0.11	0.750	0.01	0.06

Boldface values indicate statistical probability at the alpha level of 0.05

was in RS (after removing an outlier). Table 2 provides the results of the ANOVA. The main effect of stimulus was not significant, $F_{1,16} = 1.54$, $p = 0.233$. However, the main effect of space was significant, $F_{1,16} = 7.44$, $p = 0.015$ (Fig. 2e). Across both stimulus conditions, the distance between perceived and actual vertical position of the participant's index fingertip was larger when the rubber hand was in RS (mean \pm SE = 3.79 ± 1.27 cm) than when in NRS (1.98 ± 2.41 cm) (Fig. 2e). We also found an interaction effect of stimulus × space, $F_{1,16} = 4.54$, $p = 0.049$ (Fig. 2e) for which we do not at present have an explanation. Among the 18 participants who did not feel illusory ownership, neither the main effect of stimulus, $F_{1,17} = 3.40$, $p = 0.083$, nor the main effect of space was significant, $F_{1,17} = 0.42$, $p = 0.525$. The interaction effect of stimulus × space was also not significant, $F_{1,17} = 3.67$, $p = 0.072$.

Multisensory integrative processes typically privilege visual signals, as they have higher reliability and spatial acuity than tactile and proprioceptive signals (Stein and Stanford 2008). Consequently, visual signals override proprioceptive signals in so far as incongruity between the two signals does not extend beyond a threshold degree (Pavani et al. 2000; Ehrsson et al. 2004; Tsakiris and Haggard 2005; Costantini and Haggard 2007; Kalckert and Ehrsson 2012; Preston 2013). In this study, when the rubber hand was in RS, the visual signals specifying the position of the rubber hand in the horizontal plane were mostly consistent with the proprioceptive signals specifying the position of the participant's hand. Thus, the participants felt a strong sense of illusory ownership when the rubber hand was in RS. In contrast, when the rubber hand was in NRS, the visual signals specifying the horizontal position of the visible rubber hand could not override the

proprioceptive signals specifying the actual position of the participant's occluded hand. Thus, the participants did not feel illusory sense of ownership when the rubber hand was in NRS.

Given that synchronously stroking the index fingers of the participant's hand and of the rubber hand enhanced the subjectively reported illusory ownership over the index finger of the rubber hand being stroked alone, we would expect that the distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger of the participant's hand would be greater in the visual and tactile condition than in the visual condition. However, the perceived distance did not differ between the two conditions. Perhaps, this equivalence reflects the details of these two conditions. Traditionally, in the static RHI paradigm, the control involves asynchronous stroking of the index fingers of the participant's hand and the rubber hand. Alternatively, we included a visual-only condition. Given that visual signals have higher reliability and spatial acuity than tactile signals (Stein and Stanford 2008), the visual signals from the rubber hand are typically so potent that participants can develop an illusory sense of ownership from merely anticipating touch upon the observed rubber hand despite minor incongruities between the position of the rubber hand and the participant's hand. Thus, it is not surprising that several participants felt an illusory sense of ownership in the visual condition when the rubber hand was in RS. Accordingly, we suspect that inclusion of the visual-only condition, instead of an asynchronous condition, diminished the differences in the strengths of illusory ownership between the visual and visual and tactile conditions, and consequently, it also diminished the differences in proprioceptive drift between these two conditions.

Previous studies have reported that the strength of illusory ownership diminishes with the increasing lateral distance between the rubber hand and the participant's body midline (Lloyd 2007; Preston 2013; Kalckert et al. 2019), with increasing vertical distance between the rubber hand and the participant's hand (Kalckert and Ehrsson 2014b), and very recently, with increasing distance along the midline (Kalckert et al. 2019). The results of study 1 provide additional evidence that that illusory ownership is spatially bound; synchronous visual and tactile stimulation does not elicit an illusory sense of ownership over a visible fake rubber hand placed beyond self-identified RS–NRS boundary along the midline—a significant dimension along which our perception of space varies. In the following study (study 2), we examined whether our sense of agency is also spatially bound, and whether the sense of agency/ownership drives the sense of ownership/agency.

Study 2: dynamic RHI

Methods

Participants

Thirty-six undergraduate students (15 men and 21 women; mean \pm SD age = 18.8 \pm 0.6 years; all right-handed) at the University of Georgia participated in the dynamic RHI in exchange for partial course credits.

Procedure

Most experimental procedures were identical to those in the static RHI, except that each participant wore a plastic ring on the intermediate phalange of his/her right index finger. We mechanically coupled the ring on the participant's index finger with an identical plastic ring on the index finger of the rubber hand using a custom arrangement of very thin and light wooden rod(s) (Fig. 3a, b). Because of this mechanical coupling, the index finger of the rubber hand synchronously flexed/extended when the participant flexed/extended his/her index finger at the metacarpophalangeal joint.

As in the static RHI, in the dynamic RHI, each participant experienced two sensory conditions. In the “visual” condition, the experimenter repeatedly flexed/extended (tapped) the index finger of the rubber hand for 90 s as the participant stared at the index finger of the visible rubber hand and the index finger of his/her occluded hand remained still. In the “visual and kinesthetic” condition, the participant stared at the index finger of the visible rubber hand for 90 s as it flexed/extended when he/she flexed/extended (i.e., tapped) his/her index finger. As strictly regular taps could result in perfectly regular visuokinesthetic integration and

elicit weaker illusions than more irregular movements, we instructed the participant to execute quick “double taps” at frequent but irregular intervals instead of always executing a “single tap.” Also, we instructed the participant to look continually at the index finger of the rubber hand while simultaneously attending to the proprioceptive sensations of the movements of his/her index finger.

In each trial, after completing the procedure, we asked the participant to report his/her perceived vertical position of the tip of his/her [occluded] right index finger. To this end, we used a pointing task identical to that in the static RHI. We determined proprioceptive drift as the (signed) distance between the proprioceptively perceived and actual vertical position of the tip of the index finger to the nearest half centimeter.

After the pointing task, each participant filled in the RHI inventory of 12 statements examining the participant's illusory ownership and agency over the rubber hand. In the RHI inventory (Table 1), statements O-I1, O-I2, and O-I3 tested for illusory ownership, while statements O-C1, O-C2, and O-C3 served as control statements that were expected to invoke neutral responses. In addition, statements A-I1, A-I2, and A-I3 tested for agency, while statements A-C1, A-C2, and A-C3 served as control statements that were expected to invoke neutral responses. We randomized the order of presentation of the 12 statements for each trial.

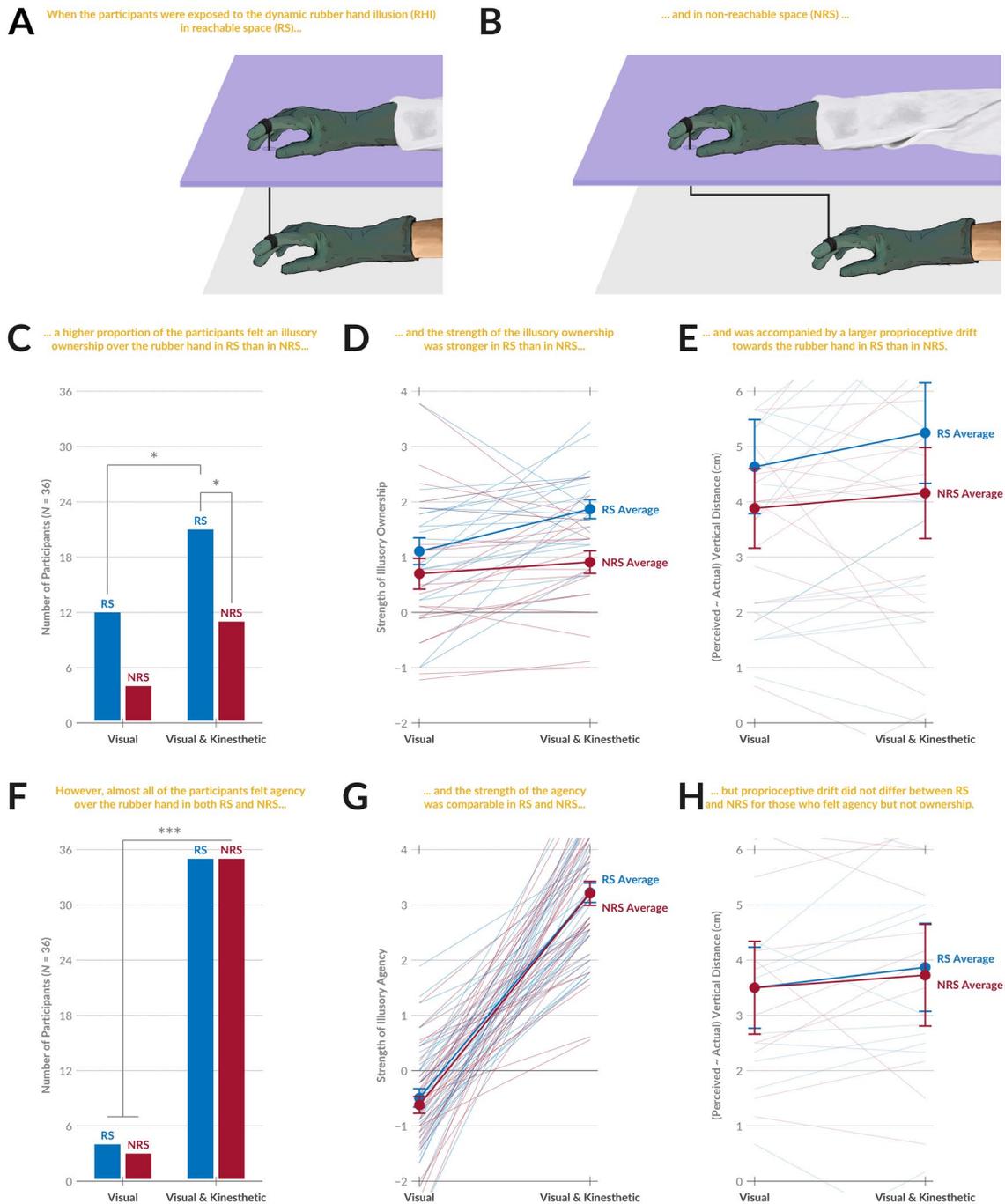
We tested each participant individually in a 60–75-min session composed of 12 RHI trials, three trials each for each of the four combinations of stimulus (visual vs. visual and kinesthetic) and space (RS vs. NRS). The visual condition always preceded the visual and kinesthetic condition. However, we randomized the order of presentation of the trials for RS and NRS for each participant.

Analysis

In addition to screening the participants for illusory ownership—as we did in the static RHI—we considered that a given participant had felt agency when his/her average rating for the agency statements was ≥ 1 . In addition to calculating the strength of illusory ownership—again, as we did in the static RHI—we also calculated the strength of agency by subtracting the average of the ratings for the agency control statements from that of the agency actual statements.

Results and discussion

First, synchronous visual and kinesthetic signals elicited a strong illusory ownership when the rubber hand was in RS but not when the rubber hand was in NRS. The sight of self-executed movements elicited an illusory ownership in a higher proportion of the participants than did the sight of movements of the rubber finger produced by



the experimenter in RS (21 out of 36 vs. 12 out of 36), $\chi^2 = 4.53$, $p = 0.033$ (Fig. 3c). [Note that the 12 participants who reported illusory ownership in the visual condition belonged to the group of 21 participants that reported illusory ownership in the visual and kinesthetic condition (i.e., they experienced illusory ownership in both conditions.) In addition, in the visual and kinesthetic condition, a higher proportion of the participants felt illusory ownership when

the rubber hand was in RS than in NRS (21 out of 36 vs. 11 out of 36), $\chi^2 = 5.63$, $p = 0.018$ (Fig. 3c).

We conducted a 2 (stimulus) \times 2 (space) repeated-measures ANOVA on the strength of illusory ownership in the 21 participants who felt illusory ownership when the rubber hand was in RS. Table 3 provides the results of the ANOVA. The main effect of stimulus was significant, $F_{1,20} = 6.50$, $p = 0.019$. Across both spaces—NS and NRS, the participants felt stronger illusory ownership in the

Fig. 3 The participants felt a strong sense of agency over a visible fake rubber hand in the dynamic RHI, regardless of whether the rubber hand was in RS or NRS, but felt a strong illusory sense of ownership only when the rubber hand was in RS. **a** The dynamic RHI procedure with the rubber hand positioned in the participant's RS. **b** The dynamic RHI procedure with the rubber hand positioned in the participant's NRS. Source: drawings by Antonio Jose Osuna Mascaró. **c** The number of participants who felt illusory ownership. A participant felt illusory ownership when the average ratings for the ownership illusion statements (O-I1, O-I2, and O-I3) was ≥ 1 . **d** The strength of illusory ownership for the 21 participants who felt illusory ownership when the rubber hand was in RS, calculated by subtracting the average of the ratings for the ownership control statements (O-C1, O-C2, and O-C3) from the average of the ratings of the ownership illusion statements (O-I1, O-I2, and O-I3). **e** The distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger for the participants who felt illusory ownership when the rubber hand was in RS. The actual vertical position of the tip of the participant's index finger is at 0. **f** The number of participants who felt agency. A participant felt agency when the average ratings for the agency actual statements (A-I1, A-I2, and A-I3) was ≥ 1 . **g** The strength of illusory agency for the 35 participants who felt agency when the rubber hand was in RS, calculated by subtracting the average of the ratings for the agency control statements (A-C1, A-C2, and A-C3) from the average of the ratings of the agency actual statements (A-I1, A-I2, and A-I3). **h** The distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger for the participants who felt agency but not illusory ownership when the rubber hand was in RS. The actual vertical position of the tip of the participant's index finger is at 0. $*p < 0.05$. $***p < 0.001$. Error bars indicate SE ($N = 36$)

visual and kinesthetic condition (mean \pm SE = 1.39 ± 0.15) than in the visual condition (0.90 ± 0.19) (Fig. 3d). The main effect of space was significant, $F_{1,17} = 6.31$, $p = 0.021$. Across both stimulus conditions—visual and visual and kinesthetic, the participants felt stronger illusory ownership in RS (1.49 ± 0.16) than in NRS (0.81 ± 0.17) (Fig. 3d). Finally, the interaction effect of stimulus \times space was also significant, $F_{1,20} = 5.51$, $p = 0.029$. The margin by which the illusory ownership was stronger in the visual and kinesthetic condition (mean \pm SE = 1.87 ± 0.17) than in the visual condition (1.11 ± 0.24) was greater when the rubber hand was in RS than the margin by which the illusory ownership was stronger in the visual and kinesthetic conditions (0.91 ± 0.20) than the visual condition (0.70 ± 0.28) when the rubber hand was in NRS (Fig. 3d).

Next, we conducted a 2 (stimulus) \times 2 (space) repeated-measures ANOVA on the distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger in the 21 participants who felt illusory ownership when the rubber hand was in RS. Table 3 provides the results of the ANOVA. The main effect of stimulus was not significant, $F_{1,20} = 4.08$, $p = 0.057$ (Fig. 3e). However, the main effect of space was significant, $F_{1,20} = 5.88$, $p = 0.025$. Across both stimulus conditions, the distance between perceived and actual vertical position of the participant's index fingertip was larger when the rubber hand

was in RS (mean \pm SE = 4.94 ± 0.62 cm) than when in NRS (4.02 ± 0.54 cm) (Fig. 3e). The interaction effect of stimulus \times space was not significant, $F_{1,20} = 0.31$, $p = 0.585$ (Fig. 3e).

In contrast to the illusory ownership, agency over the dynamic rubber hand elicited by synchronous visual and kinesthetic signals extended to NRS. The participant's sight of self-executed movements elicited an agency in a higher proportion of the participants than did the sight of movements of the rubber finger produced by the experimenter in RS (35 out of 36 vs. 4 out of 36), $\chi^2 = 53.76$, $p < 0.001$, and in NRS (35 vs. 3 out of 36), $\chi^2 = 57.07$, $p < 0.001$ (Fig. 3f). The same number of participants felt agency in the visual and kinesthetic condition, regardless of whether the rubber hand was in RS or NRS (35 out of 36 vs. 35 out of 36), $\chi^2 = 0$, $p = 1$ (Fig. 3f).

We conducted a 2 (stimulus) \times 2 (space) repeated-measures ANOVA on the strength of agency for the 35 participants who felt agency when the rubber hand was in RS. Table 3 provides the results of the ANOVA. The main effect of stimulus was significant, $F_{1,34} = 220.27$, $p < 0.001$. Across both spaces—NS and NRS, the participants felt stronger agency in the visual and kinesthetic condition (mean \pm SE = 3.21 ± 0.38) than in the visual condition (-0.56 ± 0.07) (Fig. 2g). The main effect of space was not significant, $F_{1,34} = 0.58$, $p = 0.450$ (Fig. 3g). The interaction effect of stimulus \times space was not significant, $F_{1,34} = 0.21$, $p = 0.647$ (Fig. 3g).

Finally, we conducted a 2 (stimulus) \times 2 (space) repeated-measures ANOVA on the distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger in the 14 participants who felt agency but not illusory ownership when the rubber hand was in RS. Table 3 provides the results of the ANOVA. Neither the main effect of stimulus, $F_{1,13} = 0.02$, $p = 0.886$, nor the main effect of space was significant, $F_{1,13} = 2.25$, $p = 0.152$ (Fig. 3h). The interaction effect of stimulus \times space was also not significant, $F_{1,13} = 0.11$, $p = 0.750$ (Fig. 3h).

We found that the sense of agency over the visible fake rubber hand elicited by synchronous visual and kinesthetic signals was not spatially bound as was the illusory sense of ownership elicited by the same signals. Incongruence between the visual signals specifying the position of the rubber hand in the horizontal plane and the proprioceptive signals specifying the position of the participant's hand did not impose constraints on the development of agency. Furthermore, the agency did not require any recalibration of the proprioceptive signals. The 14 participants who felt agency but not illusory ownership when the rubber hand was in RS exhibited no space-related differences in the distance between the actual position and proprioceptively perceived vertical position of the tip of the index finger. In contrast, the 21 participants who felt both illusory ownership and agency

perceived their biological hand and the rubber hand closer when the rubber hand was in RS than when it was in NRS. This result provides strong evidence that the proprioceptive signals specifying the actual location of one's hand do not impose constraints on the development of the sense of agency as they impose on the development of the sense of ownership. This finding explains why the sense of agency is not accompanied by any sense of ownership over a grasped tool, a prosthetic hand, or a virtual rendering of the hand (Farnè and Làdavas 2000; Berti and Frassinetti 2000; Holmes et al. 2004; Gallivan et al. 2013; Martel et al. 2016; D'Angelo et al. 2018).

Discussion

We used the rubber hand illusion (RHI) to study the relationship between our sense of ownership, sense of agency, and our categorization of space surrounding the body. Consistent with the predictions from our hypotheses, illusory ownership of a visible fake rubber hand elicited by synchronous visual and tactile signals in the static RHI, or by synchronous visual and kinesthetic signals in the dynamic RHI, did not extend beyond the space within reach of the unaugmented hand (reachable space, RS). We found that when the participants experienced synchronous visual and tactile signals in the static RHI, and synchronous visual and kinesthetic signals in the dynamic RHI, they felt illusory ownership when the rubber hand was in RS but not when it was in NRS (non-reachable space). Conversely, when the participants experienced synchronous visual and kinesthetic signals in the dynamic RHI, they felt agency, regardless of the rubber hand's location. In addition, illusory ownership was accompanied by proprioceptive drift, but agency was not accompanied by proprioceptive drift. These findings add to the accumulating evidence in support of the perspective that our sense of ownership is spatially bound and cannot extend beyond the space reachable by the unaugmented hand, whereas our sense of agency is not spatially bound and can extend much farther away from the body. We add to this perspective by proposing that the two senses may be differently related to the psychological processes underlying how we perceive a region of space surrounding our body as reachable or non-reachable. While synchronized multisensory afferent signals contribute to our sense of ownership and our perception of space as reachable in the Euclidean framework, the combination of efference copy and reafference signals contributes to our sense of agency. The spatial independence of our sense of agency reflects the coupling between our actions and perception of the environment, such as while using handheld tools as extensions of our body. A recently published perspective emphasizes that RS

reflects a set of graded fields describing the relevance of actions to creating or avoiding contact between the body and the environment (Bufacchi and Iannetti 2018). This perspective incorporates the concept of RS into the ecological approach to behavior that acknowledges the role of the coupling between our actions and perception of the environment in shaping our behavior (Gibson 1966, 1977, 1979). Furthermore, this perspective fits well within the systems-level understanding of brain function: parieto-premotor circuits are responsible for selecting the most relevant action among potential actions (Cisek and Kalaska 2010; Pezzulo and Cisek 2016), and the categorization of space into reachable or non-reachable reflects the relevance of the potential actions in two ways: (1) based on the current ability to act in RS with the unaugmented hand, and (2) based on the need to extend one's reach to act upon a currently NRS, for instance, using a handheld tool.

Our study (as well as previous studies investigating the spatial limits on our senses of ownership and agency) has a potential confound. We fixed the two positions of the rubber hand for each participant. Therefore, we cannot discard the possibility that the effect of space on the strength of illusory ownership and agency over the rubber hand is simply one of the Euclidean distances, rather than of reachability. Future work can dissociate the effects of Euclidean distance and reachability on the strengths of illusory ownership and agency, for example, by placing a wire mesh or a transparent screen between the participant and the rubber hand. If ownership is not associated with an individual's categorization of the space as reachable vs. non-reachable—as we propose in the present study—then placing a wire mesh or a transparent screen between the participant and the rubber hand should not affect illusory ownership over the rubber hand.

Although we typically experience our body and the surrounding space seamlessly, we show that the psychological processes underlying our senses of body ownership and agency are entirely dissociable. Our sense of ownership, while malleable enough to incorporate visible non-corporeal objects resembling a body part, is spatially constrained by proprioceptive signals specifying that body part's actual location. In contrast, our sense of agency can incorporate a visible non-corporeal object, independent of its location with respect to the body. The spatial independence of our sense of agency is associated with the malleability of our perception of space surrounding the body as reachable or non-reachable, such as while using handheld tools as extensions of our body. We propose that the psychological processes mediating our senses of ownership and agency are differentially related to our perception of space surrounding the body as reachable or non-reachable: (1) based on the current ability to act in RS with the unaugmented hand, and (2) based on the need to extend the reach to act upon a currently NRS, for instance, using a handheld tool.

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Compliance with ethical standards

Conflict of interest The authors declare that no competing interests exist.

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