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You or me? Disentangling perspectival, perceptual, and integrative mechanisms in heterotopagnosia



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ABSTRACT

Heterotopagnosia-without-Autotopagnosia (HwA) is characterized by the incapacity to point to body parts on others, but not on one's own body. This has been classically interpreted as related to a self-other distinction, with impaired visual representations of other bodies seen in third person perspective (3PP), besides spared own body somatosensory representations in 1PP. However, HwA could be impacted by a deficit in the integration of visual and somatosensory information in space, that are spatially congruent in the case of one's own body, but not for others' body.

Here, we test this hypothesis in a rare neurological patient with HwA, H+, as well as in a control patient with a comparable neuropsychological profile, but without HwA, and in age-matched healthy controls, in two experiments. First, we assessed body part recognition in a new task where somatosensory information from the participant's body and visual information from the target body shown in virtual reality was never aligned in space. Results show that, differently from the flawless performance in controls, H+ committed errors for not only the body of others in 3PP, but for all conditions where the information related to the real and the target body was not spatially congruent.

Then, we tested whether the integration between these multisensory bodily cues in space, as during visuo-tactile stimulation in the full-body illusion, improves the patient's performance. Data show that after the stimulation prompting visuo-tactile integration, but not in control conditions, the patient's abilities to process body parts improved up to normal level, thus confirming and extending the first findings. Altogether, these results

¹ The authors contributed equally to this work.

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Abbreviations: HwA, heterotopagnosia without autotopagnosia; VR, virtual reality.

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support a new interpretation of HwA as linked to the matching between somatosensory inputs from one's body and visual information from a body seen at a distance, and encourage the application of multisensory stimulation and virtual reality for the treatment of body-related disorders.

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1. Introduction

We take the recognition of our body and its parts for granted: I perceive that this is my right hand with which I am typing on the computer's keyboard and that my nose is in the middle of my face. We also perceive the body of others and, similarly, recognize their body parts generally with great ease. Yet, rare cases of patients with selective body recognition disorders have provided strong evidence that the perception and recognition of one's own body and those of other people cannot be taken for granted and rely on highly specialized brain mechanisms that, once disrupted, lead to striking deficits. Indeed, focal brain damage can lead to deficits that selectively impair the recognition of one's own body, while leaving the recognition of the body of another person, as well as visual, auditory, or other cognitive functions, that do not concern human bodies, unimpaired (Felician, Ceccaldi, Didic, Thinus-Blanc, & Poncet, 2003). Notorious examples of such body recognition disorders are deficits in identifying body parts. Such patients are typically asked to indicate specific body parts on their own body or on another person's body (e.g., (Semenza & Goodglass, 1985), Fig. 1, panel a) and are impaired at indicating body parts on their own body, while behaving normally when asked to indicate the corresponding body parts of another person (i.e., autotopagnosia without heterotopagnosia, AwH, Corradi-Dell'Acqua & Tessari, 2010; Felician et al., 2003; Wicky, 2005). The opposite deficit, i.e., an impairment to indicate body parts of another person, with a preserved ability for one's own body parts, has also been described (i.e., heterotopagnosia without autotopagnosia, HwA (Corradi-Dell'Acqua & Tessari, 2010; Degos, Bachoud-Levi, Ergis, Petrissans, & Cesaro, 1997; Felician et al., 2003). These processes are dissociable and caused by focal brain damage, with HwA mainly arising from damage to the left inferior parietal cortex and AwH mainly from damage to the left superior parietal cortex (Corradi-Dell'Acqua & Tessari, 2010; Felician et al., 2003; Wicky, 2005).

Although AwH and HwA are typically caused by damage in the left hemisphere, neuropsychological studies have demonstrated that they do not depend on language deficits, as patients are generally able to name the body parts that they cannot point to (e.g., Auclair, Noulhiane, Raibaut, & Amarenco, 2009; Sirigu, Grafman, Bressler, & Sunderland, 1991). AwH and HwA also do not depend on general spatial deficits or the inability to analyze part—whole relationships, given that patients can correctly identify parts on non-human objects, i.e., different parts of a bike or car (De Renzi & Scotti, 1970; Felician et al., 2003). Instead, Felician and colleagues proposed in their seminal clinical studies that AwH/HwA are related to selective deficits in self-other distinction, so that HwA is due to an impaired representation of the body of others, affecting mainly visual bodily processing, while leaving somatosensory processing intact, and that AwH is based on impaired somatosensory processing affecting the representation of one's own body, while sparing visual bodily processing for bodies of other people.

Likely due to the rarity of HwA/AwH patients, this seminal proposal has not been systematically tested. Moreover, other factors may also be involved: while we experience our own body from a first-person perspective (1PP), where somatosensory and visual inputs are spatially aligned, we perceive the body of others from a more distant third-person perspective (3PP), where visual information about the other's body is not spatially congruent with somatosensory cues from

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Fig. 1 – Heterotopagnosia without autotopagnosia (HwA). Panel a represents the classical neuropsychological procedure for detecting HwA without virtual reality, i.e., pointing the target body parts verbally requested by the examiner on patient's own body (on the left) and on the examiner's body (on the right). Panel b, on the right, shows H+'s significant dissociation between pointing to his own (preserved) or to the examiner's (impaired) body parts (see **Supplementary Table 1**) under the classical HwA testing (panel a). The image on the right shows CT scan of H+, revealing his left hemispheric brain damage in the occipital-parietal lobe (R: right; L: left).

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the observer's own body. Thus, it is possible that the processing of one's own and other bodies is differently impacted by the perspective from which the target body is perceived and/or by differences in visual-somatosensory integration as perceived from these different perspectives. The integration of bodily multisensory cues from one's own body is considered an important mechanism for bodily self-consciousness and used to differentiate it from the other persons' bodies, as demonstrated by many examples of illusory feeling of ownership induced by manipulating the congruency between somatosensory signals from one's own body and visual stimuli from another person's body or avatar (e.g., Blanke, Slater, & Serino, 2015). According to this view, when identifying body parts on another person's body, another mechanism not considered in previous interpretations, could play a major role: a matching process linking visual information of the other person's body with somatosensory inputs from one's own body that are not spatially congruent (e.g., Beck, Bertini, Haggard, & Ladavas, 2015; Heed & Röder, 2012; Sirigu et al., 1991, see Fig. 2, panel a). If this were the case, a deficit in recognizing body parts on another person as in HwA, may be a deficit in integrating visual and somatosensory bodily information, rather than a deficit of visual processing with preserved somatosensory processing. If so, manipulations facilitating the integration between somatosensory bodily cues on one's own body and visual information from another body should improve HwA.

Here, we had the rare opportunity to study a patient (H+) in whom these hypotheses could be experimentally tested. Based on repeated standard neuropsychological assessments, patient H+ showed a specific disorder of indicating body parts on others, but had no difficulties in identifying body parts on his own body (HwA), due to a stroke affecting his left occipital-parietal cortex (Fig. 1). In order to investigate whether HwA depends on visual-somatosensory integration mechanisms, we here adopted recent virtual reality (VR) technology for research in the field of body recognition. This allowed us to manipulate separately the identity and the perspective of the target body (Fig. 2, panel a). In Experiment 1, we asked H+ to identify body parts of a virtual body of which we manipulated in a factorial design the identity (either the patient's own body or another person's body was shown) and the perspective from which the body was shown (in either 1PP or 3PP). According to current definitions of HwA, defined as a selective deficit for the recognition of another person's body, sparing one's own body representation (Auclair et al., 2009; Corradi-Dell'Acqua & Tessari, 2010; Felician et al., 2003; Wicky, 2005), H+ should not show any deficit in identifying body parts on his own body both when stimuli are shown from 1PP (self 1PP) or 3PP (self 3PP) in VR. Moreover, H+ should exhibit a deficit in recognizing body parts on another person's body from either perspective (other 1PP and other 3PP). Alternatively, it might be the case that HwA-symptoms rather emerge from a deficit in integrating visual and somatosensory bodily signals characterized by errors in processing visual bodily information when presented in 3PP and in linking such visual signals to somatosensory signals, regardless of the identity of the observed body (self or other). In that case, H+'s performance should be also impaired for his own body.

b Body part recognition in VR 100 80 60 40 20 0 OTHER SELF OTHER SELF SELF OTHER SELF OTHER SELF SELF OTHER OTHER 1PP 3PP 1PP 3PP 1PF 3PP H+ H-CG Percentage of incorrect responses Percentage of correct responses

Fig. 2 – Experiment 1: body part recognition in virtual reality. When HwA is tested through a virtual reality (VR) head mounted display, HMD, (panel a), somatosensory information from one's own body (represented here as the person wearing the HMD) and visual inputs related to target body (displayed in the black square, i.e., the monitor of the HMD) are never coincident in space, independently of the visual perspective (1PP, on the left or 3PP, on the right) or the identity of the body (own body, in red, others' body, in blue). If the matching between somatosensory information from one's own body and visual inputs from another body is impaired in HwA, a patient with HwA could make errors in all these conditions and not only in other body conditions. Here the observed bodies are represented as avatar in virtual reality just for illustrative purpose, please refer to Supplementary Fig. 1 for an example of the visual stimuli (photos) used in Experiment 1. Panel b shows the performance (percentage of correct and incorrect responses) of H+, the control patient (H-), and the healthy controls (CG) when indicating body parts on a photo of their own or of another person's body in 1PP and 3PP in VR. While H- and the CG never made errors (standard deviation equal to zero), H+ had difficulties in executing the task in all conditions, independently of identity or perspective.

Results from Experiment 1 revealed that H+'s HwA is not limited to the visual representation of other bodies (Auclair et al., 2009; Corradi-Dell'Acqua & Tessari, 2010; Felician et al., 2003), not a selective deficit in self-other discrimination, and not a selective perspectival deficit. Importantly, data from Experiment 1 suggested that HwA depends on the inability to integrate somatosensory inputs from one's own body with non-spatially congruent visual inputs of another (virtual) body observed at a distance (see Fig. 2). To further investigate this proposal, we next tested whether a procedure able to enhance the integration between



Fig. 3 - Experiment 2: full-body illusion (FBI). If HwA is a deficit of the matching between somatosensory information from one's own body and visual inputs from another person's body, it could be restored by the integration between the vision of a body seen at a distance and somatosensory information related to one's own body prompted by synchronous (seen and felt stroking are synchronous, on the left, red) but not asynchronous (on the right, blue) visuo-tactile stimulation during full-body illusion (panel a, Experiment 2). On panel b, on the left, H+'s performance in indicating body parts on a virtual projection of his own (self) or another person's (other) body are shown, before (baseline) and after (POST) synchronous (SYNC) or after asynchronous (ASYNC) visuo-tactile stimulation. Two experiments with visuo-tactile stroking were performed, by showing on the head-mounted display once the own body (above) and once the body of another person (below). Note that only after SYNC-FBI-self (arrow) H+'s deficit in indicating body parts disappeared. On the right, the changes in self-location are shown for H+ in the same conditions and compared to those of the CG (mean \pm standard error). Positive values indicate a higher drift toward the virtual body in SYNC versus ASYNC condition, as expected. Note that this was the case for both the CG and H+ after FBI-self, but not for the patient after FBI-other.

visual and somatosensory bodily inputs would ameliorate H+'s HwA (Fig. 3, panel a). To test this hypothesis, in Experiment 2 we sought to alter H_+ 's performance experimentally by adapting a well-established VR protocol based on the integration of visual signals from a body seen at a distance and somatosensory information related to one's own body for the first time to the study of HwA. In the so-called full-body illusion (FBI) (Blanke, 2012; Blanke et al., 2015; Lenggenhager, Tadi, Metzinger, & Blanke, 2007), participants receive tactile stimulations on their back while they observe the stroking of a human body presented in VR as if it were standing in front of them at a distant location. Previous studies have demonstrated that when exposed to the FBI, participants selfidentify with the seen virtual body, show a drift in selflocation (i.e., perceiving themselves to be located towards the position occupied by the virtual body), and, importantly, more strongly integrate multisensory visuo-tactile stimuli between their own and the virtual body (Aspell, Lenggenhager, & Blanke, 2009; Noel, Pfeiffer, Blanke, & Serino, 2015; Salomon et al., 2017). In Experiment 2, we tested whether multisensory visuo-tactile stimulation, as administered through the FBI protocol between H+'s body and a virtual body (seen in 3PP using VR), would ameliorate H+'s HwA, corroborating our data and interpretation from Experiment 1.

2. Materials and methods

2.1. Participants

Case report. H+, a 60-years-old ambidextrous man, was seen at the Clinique Romande de Réadaptation for rehabilitation, 1 month after a left occipito-parietal stroke and an occipital craniotomy to remove a cerebral arteriovenous malformation (Fig. 1). In the acute phase, the neurological exam showed preserved motor and somatosensory functions, right homonymous hemianopia and right hemispatial neglect. No visual, nor tactile extinction to double stimulation was detected. A detailed neuropsychological evaluation revealed cognitive impairments in language (fluent aphasia), memory (episodic memory), executive functions (deficit in the inhibition, planning and abstraction, perseveration), signs of apraxia (constructional and ideomotor apraxia) and visual agnosia (with pathological scores in the Visual Object and Space Perception test, VOSP, Warrington & James, 1991, for sub-tests concerning object perception, i.e., incomplete letters and silhouettes, and spatial perception, i.e., dot counting and cube analysis, and at the Poppelreuter-Ghent Overlapping Figures Test, De Renzi, Scotti, & Spinnler, 1969). There was no prosopagnosia. Moreover, at that time, he showed an impairment in pointing towards another person's body parts (i.e., examiner's body, 12 errors out of 20 trials), on a human body shown on a photo (8 errors out of 20), on a drawing of a human body (12 errors out of 18), and on a doll (8 errors out of 20). In contrast, H+ was able to correctly point to the same body parts on his own body (only 1 error out of 20; examiner's body versus H+'s body: χ^2 (1) = 13.79, *p* = .0002, Fig. 1) (see Supplementary Table 1 for further details and statistics), a self-other dissociation typically reported in HwA. Further tests were carried out,

because H+'s deficit in pointing to another person's body parts could potentially be caused by other cognitive deficits such as language impairment or general spatial problems. First, his deficit was not due to an overall language impairment (Dennis, 1976), because his ability to name body parts being pointed on his own or another person's body was comparable in the two conditions $[\chi^2 (1) = 2.06, p = .15]$. Importantly, he was able to correctly name all body parts, including those he could not indicate on another person's body. Second, H+ was able to locate the different parts of a non-human object, e.g., an animal (15 correct answers out of 15 trials, 3 animals: horse: eye, ear, mane, tail, shoe; duck: beak, leg, neck, wing, eye; elephant: tail, trunk, tusks, ear, eye), ruling out the account that the HwA deficit reflects rather a general spatial impairment such as an incapacity to analyze the whole into its components (Auclair et al., 2009; De Renzi & Scotti, 1970; Felician et al., 2003; Sirigu et al., 1991). Altogether, these observations suggest that H+'s difficulties were specifically related to process bodily information related to the body of others, consistently with the definition of HwA (e.g., Corradi-Dell'Acqua & Tessari, 2010; Felician et al., 2003; Wicky, 2005) (see Supplementary Table 1). Interestingly, during all the tests when the patient was asked to point to another person's body parts, he often referred to his own corresponding body parts. More precisely, instead of touching the examiner's body, H+ was searching on his own body the target body parts to point on the other person. This behavior, called "self-referencing behaviour", have been previously described in patients with heterotopagnosia (Degos et al., 1997; Felician et al., 2003) and thus further confirm here the diagnosis.

Control patient and control healthy participants. Another stroke patient with left (temporo-parietal) brain damage and similar neuropsychological deficits as H+, but without HwA (H-, the pointing to her own or examiner's body was flawless, i.e., 18/18 correct responses) was included in the study as a control patient (see Supplementary Table 2 for full neuropsychological profile of the two patients). H- underwent the Experiment 1 and the baseline (testing) task of the Experiments 2 (see below) in a single session within one day, while an extra day was dedicated to neuropsychological assessment (Supplementary Table 2). In addition, eight (4 males) agematched (mean age: 63.4, SD: 3.7, range: 58-69) neurologically unimpaired volunteers (Mini Mental State Examination scores always higher than the cut-off (Kalafat, Hugonotdiener, & Poitrenaudl, 2003) were also tested as control group (CG). All participants had normal or corrected to normal vision. Participants in the CG underwent Experiment 1 and 2 in a single experimental session within one day.

Patients and healthy participants were naive to the purpose of the work and they gave their written informed consent to participate to the study, which was approved by the local ethics committee (Ethics Committee of the canton of Valais, Switzerland) and was performed in accordance with the Declaration of Helsinki (2008 version).

2.2. Procedure

Four months after the initial neuropsychological evaluation (5 months post-stroke), we tested H+'s HwA-related symptoms in a body part task in VR by manipulating identity and

perspective (Experiment 1, Fig. 2, panel a) and the possibility of ameliorating his deficit through the FBI paradigm (Experiment 2, Fig. 3, panel a). H+'s scores were compared with those obtained in the control patient (H-) and the healthy control group (CG). We note that neuropsychological evaluation of H+ at the time of the experimental testing (Supplementary Table 2) revealed an overall amelioration in cognitive functions with respect to the initial assessment that was performed 1 month after stroke (paragraph 2.1). In particular, H+'s scores testing for neglect (i.e., Bell cancellation test, Gauthier, Dehaut, & Joanette, 1989, of the BEN battery, Batterie d'Évaluation de la Négligence unilatérale du Geren, Rousseaux et al., 2001) was not abnormal anymore (3 omissions, with left minus right difference <2, versus 29 omissions at the first neuropsychological evaluation, 1 month from stroke). Moreover, hemianopia was partially compensated thanks to trunk and head movements. Clinical HwA was still present when tested with standard neuropsychological evaluations at the time of the experiment [i.e., examiner's body, 4 errors out of 26 trials versus one's own body, 0 errors out of 28 trials, χ^2 (1) = 4.01, p = .045].

Experiment 1: body part tasks. To test if the ability to indicate body parts on one's own or on another person's body was modulated by the origin of visual information, i.e., visual perspective from where the body is seen, or the identity of the target body, i.e., either the patient's own body or another person's body, we used VR to present H+ and control participants with photos of their own body or of another person's body, either from 1PP or 3PP (Fig. 2, panel a), in different experimental blocks. All participants, except two subjects in the CG, explicitly noticed the identity of the observed body.

Participants (H+, H–, CG) were standing and wore a virtual reality head mounted display (HMD, Oculus Development Kit 1, 640 \times 800 resolution per eye, 110° Field of View (nominal), refresh rate 60 Hz, Oculus VR, Menlo Park, CA, USA). An inhouse software (ExpyVR, http://lnco.epfl.ch/expyvr) was used for stimulus presentation.

In the 1PP condition, participants had the head tilted downwards as if to look at their feet (as we do in daily life when looking down to our body) and observed in the HMD a photo depicting either their own or another body (gendermatched), extending from the chest to the feet. In the 3PP condition, the participants looked in front of them and saw a photo showing their own body or another body (gendermatched) facing them. The body displayed covered almost the entire vertical field of view of the HMD (~60°) and therefore appeared to be approximately at a distance of 1 m.

Capital letters (randomly selected) were superimposed on all the target body parts represented in the photo (see **Supplementary Figure 1**), so that participants could designate the target body part by naming the letter placed over the corresponding body part. Visually, the letters covered approximatively 5° and 3° of the HMD field of view in the 1PP and 3PP conditions, respectively. Before starting the task, we checked that all participants understood well the instructions, and were able to perceive and read the letters. For each trial, the experimenter verbally named the body part to recognize and the participant verbally indicated the letter corresponding to the target body part. In all conditions, the photos were shown for the time necessary for indicating all the target body parts (around 2 min for H+).

Sixteen targets were tested in 1PP (8 for self, 8 for other) and 26 in 3PP (13 for self, 13 for other). We compared the number of correct and wrong answers across conditions and between participants by means of the chi-squared test, with Bonferroni corrections for multiple comparisons.

Experiment 2: FBI: body-related visuo-tactile integration in HwA. The FBI experiment was carried out 10 days after Experiment 1 and consisted in two phases, a testing and a stimulation phase. For both phases, the participants observed an on-line virtual projection of their own body (self) or of another person's body (other) as filmed from the back and seen at a 2 m distance through the HMD. The body was filmed with two cameras (Logitech HD Webcam C270, 1280-720 pixels, Logitech Fluid Crystal Technology), placed on a tripod positioned 2 m behind the participant's own or the other person's body. The stereoscopic stimulus was presented in real-time (<50 msec latency) using our in-house software (ExpyVR, http://lnco.epfl.ch/expyvr, see https://doi.org/10. 17605/OSF.IO/WCJSF).

Testing. In the testing phase, to measure the patient's ability to recognize body parts before and after exposure to the FBI, we used a body part task similar to that used in Experiment 1. To follow standard FBI protocol, the task was adapted in this way: the body was seen from behind (and not from the front), and photos were replaced by online video stream of cameras showing the body. The task consisted of indicating the respective body part by indicating the letter placed on the image of one's own or another person's body (gendermatched), similarly to Experiment 1 (see Supplementary Figure 1). The letters were written on plastic cards (7 \times 7 cm) attached on participant's/experimenter's back, arms and legs. H+ executed this task (self and other condition) before and after the FBI (see below). The control patient (H-) and the control group (CG) performed the test only at baseline (self and other conditions) during the same day in which they were tested also for the tasks of Experiment 1 (always performed as firsts). According to the purpose of the study, there was no need to test H- and CG again after FBI because their performance was flawless and thus could not improve after the stimulation. Before starting the task, we checked that all participants understood well the instructions, and were able to perceive and read the letters. The testing (before FBI) was performed on two different days at one-week interval, to ascertain consistency of the results (12 body parts in total, 6 for each session). We considered the sum of all correct answers with respect to errors in all conditions and between participants and used the chi-squared test (Bonferroni corrected).

FBI. During the FBI (e.g., Blanke, 2012; Canzoneri, di Pellegrino, Herbelin, Blanke, & Serino, 2016; Dijkerman & Lenggenhager, 2018; Lenggenhager et al., 2007; Noel et al., 2015), we used a visuo-tactile stimulation procedure in which participants felt stroking on their back administered by the experimenter with a wooden stick, while the participants observed the online virtual projection of their own body (FBIself) or of another person's body (FBI-other) on a HMD. During the whole stimulation, the participant listened to white noise presented through headphones, to exclude surrounding auditory input. Perception of tactile stimuli on the patient's back was preserved as checked before the experiment. The temporal delay between felt and seen stroking was experimentally manipulated. The stroking felt by the participant on their back was synchronous (<50 msec delay) or asynchronous (\approx 500 msec delay, where tactile stimulus preceded the visual stimulus (Lenggenhager et al., 2007) with respect to the stroking seen on the on-line virtual projection of their own body (FBI-self) or of another person's body (FBI-other). The total design of the experiment was a 2 (FBI-self, FBI-other) by 2 (synchronous, asynchronous) design, administered in different blocks (Fig. 3, panel a). H+ and the CG underwent the same standard FBI stimulation, with the exception that according to the purpose of the study, there was no need to test CG again after FBI because their flawless performance already at the baseline could no further improve (see above). Data from the CG served as a control for the effects of the wellknown FBI procedure at a behavioral level (see below selflocation task).

The effect of the illusion was assessed through the selflocation task (Aspell et al., 2009; Blanke, 2012; Lenggenhager et al., 2007; Ronchi et al., 2015) both in H+ and in the CG. Instead of an explicit measure such a questionnaire, this implicit task was chosen because of H+'s language problems. In the self-location task, after 1 min of visuo-tactile stimulation, participants were passively guided (with small steps) to another position of the testing room (1.5 m backward) and were then asked to walk back to the initial position where they were during the FBI. The distance between the position estimated by the participants and their original position during the FBI was measured in centimeters (self-location drift). We considered the difference between the self-location drift observed after synchronous and asynchronous condition (Ronchi et al., 2015) by subtracting the drift obtained after synchronous from the drift after the asynchronous condition. Higher positive values, indicating a shift of self-location towards the virtual body, are expected in the synchronous as compared to the asynchronous condition (e.g., Ronchi et al., 2015). In order to test whether the FBI induced the expected change in self-location in H+, we compared the difference between the self-location drift observed after synchronous and asynchronous (for FBI-self and FBI-other) in the controls and in H+ by means of single sample t-tests, with Bonferroni corrections for multiple comparisons.

The first FBI stimulation per condition lasted 2 min, while the following four stimulations lasted 1 min each. A 2 min stimulation has been previously reported to be sufficient to induce the illusion (e.g., Canzoneri et al., 2016; Lenggenhager et al., 2007; Noel et al., 2015). The first four repetitions of the visuo-tactile stroking were intermixed with a few trials of the testing task (3 trials per repetition, 6 for self and 6 for other), while the last repetition was followed by the self-location task (1 trial of the self-location task). For both FBI-self and FBIother, H+ performed 2 separate blocks for synchronous and asynchronous stimulation, in randomized order. The entire session (FBI-self or FBI-other), consisting in one synchronous and one asynchronous block, was performed twice on two different days at one-week interval, to ascertain consistency of the results (12 body parts in total for self and 12 for other, 2 trials for the self-location task). Similarly to the procedure

previously described for the patient, healthy controls performed two separate blocks within the same day for the synchronous and the asynchronous condition, which order was counterbalanced. Each block included 2 repetitions of visuo-tactile stroking (the first repetition lasted 2 min, while the second lasted 1 min), followed by the *self*-location task (1 trial of the self-location task per repetition, 2 in total).

Statistical analyses in Experiment 1 and 2 were performed with Statistica software, Stat Soft[®], version 10, www.statsoft.com.

3. Results

3.1. Experiment 1: the more complex nature of heterotopagnosia when tested with VR

In Experiment 1, in order to evaluate the effect of *perspective* in pointing to the body parts, independently from identity, we collapsed the self-other data and analyzed H+'s responses separately for the 1PP and 3PP condition. H+'s performance in 1PP (14 errors out of 16 items) was even worse than in the 3PP condition (7 errors out of 26 items) [χ^2 (1) = 14.54, *p* = .0001]. No evident left-right bias emerged in the distribution of the errors (see Supplementary Table 3). These data suggest that H+'s "body deficit" does not only concern other peoples' bodies (as generally assumed in HwA), not only human bodies observed in 3PP, but also extends to stimuli presented in 1PP (as H+ showed deficits in 3PP and 1PP at least under the conditions of Experiment 1).

Moreover, in order to investigate the effect of the *identity* of the body, independently from the perspective, we collapsed 1PP and 3PP data and analyzed responses separately for the self and the other condition. There was no significant difference when H+ indicated body parts on his own (12 errors out of 21 items) as compared to on the other person's body (9 errors out of 21 items), with performance in both conditions being equally poor [χ^2 (1) = .86, p = .35]. This result indicates that H+'s deficit is not limited to processing body parts on another person's body, but also extends to body parts on his own body (see Supplementary Results for separate analyses on the four conditions).

We compared H+'s performance with that of a control stroke patient with left (temporo-parietal) brain damage and similar concurrent neuropsychological profile as H+, but, critically, without HwA (control patient, Supplementary Table 2). H+'s performance was also compared with the performance of a group of eight healthy age and gender matched participants (control group, CG). We note that in all conditions, H+ had a higher percentage of errors than the flawless performance (i.e., no errors) recorded both in the control patient or in the healthy controls [self, both perspectives: χ^2 (1) = 17, p < .00001; other, both perspectives: χ^2 (1) = 11.45, p = .0007; 1PP, self and other: χ^2 (1) = 24.89, p < .0001; 3PP, self and other: χ^2 (1) = 8.09, p = .0045; Bonferroni-corrected, alpha set at .0125] (Fig. 2, panel b).

Altogether, these data show that H+'s body part recognition deficit is not only characterized by an inability in processing information related to body parts shown on another person's body, as one might have expected based on the results of his neuropsychological testing, as well as clinical HwA definitions and past HwA cases. Moreover, H+'s deficit is not only determined by an inability in processing visual information from a body seen from 3PP, that is the perspective in which HwA has been previously tested. Instead, it seems that H+'s deficit may depend on the inability of mapping somatosensory inputs of one's own body and non-spatially congruent body-related visual inputs from other bodies. Indeed, what is common in all the tested conditions was the necessity to integrate somatosensory information of one's own body with visual information of the target body, independently of the identity or perspective of the target body. Crucially, in all the conditions tested with the present VR setup, somatosensory information of one's own body (in the real world) and visual information of the target bodies (in virtual reality, and regardless of identity and perspective) were never spatially congruent.

3.2. Experiment 2: body-related multisensory integration improves heterotopagnosia

Baseline. In the testing phase before the FBI (i.e., identifying body parts on the virtual projection of his own body or on another person's body), in line with data from Experiment 1, H+ made errors regardless of whether he had to identify body parts on his own body (self condition, 8 errors out of 12 items) or on another person's body [other condition, 7 errors out of 12 items; self-other comparison: χ^2 (1) = .18, p = .67]. In addition, in all conditions H+'s performance was significantly worse than the flawless performance of H– and the CG [self: χ^2 (1) = 12, p = .0005; other: χ^2 (1) = 9.88, p = .0017; Bonferronicorrected, alpha set at .016]. No evident left-right bias emerged in the distribution of the errors (see Supplementary Table 3). This finding confirms the results of Experiment 1 by showing that H+'s deficit involved recognition of body parts both on his own and on another person's body, independently if tested through static images, as in Experiment 1, or with online video recordings, as in experiment 2.

Body part recognition after FBI. After synchronous visuotactile stimulation, a condition promoting visuo-tactile integration and inducing the emergence of the FBI (Aspell et al., 2009), in the FBI-self condition, H+'s performance in indicating body parts on his own virtual body was strongly improved. Differing with his poor score obtained at baseline (8 errors out of 12 trials), H+ now named all body parts correctly [after the synchronous FBI-self condition: 0 errors out of 12 trials; $\chi^2(1) = 12$, p = .0005, Bonferroni-corrected]. Importantly, this improvement was specific for synchronous visuo-tactile stimulation, because no improvement in body part recognition occurred after asynchronous visuo-tactile stimulation (i.e., the control visuo-tactile condition that does not promote visuo-tactile integration and does not induce the FBI) in the FBI-self condition stimulation [after asynchronous FBI-self condition: 6 errors/12, χ^2 (1) = .69, p = .41]. Such changes were only observed when recognition was tested for his own body parts, since H+'s performance for another person's body parts after the FBI-self condition did not change [other condition at baseline: 7 errors/12; after synchronous: 7 errors/12; after asynchronous: 4 errors/12, χ^2 (1) = 1.51, p = .22]. Moreover, H+'s performance did not change after any of the FBIother conditions, neither after the synchronous nor the

asynchronous condition (*p* always higher than .41 in all conditions, see Fig. 3, panel b). We note that the order of the conditions (synchronous/asynchronous) was always randomized and that the FBI-induced improvement of H+ was constant as confirmed in two testing sessions separated by 1 week: that is, there were no errors after the FBI-self condition, while errors persisted after the FBI-other condition, independently of the time of testing.

Self-location after FBI. In order to measure the effectiveness of visuo-tactile stimulation in inducing the FBI, we analyzed the drift in self-location (i.e., the differential drift in synchronous and asynchronous FBI, see Materials and methods) and we found that H+ showed a positive drift after the synchronous FBI-self condition (\approx 50 cm), which was higher than that in the asynchronous condition (\approx 42 cm). This synchronous-asynchronous difference in H+ (\approx 8 cm) did not differ from and was comparable in magnitude to that found in healthy controls (mean \pm S.E.: 12.44 \pm 1.9 cm, t = 2.35, p > .05), showing that H+ had the same and expected drift in selflocation. Conversely, this was not the case after the FBIother condition: the difference between synchronous and asynchronous stimulation was again present in healthy controls (mean \pm S.E.: 7.5 \pm 2.44 cm), but not in H+ (-.5 cm, t = 3.28, p = .013, Bonferroni-corrected, alpha set at .025). As expected, in healthy controls, the drift was always higher in the synchronous as compared to the asynchronous condition, both in FBI-self (t = 6.57, p < .01) and in FBI-other (t = 3.08, p = .018, Bonferroni-corrected, alpha set at .025, Fig. 3, panel b) conditions. Thus, in contrast with the self-condition, visuotactile stimulation was not effective in inducing the FBI in H+ in the FBI-other condition.

4. Discussion

HwA is classically described as the inability of pointing to body parts seen on another person's body caused by a deficit in visual body representation, while the ability to identify the same body parts on one's own body is strikingly preserved, based on spared mechanisms of somatosensory body perception (see for reviews Corradi-Dell'Acqua & Tessari, 2010; Wicky, 2005). However, in the tasks typically used to detect HwA, the other person's body is generally seen in 3PP, that is, shown in full front-view and at some distance from the patient's body. This is in contrast with body parts of the patient's own body that are tested in 1PP, that is, in a partial and non-distant front-view. Therefore, the classical HwA behavioral pattern of impaired-other versus unimpaired-self recognition may actually imply a difference in processing bodily information from 1PP versus 3PP and associated differences in visual-somatosensory integration. Using VR technology to systematically manipulate perspective and identity, the data from experiments 1 and 2, demonstrate that H+'s HwA is based on an inability to integrate visual and somatosensory bodily cues, rather than a selective deficit in visual body representation.

Testing HwA for the first time in different experimental VR conditions, we were able to present to the patient an image of either his own or another person's body, and to present each observed body at the same distance (in VR) from the patient's body. In these conditions, H+ consistently made errors not only for body parts on the body of other people and when shown in 3PP, as predicted by his HwA deficit according to standard neuropsychological assessment. Tested in VR, H+ now also made many errors for body parts shown on his own body and, moreover, his errors were observed from 1PP and 3PP. Control data showed that his performance was significantly impaired with respect to that of a group of age-matched healthy adults and a control stroke patient (with a similar neuropsychological profile caused by left hemisphere brain damage, but without HwA). These findings from experiment 1 demonstrate that H+'s HwA is not a selective or predominant deficit in indicating body parts on other people's bodies (selfother deficit, Auclair et al., 2009; Corradi-Dell'Acqua and Tessari, 2010; Felician et al., 2003; Wicky, 2005), not in the processing of visual body-related information (Felician et al., 2003), and not in the processing of bodily stimuli in 3PP. Instead, we argue that H+'s HwA depends on an inability to integrate somatosensory self-related bodily signals (which are predominantly perceived in 1PP coordinates in real life conditions) with visual signals related to bodies perceived at a distance (which are predominantly perceived in 3PP coordinates in real life conditions).

This indicates that pointing to a location on another person's body relies on a matching process between own body related somatosensory cues and non-spatially aligned visual information from the other person's body, implying an engagement of own body signals when perceiving the body of others. Obviously, the involvement of own body representation is not sufficient to recognize other person's body parts per se, but requires an additional mechanism that matches or remaps bodily information from one's own body with those of the other person's body. In line with this interpretation, our findings also show that body part recognition was impaired when H+'s somatosensory inputs were presented with spatially non-matching stimuli from a target body shown at the same distance than another person's body in VR (experiment 1 and 2). This new proposal for interpreting HwA, as a problem in matching signals from one's own and another person's body, can also account for the performance of earlier HwA cases that was difficult to reconcile with previous interpretations, such as errors in identifying body parts of one's own body in a mirror test (Cleret de Langavant, Trinkler, Cesaro, & Bachoud-Lévi, 2009) and the "self-referencing behavior" (i.e., pointing to one's own corresponding body part when asked to point to a body part of the examiner, e.g., Cleret de Langavant et al., 2009; Degos et al., 1997; Felician et al., 2003). Although the majority of patients with HwA suffered from lesions involving the left parietal lobe (as H+), several patients also had damages to other areas, making it possible that in some cases HwA may depend on self-other discrimination deficit due to interference with different brain regions (e.g., occipito-parietal damage in H+, lesion in inferior parietal lobule (BA 39/40) in Felician et al., 2003; posterior parietal lesion in Degos et al., 1997; lesion in parietooccipital junction and insula in Cleret de Langavant et al., 2009; parieto-occipital lesion, or more in details, damages in parietal lobe, precuneus, part of the superior parietal gyrus and the posterior forceps of the corpus callosum, in Auclair et al., 2009).

The matching between signals from one's own body and visual inputs related to another body or body parts is also a crucial multisensory mechanism in body ownership, selfidentification, and self-location (Blanke et al., 2015), as tested in a large variety of bodily illusions ("full-body," "outof-body," or "body-swap" illusions: e.g., Aspell et al., 2009; Ehrsson, 2007; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008; rubber hand illusion: e.g., Botvinick & Cohen, 1998; De Vignemont, 2011; Kilteni, Maselli, Kording, & Slater, 2015; Serino et al., 2013; Tsakiris, 2010; for a review Blanke et al., 2015). These protocols have used VR to show another person's body in 3PP or 1PP (as in experiment 1) and additionally applied prolonged multisensory stimulation between one's own physical body and to an external visual (or virtual) body observed at a distance. In experiment 2, in order to experimentally alter mechanisms of visuo-somatosensory processing in H+ and to directly test our hypothesis of a deficient matching process between somatosensory and visual bodily cues that is at the core of HwA, we adopted a prolonged visuotactile stimulation in the FBI to prompt the integration between one's own body and the target body observed at a distance (i.e., Aspell et al., 2009; Noel et al., 2015; Salomon et al., 2017). These FBI data in patient H+ significantly extend those of Experiment 1 and demonstrate that visuotactile stimulation dramatically improves H+'s performance in indicating body parts, revealing that enhanced integration between somatosensory and visual bodily stimuli improves HwA through enhanced matching between one's own body and a virtual body observed at a distance.

A major finding in the present study was that the improvement in the processing of bodily stimuli through visuo-tactile stimulation that we observed in experiment 2 was highly selective. First, no improvements of H+'s HwA occurred after the asynchronous visuo-tactile stimulation, which is a control condition not inducing the FBI (see e.g., Blanke, 2012; Blanke et al., 2015; Lenggenhager et al., 2007). Second, no changes were observed in recognizing body parts on another person's body, when the FBI was induced while viewing the own body at a distance in VR, suggesting that the improvement was related only to the visual stimuli used to trigger the illusion (i.e., the patient's body observed during the FBI). Third, both the experimentally-induced improvement in HwA, and the experimentally-induced change in self-location (used to measure the occurrence of the FBI), were absent when H+ saw another person's body during VR exposure, even if the seen stimulation matched tactile stimulation on his back. These data consistently show that only stimulation patterns inducing the FBI and thus, favoring the integration of visual and somatosensory related bodily-cues, were related to HwA and able to improve H+'s performance. This extends previous efforts to improve body parts specific neurological symptoms through multisensory illusions such as rubber hand illusion for somatoparaphrenia or pathological embodiment (e.g., Bolognini, Ronchi, Casati, Fortis, & Vallar, 2014, 2015; Fossataro et al., 2018; Jenkinson, Haggard, Ferreira, & Fotopoulou, 2013) and through self-observation in a mirror for anosognosia for hemiplegia and somatoparaphrenia (Fotopoulou et al., 2011; Fotopoulou, Rudd, Holmes, & Kopelman, 2009). The present data are of relevance not only for clinical observations and

possible future therapeutic applications, but also for studies in healthy participants revealing the recruitment of one's own body representations in the processing of the others' body. For instance, previous works have shown an influence of one's own hand processing in judging the laterality of other people's hands (e.g., Candini et al., 2016; Ionta, Sforza, Funato, & Blanke, 2012). Similarly, activations in cortical areas generally implicated in first-person self-related processing (cortical midline structures) or in HwA (left inferior parietal lobe) have been reported during the pointing to body parts on another person body (i.e., Corradi-Dell'Acqua & Tessari, 2010; Felician et al., 2009; Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015; Vogeley & Fink, 2003). Our present data extend these previous results by revealing the role of own body representations in body cognition and, especially, that somatosensory cues from one's own body have to be properly integrated with visual inputs related to the target body for the correct recognition of body parts.

In conclusion, the present results offer a new interpretation of HwA, superseding previous accounts of HwA based on abnormal self-other distinction or interference between visual versus somatosensory processing (Auclair et al., 2009; Corradi-Dell'Acqua & Tessari, 2010; Felician et al., 2003; Wicky, 2005).

We argue, instead, that a deficit in matching somatosensory stimuli from one's own body with visual bodily stimuli of a body with different perspectival and other spatial attributes is the core deficit in HwA. VR technology allowed us to demonstrate this matching process by systematically dissociating identity as well as the perspectival and spatial congruency between cues from own and other bodies.

The perspectival, perceptual, and integrative multisensory mechanism in body recognition we have described may also be of relevance for other social functions such as action understanding and imitation (e.g., Buccino, 2014; De Vignemont & Haggard, 2008; Jeannerod, 2001, 2003; Rizzolatti & Craighero, 2004), as well as empathy, perspective taking, and theory of mind (e.g., De Vignemont & Singer, 2006; Keysers, Gazzola, Dulac, & Rizzolatti, 2009). Our data also show that VR is an important new research tool for body recognition and social cognition that requires the testing of human stimuli, social situations and complex human interactions. VR allows to test social situations in controlled laboratory conditions, in healthy and neurological participants. Such testing will likely become increasingly relevant because today's ubiquitous media technologies (e.g., skyping, gaming, VR, augmented reality, smartphones, selfies) are not only changing the constancy of perspectival and other spatial differences in the processing of one's own versus other bodies, but increase the amount and variability of readily available digital stimuli about one's own and other people's bodies the human brain is exposed to.

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Declaration of interests

The authors report no commercial or competing interests.

Open practices

We have reported all inclusion/exclusion criteria for the recruitment of patients and controls, all manipulations, and all measures in the manuscript. No data exclusions criteria or sample size estimation were applied. It has not been possible to pre-register part of the study procedures or analyses prior to the research being conducted.

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the study are available at https://doi.org/10.17605/OSF.IO/WCJSF.

CRediT authorship contribution statement

Michela Bassolino: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing - original draft, Writing - review & editing. Aurélie Bouzerda-Wahlen: Data curation, Formal analysis, Investigation. Viviane Moix: Investigation. Anne Bellmann: Investigation. Andrea Serino: Conceptualization, Writing - original draft, Writing - review & editing. Olaf Blanke: Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing.

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Supplementary data

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