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Hierarchical and dynamic relationships between body part ownership and full-body ownership

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ABSTRACT

What is the relationship between experiencing individual body parts and the whole body as one's own? We theorised that body part ownership is driven primarily by the perceptual binding of visual and somatosensory signals from specific body parts, whereas full-body ownership depends on a more global binding process based on multisensory information from several body segments. To examine this hypothesis, we used a bodily illusion and asked participants to rate illusory changes in ownership over five different parts of a mannequin's body and the mannequin as a whole, while we manipulated the synchrony or asynchrony of visual and tactile stimuli delivered to three different body parts. We found that body part ownership was driven primarily by local visuotactile synchrony and could be experienced relatively independently of full-body ownership. Full-body ownership depended on the number of synchronously stimulated parts in a nonlinear manner, with the strongest full-body ownership illusion occurring when all parts received synchronous stimulation. Additionally, full-body ownership influenced body part ownership for nonstimulated body parts, and skin conductance responses provided physiological evidence supporting an interaction between body part and full-body ownership. We conclude that body part and full-body ownership correspond to different processes and propose a hierarchical probabilistic model to explain the relationship between part and whole in the context of multisensory awareness of one's own body.

1. Introduction

Multisensory bodily illusions (Ehrsson, 2022), such as the rubber hand illusion (Botvinick & Cohen, 1998) and the full-body ownership illusion (Petkova & Ehrsson, 2008), provide a unique opportunity to experimentally manipulate perceptions of one's own body in healthy participants. In these illusions, a combination of repeated visual stimulation to a rubber arm (Botvinick & Cohen, 1998) or a mannequin (Petkova & Ehrsson, 2008) that is viewed from the natural (first person) point of view with synchronous tactile stimulation of the real arm or body at corresponding locations triggers the illusory sensation that the fake arm or body is one's own. These illusions occur due to the perceptual binding of visual, tactile and proprioceptive signals that are spatiotemporally centred on the fake limb or body, so that tactile and proprioceptive sensations seem to originate from the rubber hand or mannequin (Ehrsson, 2012; Ehrsson, Spence, & Passingham, 2004; Petkova & Ehrsson, 2008). With regard to both body parts and whole bodies, these experimental paradigms permit the study of the sense of body ownership (Blanke, Slater, & Serino, 2015; Ehrsson, 2012, 2020; Tsakiris, Carpenter, James, & Fotopoulou, 2010) and multisensory bodily awareness under controlled research settings (Ehrsson, 2022). A great deal of research has focused on the basic multisensory processes associated with the elicitation of these bodily illusions and the relationship between the subjective sense of body ownership and multisensory integration (Blanke et al., 2015; Ehrsson, 2020; Kilteni, Maselli, Kording, & Slater, 2015; Makin, Holmes, & Ehrsson, 2008; Tsakiris, 2010). For example, the rubber hand illusion and the full-body ownership illusion depend on the temporal and spatial congruence of sensory signals in different sensory modalities (Costantini & Haggard, 2007; Ehrsson et al., 2004; Ehrsson, 2020; Lloyd, 2007; Petkova et al., 2011b; Petkova & Ehrsson, 2008; Shimada, Fukuda, & Hiraki, 2009) in a manner reminiscent of the spatiotemporal principles of multisensory integration (Blanke et al., 2015; Holmes & Spence, 2005; Stein & Stanford, 2008). Indeed, the classic way to elicit the rubber hand illusion and the full-body ownership illusion with a mannequin is by using synchronous visuotactile stimulation, which is contrasted with asynchronous visuotactile stimulation - which reduces the illusion - in otherwise equivalent experimental conditions (Botvinick & Cohen,

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1998; Petkova et al., 2011b; Preston, Kuper-Smith, & Ehrsson, 2015; Reader, Trifonova and Ehrsson, 2021b; van der Hoort, Guterstam, & Ehrsson, 2011). More recent probabilistic multisensory models of body ownership have focused not on fixed temporal and spatial rules but rather on the information conveyed by the correlated sensory signals and how these signals are interpreted in a probabilistic fashion. In Bayesian causal inference models (Körding et al., 2007; Sato, Toyoizumi, & Aihara, 2007) of body ownership (Chancel, Ehrsson and Ma, 2022a; Kilteni et al., 2015; Noel et al., 2019; Samad, Chung, & Shams, 2015), the most likely cause of the sensory signals is estimated based on spatiotemporal correspondence, sensory uncertainty and prior experiences, and this process of causal inference determines the automatic perceptual decision regarding whether to combine or segregate visual and somatosensory signals into a coherent multisensory representation of one's own body part.

Although previous work has focused on how vision, touch and proprioception contribute to the multisensory perception of one's own body, given the importance of these senses for localising and identifying body parts in space, other senses also contribute. Bodily illusions such as the rubber hand illusion and the full-body ownership illusion are influenced by congruent versus incongruent combinations of sensory information in sensory channels, such as vision and sensed bodily movement (kinaesthesia) (Kalckert & Ehrsson, 2012; Slater, 2008; Walsh, Moseley, Taylor, & Gandevia, 2011), vision and felt static bodily posture (proprioception) (Carey, Crucianelli, Preston, & Fotopoulou, 2019; Ide, 2013), vision and vestibular information (Preuss & Ehrsson, 2019), vision and thermosensory information (Crucianelli, Enmalm, & Ehrsson, 2022), and vision and various forms of interoceptive signals (Monti, Porciello, Tieri, & Aglioti, 2020; Crucianelli, Krahé, Jenkinson, Fotopoulou, 2018; Crucianelli & Ehrsson, 2023). Top-down knowledge and prior experience modulate these multisensory illusory processes (Chancel et al., 2022a; Tsakiris, 2010), and individual differences in multisensory integration (Chancel et al., 2022a; Costantini et al., 2016; Horváth et al., 2020; Shimada et al., 2009) and cognition (Germine, Benson, Cohen, & Hooker, 2013; Marotta, Tinazzi, Cavedini, Zampini, & Fiorio, 2016; Slater & Ehrsson, 2022) can also influence subjective illusion strength. Furthermore, body ownership illusions themselves can also lead to changes in body representation that range beyond changes in multisensory bodily awareness, thus influencing body representations for emotional and motoric processing. For example, illusions pertaining to arm and hand ownership bias goal-directed voluntary movement (Heed et al., 2011; Newport, Pearce, & Preston, 2010; Preston & Newport, 2011; Rossi Sebastiano et al., 2022; Zopf, Truong, Finkbeiner, Friedman, & Williams, 2011)(but not simple movement; Reader, Trifonova and Ehrsson, 2021a) and sensorimotor predictions (Kilteni & Ehrsson, 2017; Padrao, Gonzalez-Franco, Sanchez-Vives, Slater, & Rodriguez-Fornells, 2016); such illusions also impact emotional processes (Fourcade, Schmidt, Nierhaus, & Blankenburg, 2022; Preston & Ehrsson, 2018) and emotional defence reactions to physical threats (Armel & Ramachandran, 2003; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Petkova & Ehrsson, 2008). Other researchers have demonstrated that these illusions can even cause changes in self-related higher cognition (Pyasik, Ciorli, & Pia, 2022), such as self-concept (Banakou, Hanumanthu, & Slater, 2016; Maister, Slater, Sanchez-Vives, & Tsakiris, 2015; Tacikowski, Weijs, & Ehrsson, 2020) and episodic memory (Iriye & Ehrsson, 2022).

A fundamental aspect of the perception of one's own body is the unitary experience of the entire body; we do not experience our bodies as a set of disconnected parts but rather as a single body. However, relatively little attention has been given to the relationship between multisensory perceptions of one's individual body parts and such perceptions of the body in its entirety, especially in the experimental literature. Research conducted in the multisensory integration theoretical framework discussed above has suggested that the difference between body part ownership and full-body ownership is related to the spatial extent over which perceptual binding of multisensory body-related information occurs (Blanke et al., 2015; Ehrsson, 2012; Petkova et al., 2011a): a coherent multisensory representation of one's entire body requires the integration of multisensory information across multiple limbs and body segments (Blanke et al., 2015; Gentile, Björnsdotter, Petkova, Abdulkarim, & Ehrsson, 2015; Petkova et al., 2011a), whereas a coherent multisensory representation of a limb or restricted body part primarily requires the binding of multisensory information regarding that body part (Chancel, Blanchard, Guerraz, Montagnini, & Kavounoudias, 2016; Collins, Refshauge, Todd, & Gandevia, 2005; de Vignemont, Tsakiris, & Haggard, 2005; Ehrsson et al., 2004; Gentile, Petkova, & Ehrsson, 2011, Gentile et al., 2015; Limanowski & Blankenburg, 2016; Lloyd, 2007). However, although differences in the spatial extent of multisensory integration probably contribute to differences in multisensory perception between body parts and whole bodies, they do not explain the specific relationships between part and whole or how full-body ownership is established based on the ownership of parts.

Thus, the question of the relationship between parts and whole in the context of body ownership deserves more attention, and several arguments can be made to support the idea that body part ownership and full-body ownership may be different. First, the distinction between part and whole, according to which the whole is fundamentally something other than the sum of its parts, has long been at the core of gestalt psychology (Koffka, 2013; Pinna, 2010; Rescher & Oppenheim, 1955; Wagemans et al., 2012). Thus, conceptualising the perception of one's entire body as a "whole-body perceptual gestalt" (Gentile et al., 2015) based on gestalt principles of perceptual organisation would indicate the existence of a representation of the owned body in its entirety that is different from or more than the sum of the composite body parts (O'Kane & Ehrsson, 2021). Second, the notion that the relationship between the whole and parts may differ from the relationships among parts is in line with philosophical work on "body mereology" (derived from the Greek meros, meaning "part") (de Vignemont et al., 2005), which aims to clarify how the body as a whole is organised into parts and how body parts relate to each other within the whole (Bermúdez, 2011, 2017, 2018; Munro, 2021). Recent experimental studies in this direction have revealed that tactile localisation (Cholewiak & Collins, 2003; Miller et al., 2022) and two-point discrimination are most precise near the boundary between different segments of limbs (e.g., between hand and forearm) rather than within the same segment, illustrating the common parcellation of the body representation into parts (de Vignemont, Majid, Jola, & Haggard, 2009; Le Cornu Knight, Cowie and Bremner, 2017; de Vignemont, 2017). As noted by Bermúdez (2017), although bodily events are typically experienced relative to the body as a whole, they are also mapped onto individual limbs and body parts based on a hierarchical spatial model of the body, according to which parts are defined by joints. Finally, evidence to support the existence of processes that are specific to body parts versus the whole body is abundant within the neurological and neuropsychiatric literature. Examples of disturbances in the ownership of one's own body part include poststroke limb disownership syndromes, which are characterised by the feeling that a body part no longer belongs to oneself (somatoparaphrenia and asomatognosia) (Feinberg & Venneri, 2014; Moro et al., 2023; Vallar & Ronchi, 2009), and body integrity dysphoria, a neuropsychiatric condition characterised by dissatisfaction with one's body, which is often associated with the desire to amputate a body part, alongside feelings of disownership for that unwanted body part (Romano, Sedda, Brugger, & Bottini, 2015; Saetta et al., 2020). Disturbances can also affect more global aspects of bodily awareness. Reports of such disturbances have been documented in depersonalisation-derealisation disorder (Hunter, Phillips, Chalder, Sierra, & David, 2003), posttraumatic stress disorder (Ataria, 2016) and schizophrenia (Kean, 2009; Klaver and Dijkerman, 2016). Neurological research into autoscopic phenomena, such as out-of-body experiences, has indicated that changes in the spatial experience of the bodily self as a whole may occur following brain damage and focal epileptic seizures involving parietal and temporal brain regions (Blanke & Mohr 2005; Blanke, Landis, Spinelli, & Seeck, 2004; Blanke, Faivre, & Dieguez, 2016; Brugger, 2006; Brugger, Agosti, Regard, Wieser, & Landis, 1994). Collectively, these streams of literature have suggested that functional relationships between part and whole in bodily awareness can be selectively interrupted by structural brain damage and changes in neurophysiological functioning.

However, based on empirical studies on bodily illusions, our knowledge of the relationship between body part and full-body ownership remains quite limited. In rubber hand illusion studies, body ownership has been investigated in the context of a single body part, the hand, and in most previous studies on the full-body illusion (Petkova et al., 2011a; Petkova & Ehrsson, 2008), subjective body ownership of the body is assessed without distinguishing between parts and the whole. Indeed, previous studies involving full-body illusions have typically asked participants to rate their experiences of the fake body in view as their own without explicitly investigating the feeling of ownership pertaining to individual body parts versus that pertaining to the body in its entirety. We know that a comparable full-body ownership illusion can be elicited by synchronous visuotactile stimulation applied to one (Gentile et al., 2015; Petkova et al., 2011a), two, or three body parts simultaneously (O'Kane & Ehrsson, 2021) and that it does not appear to matter which body part(s) – arm, leg or trunk/torso – are synchronously stimulated (Gentile et al., 2015; Petkova et al., 2011a; van der Hoort et al., 2011). A moderately strong full-body illusion can sometimes be elicited simply by looking at a mannequin (without stroking it) that is placed in an anatomically and spatially congruent position presumably through the visuo-proprioceptive integration of spatially congruent visual and proprioceptive cues (Carey et al., 2019). Notably, during the visuotactile full-body illusion, subjective ownership seems to "spread" across body parts (Gentile et al., 2015; Petkova & Ehrsson, 2008); thus, if the full-body illusion is induced by synchronously stroking one body part, ownership ratings for nonstimulated body parts are also significantly influenced. However, little is known about the mechanism underlying this effect, and even if it has been assumed to reflect an aspect of the full-body illusion in some way, its relationship to full-body ownership versus the ownership of other stimulated body parts has not been examined.

Previously, O'Kane and Ehrsson (2021) developed questionnaire ratings specifically designed to quantify full-body ownership and body part ownership during a full-body illusion experiment and found both of these sensations of ownership to be driven by visuotactile synchrony and to be correlated; ownership ratings were also enhanced for body parts that did not receive visuotactile stimulation, and these ratings were also positively correlated with illusory full-body ownership ratings. Thus, although previous studies have shown that congruent multisensory signals drive illusory ownership of both body parts and the whole body, we still know little about the basic principles that determine how a full-body ownership sensation arises from ownership of parts. Conceptualising body part and full-body ownership as local versus global multisensory processes and assuming that full-body ownership is more than the sum of the parts (O'Kane & Ehrsson, 2021; Petkova et al., 2011a) implies that it should be possible to dissociate body part and full-body ownership; a person should be able to perceive (or not perceive) ownership of a single body part regardless of whether full-body ownership is experienced. Addressing these questions would require an experimental paradigm that is lacking in the literature: an experiment that independently manipulates ownership of different body parts simultaneously using a combination of synchronous or asynchronous visuotactile stimulation and varies the numbers of parts associated with illusory ownership to clarify the relationship between this phenomenon and the full-body illusory experience. Such an experiment would allow us to specifically investigate whether it is possible to dissociate body part and full-body ownership, identify how many parts of the body must be experienced as one's own before a full-body ownership illusion is triggered, and test the hypothesis that full-body ownership arises in a nonlinear fashion with respect to body part ownership.

To address these questions, we manipulated the temporal congruence (synchronous or asynchronous) of visual and tactile stimuli delivered concurrently to three distinct body parts—the right arm, the trunk, and the right leg—within an adapted version of the full-body illusion paradigm with a mannequin viewed from the first-person perspective (1PP) (O'Kane & Ehrsson, 2021; Petkova et al., 2011b; Petkova & Ehrsson, 2008). Crucially, in eight (Experiment 1) or four (Experiments 2 and 3) experimental conditions we systematically varied the relative number of body parts receiving synchronous versus asynchronous stimulation (from all synchronous to all asynchronous). In this experimental paradigm, we quantified the subjective experience of body ownership for five different body parts (the right arm, the left arm, the trunk, the right leg and the left leg) and for the body as a complete whole using questionnaire ratings that were specifically designed to assess body part ownership and full-body ownership (Experiments 1 and 2). As an indirect physiological index of the multisensory bodily illusion (O'Kane & Ehrsson, 2021; Petkova & Ehrsson, 2008), we also registered the skin conductance responses (SCRs) triggered by physical threats to the mannequin's right arm in different conditions when ownership of the right arm and ownership of the entire body were manipulated (Experiment 3). Based on the multisensory theoretical framework outlined above, we formulated three hypotheses regarding the psychometric data. First, we posited that body part ownership would be driven primarily by visuotactile synchrony (versus asynchrony) for each body part relatively independently and that body part ownership would be reported even when full-body ownership was not. Second, we hypothesised that full-body ownership would be related to visuotactile synchrony delivered to multiple body parts with the strongest full-body illusion elicited when all stimulated parts receive synchronous visuotactile stimulation, but, critically, that the relationship to the number of synchronously stimulated parts would be nonlinear. Third, we posited that the full-body ownership illusion would enhance illusory body part ownership ratings for nonstimulated body parts (the left arm and the left leg) and that this "spread of ownership" would be related to subjective full-body ownership and thus exhibit a similar nonlinear relationship to the number of synchronously stimulated parts as illusory full-body ownership. Finally, we hypothesised that the SCR evoked by threats to the mannequin's right hand should follow the pattern of the subjective ratings of hand ownership identified in the previous experiments (Fan, Coppi, & Ehrsson, 2021; Gentile, Guterstam, Brozzoli, & Ehrsson, 2013; O'Kane & Ehrsson, 2021; Petkova & Ehrsson, 2009) and thus potentially serve as a physiological index of arm ownership (or the lack thereof) irrespective of full-body ownership; however, previous studies have also suggested that threat-evoked SCRs reflect full-body ownership (Guterstam et al., 2015; Petkova & Ehrsson, 2008), and so this measure may instead follow the pattern of subjective ratings for full-body ownership or reveal an interaction between the body part and full-body ownership effects.

We report the results of the three experiments in chronological order in terms of when they were planned and conducted; the specific aims, experimental designs, and analyses are described in the corresponding sections below. Finally, inspired by recent developments in probabilistic computational models of body ownership (Chancel et al., 2022a; Chancel & Ehrsson, 2023; Kilteni et al., 2015; Preuss Mattsson, Coppi, Chancel, & Ehrsson, 2022; Samad et al., 2015) (see also human experiment in Fang et al., 2019), we extended these models and developed a hierarchical Bayesian model to explain our findings and characterise the relationship between part and whole according to this influential theoretical framework.

2. Experiment 1 - Aims and rationale

The aim of the first questionnaire experiment was to examine the relationship between illusory feelings of ownership of parts and the whole body when different combinations of synchronous and asynchronous visuotactile stimulation are delivered to multiple body parts in the context of a full-body illusion paradigm involving a mannequin viewed from the first-person perspective through a head-mounted display (HMD) (O'Kane & Ehrsson, 2021; Petkova et al., 2011b; Petkova & Ehrsson, 2008). Accordingly, we designed the most extensive and systematic investigation of body part and full-body ownership to date. Experiment 1 consisted of eight experimental conditions during which synchronous or asynchronous visuotactile stimulation was delivered to the right hand, trunk or right leg of a mannequin and the participant in *all possible* combinations. The three body parts chosen for stimulation were in keeping with previous full-body ownership illusion studies (Gentile et al., 2015; O'Kane & Ehrsson, 2021; Petkova et al., 2011a). Thus, the experiment included one condition of fully synchronous stimulation, three configurations of two synchronous and one asynchronous stimulation, three configurations of one synchronous and two asynchronous stimulations, and one condition of fully asynchronous stimulation. The subjective experiences of body part and full-body ownership were quantified in all conditions based on separate questionnaire items that investigated body ownership of the five body parts and the whole body (O'Kane & Ehrsson, 2021).

As mentioned above, we examined the hypotheses that the synchronicity of visuotactile stimulation determines whether a particular body part is perceived as one's own, that the strongest full-body ownership sensation is elicited when all three body parts receive synchronous stimulation, and that full-body ownership does not reflect a linear summation of body part ownership but rather exhibits greater illusory increases in cases in which more parts receive synchronous as opposed to asynchronous stimulation (i.e., a non-linear relationship). Additionally, we explored the hypothesis that body part ownership regarding nonstimulated body parts increases when full-body ownership is experienced, and that a similar non-linear relationship exists between ownership for nonstimulated body parts and the number of synchronously stimulated body parts as in the case of full-body ownership.

3. Experiment 1 - Methods & materials

3.1. Experiment 1 - Participants

Forty-eight healthy adults (17 females, 31 males; average age: 26.3 ± 4.2 years; age range: 21–41 years; 47 right-handed, 1 left-handed, self-reported) were recruited via online and poster advertisements to participate in the experiment, which lasted for approximately 30 min; these participants were compensated with one cinema ticket. The sample size was based on a previous study (O'Kane & Ehrsson, 2021) and predetermined before the data collection commenced. All participants were naïve to the full-body ownership illusion and provided written informed consent upon arrival. The study was approved by the Swedish Ethical Review Authority (https://etikprovningsmyndigheten.se/).

3.2. Experiment 1 - Visual stimulation and HMD

Experiment 1 comprised eight experimental conditions that all included identical visual stimulation consisting of a two-minute prerecording of a life-sized male mannequin's body lying on a bed from the first-person perspective (Fig. 1). In this prerecorded movie, a trained experimenter (SO) applied sixteen independent strokes along a 15 cm trajectory to three body parts of the mannequin's body simultaneously. As previously mentioned, the three body parts were the mannequin's right arm, trunk, and right leg. The three strokes were delivered using three spherical tactile stimuli that were connected to sticks of one metre in length that were held by the experimenter (as described in further detail below). Since all video recordings presented to the participants in the eight conditions included in the current study were identical to the three synchronous ("3S") experimental condition used in a previous study, please refer to (O'Kane & Ehrsson, 2021) for a detailed description of its construction. In brief, this visual stimulation was prerecorded using two Go Pro Hero Black 10 cameras (GoPro Inc., USA) and assembled using Final Cut Pro X software (Apple, USA) to create a 3D stereoscopic image of a male mannequin lying in a supine position on a bed against a blue background and receiving repeated touch stimulation. The movie had a duration of two minutes and was presented to the participants using an HMD (Oculus Rift DK2) via a graphical user interface developed by our inhouse engineer.

3.3. Experiment 1 - Visuotactile stimulation

Tactile stimulation was delivered to the right arm, trunk and right leg

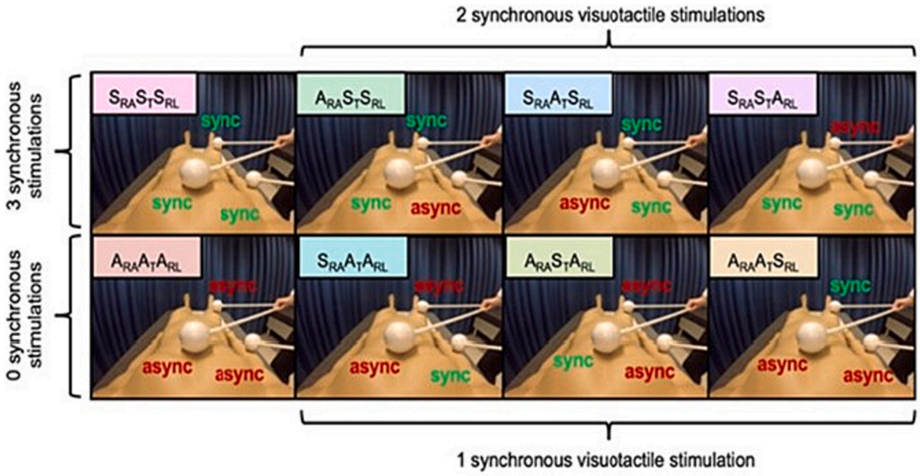

Fig. 1. The eight experimental conditions used in Experiment 1. The visual stimulation was identical in all experimental conditions. It consisted of an immersive, naturalistic, stereoscopic high-resolution video of a mannequin lying on a bed receiving repetitive and simultaneous strokes on three body parts. The participant lay on the same bed in the same room as shown in the videos and wore a head-mounted display (HMD) that showed the videos; the participant's head was tilted forward as if he or she were looking down on his or her body. The tactile stimulation applied to the right arm (RA), trunk (T), and right leg (RL) of participants' unseen real bodies was either synchronous (S) or asynchronous (A). $S_{RA}S_TS_{RL}$ represents the delivery of three synchronous visuotactile stimulations simultaneously, $A_{RA}S_TS_{RL}$, $S_{RA}A_TS_{RL}$ and $S_{RA}S_TA_{RL}$ represent the delivery of two synchronous and one asynchronous visuotactile stimulations, $S_{RA}A_TA_{RL}$, $A_{RA}S_TA_{RL}$ and $A_{RA}A_TS_{RL}$ represent the delivery of one synchronous and two asynchronous visuotactile stimulations, and $A_{RA}A_TA_{RL}$ represents the delivery of zero synchronous (and three asynchronous) visuotactile stimulations. Stimulus onset asynchrony (SOA) during asynchronous visuotactile stimulation was always precisely 2 s (the visual event always preceded the tactile stimulation). Note: Monocular view for illustrative purposes; a 3D binocular view was achieved using the HMD worn by the participants.

of participants' real bodies using the same custom-made tactile stimuli shown in the prerecorded 3D videos, which were hand-held plastic probes with polystyrene spheres that came into contact with the participants' bodies (Fig. 1). In each condition, sixteen individual strokes (1 s in duration) were delivered in intervals ranging from two to six seconds, with the first tactile stimulation occurring at twelve seconds. Prior to the first tactile stimulation, participants simply viewed a still image of the mannequin's body within the HMD, while the experimenter (SO) prepared to apply the tactile stimuli associated with each experimental condition (in eight possible combinations; see further details below). For synchronous visuotactile stimulation, the timing and duration of the delivered strokes were matched as closely as possible to those viewed by participants in the HMD. For asynchronous stroking in the mixed synchronicity conditions or the fully asynchronous control condition (see the following section), the stimulus onset asynchrony (SOA) between the seen and subsequently felt touches was always precisely two seconds, thus ensuring that there was no temporal overlap between what was seen and what was felt as well as that the experimenter had ample time to stimulate multiple body parts and guarantee the synchronous and synchronous elements of the experiment. When multiple asynchronous stimulations were provided, they occurred simultaneously, as was the case for synchronous stimulations. That is, the visual stimuli on the three body parts were always presented at the same time in all conditions; the only distinction for the asynchronous stimulations was the delayed tactile stimulations. The frequency of the delivery of the visuotactile stimulations was identical to the frequency employed in a previous study (O'Kane & Ehrsson, 2021) to ensure the complete temporal separation of the visual and tactile stimuli impacting a particular limb between each stroke stimulus, as was the case in the asynchronous condition; thus, the intertrial interval ranged from 4 to 9 s in duration (6.5 s on average) to avoid a predictable temporal pattern and to ensure a sufficiently long interval with regard to the minimum delay to enable the experimenter to stimulate the body part(s) asynchronously immediately after stimulating the other body part(s) synchronously in the mixed synchronicity conditions. Throughout the two-minute span of each of the eight stimulation configurations (see below), the timing and duration of all tactile stimulations applied to participants' real bodies were controlled by audio instructions produced using Audacity 2.3.3 software (Audacity Inc., USA) and supplied only to the experimenter (SO) through noise-cancelling headphones. The audio instructions included a metronome played at 120 bpm, such that two beats correspond to one second in real-time, i.e., the duration of one stroke. This was approach made it easy for the experimenter to deliver asynchronous stimulation simply by delaying the strokes with respect to the visual stimulation by 2 s, i.e., four metronome beats. To deliver the stimuli, the experimenter held one touch probe in the left hand to stimulate the participant's right arm and used the other two probes (which were attached to one another using elastic bands and positioned between the thumb and the index as well as between the middle and the third finger, thereby resembling the grip used by percussionists) to stimulate the trunk and right leg (O'Kane & Ehrsson, 2021). The experimenter (SO) was highly trained to ensure that the tactile stimuli were delivered precisely and reliably using this technique; the same experimenter applied the stimuli in all experiments. Participants wore earplugs during the experiment to ensure that none of the sounds of the stimulation were audible, which could otherwise potentially influence the illusion (Radziun & Ehrsson, 2018).

3.4. Experiment 1 - Experimental conditions

Eight conditions were included in the experiment. In each condition, repeated visuotactile stimulation was always applied to three body parts: the right arm (RA), trunk (T), and right leg (RL). The stimuli applied to each body part varied systematically between synchronous (S) and asynchronous (A). Thus, the conditions were as follows: (i) synchronous stimulation of all three body parts ($S_{RA}S_{T}S_{RL}$); (ii) synchronous stimulation of the trunk and the right leg, asynchronous stimulation of the right arm ($A_{RA}S_{T}S_{RL}$); (iii) synchronous stimulation of the right arm and the right leg, asynchronous stimulation of the trunk ($S_{RA}A_{T}S_{RL}$); (iv) synchronous stimulation of the right arm and the trunk, asynchronous stimulation of the right leg ($S_{RA}S_{T}A_{RL}$); (v) synchronous stimulation of the right arm, asynchronous stimulation of the trunk and the right leg ($S_{RA}A_{T}A_{RL}$); (vi) synchronous stimulation of the trunk, asynchronous stimulation of the right arm and the right leg ($A_{RA}S_{T}A_{RL}$); (vii) synchronous stimulation of the right leg, asynchronous stimulation of the trunk and the right arm ($A_{RA}A_{T}S_{RL}$); and asynchronous stimulation of all three body parts ($A_{RA}A_{T}A_{RL}$). The eight experimental conditions are illustrated in Fig. 1.

3.5. Experiment 1 - Questionnaire

After each experimental condition, participants completed the same 10-item questionnaire as used in a previous study (O'Kane & Ehrsson, 2021). Upon each presentation, the items were rearranged in a different order. These items were specifically crafted to capture participants' experiences of sensing the touches at the locations they observed on the mannequin's body (referral of touch) (Q1, Q2), the sense of full-body ownership (Q8), and the sense of ownership over isolated body parts (Q3-Q7) (Table 1). Additionally, two control questions (Q9, Q10) addressed 'fake experiences' not associated with the illusion. Responses were scored on a 7-point Likert scale in which −3 indicated 'strongly disagree' and + 3 indicated 'strongly agree'.

3.6. Experiment 1 - Procedure

After providing written informed consent, participants assumed a supine position on a bed and put on the HMD, which showed a stereoscopic view of a mannequin's body from the first-person perspective (Petkova et al., 2011b). After participants adjusted the HMD to ensure optimal clarity and comfort, they were instructed to lie as still as possible in a position analogous to that of the mannequin's body. Participants' heads were tilted slightly forward (approx. 20 degrees) and supported by pillows to convey the impression that they were looking down on the mannequin's body in the HMD. After participants inserted a pair of earplugs and indicated that they were ready to begin, the experimenter (SO) initiated the prerecorded visual stimulation and administered one of the experimental conditions as previously described. Each condition consisted of an identical two-minute visual stimulation with a corresponding condition-specific configuration of tactile stimulation, and each of these eight conditions was presented only once to the participant. Immediately after each condition, participants removed the HMD and completed the questionnaire on paper by hand; the 10 questions were presented in a novel order upon each

Table 1
Questionnaire statements used for the full-body ownership illusion.

Item	Statement	Purpose
Q1	I felt the touch(es) given to the mannequin's body	Referral of touch
Q2	It seemed as though the touch(es) I felt were caused by the probe(s) touching the mannequin's body	Referral of touch
Q3	I felt as though the mannequin's right arm were my arm	Body part ownership
Q4	I felt as though the mannequin's left arm were my arm	Body part ownership
Q5	I felt as though the mannequin's trunk were my trunk	Body part ownership
Q6	I felt as though the mannequin's right leg were my leg	Body part ownership
Q7	I felt as though the mannequin's left leg were my leg	Body part ownership
Q8	I felt as though the mannequin's whole body were my own body	Full-body ownership
Q9	I felt as though my real body were turning into a plastic body	Control
Q10	I felt naked	Control

presentation (Table 1). The participants then returned to a supine position wearing the HMD in preparation for the next experimental condition. The eight experimental conditions were pseudorandomised, and their presentation order was counterbalanced across all 48 participants, such that no two individuals experienced the same order of conditions.

3.7. *Experiment 1 - Statistical analyses and data availability*

For clarity, we describe the various statistical analyses conducted in the corresponding results section below and in the Supporting Information – Experiment 1. The basic analytical strategy was based on the fact that we had hypotheses that we tested using planned pairwise comparisons across conditions and additional post hoc comparisons among conditions that we also report for the sake of completeness and exploratory purposes. Pairwise comparisons among the experimental conditions were developed using R Version 4.2.2 "Funny-Looking Kid". We controlled for multiple comparisons using the Benjamini–Hochberg false discovery rate (FDR) method (FDR = 0.05) (McDonald, 2014) but also reported uncorrected *p* values because many of our tests were based on a priori hypotheses. We additionally used $r = Z/\sqrt{N}$ (Rosenthal, 1994) as a measure of effect size and performed Bayesian paired *t*-tests to evaluate the Bayes factor (BF10) associated with each comparison (JASP 0.9.2, JASP team, 2023). In this study, Bayes factors (BFs) are utilized purely descriptively, primarily to facilitate a deeper understanding of negative findings. All hypothesis testing and inferential analyses, however, are conducted using frequentist statistical methods. These results are fully presented in the Supporting Information Tables 1-4. We used mixed effects linear modelling to test the hypothesis that the number of synchronously versus asynchronously stimulated parts would influence full-body ownership and the ownership of nonstimulated parts using data concerning all conditions (with the support of clmm2 function of the ordinal package for R) (Christensen, 2019; Taylor, Rousselet, Scheepers, & Sereno, 2022). For Experiment 1, a mixed effects linear model was also used to investigate whether the nonstimulated body parts ownership ratings could be predicted most effectively by illusory full-body ownership ratings, averaged stimulated body part ownership ratings, or an interaction between these two outcome measures. Although our hypotheses were often directed (i.e., they proposed that synchrony should increase the body part or full-body illusion compared to asynchrony), we always used two-tailed tests to ensure consistency and because the current paradigm has not previously been tested. All questionnaire data are publicly available: https://osf.io/nxpvy/?view_only=e70f00a9354d4331b7c9e58bf0ddc235.

4. Experiment 1 – Results

4.1. *Experiment 1 - Descriptive overview of the questionnaire results*

For descriptive purposes and to facilitate comparison with previous studies (O'Kane & Ehrsson, 2021; Petkova & Ehrsson, 2008), mean ratings for all questionnaire items (Q1 – Q10) across all eight experimental conditions (Fig. 1) are displayed in Fig. 2 below. Boxplots for illusory full-body ownership ratings, illusory right arm ownership ratings, illusory trunk ownership ratings, and illusory right leg ownership ratings across the eight experimental conditions are presented in Fig. 3. A visual inspection of these data reveals that the synchronous stimulation of a particular body part is associated with positive (affirmative) mean body part ownership ratings for the stimulated part, whereas asynchronous stimulation leads to lower and negative (nonaffirmative) ratings for the stimulated part. Full-body ownership receives the strongest affirmative ratings in the condition in which all three body parts receive synchronous stimulation and exhibits a gradual relative reduction as more parts receive asynchronous stimulation. The left nonstimulated limbs receive weaker body part ownership ratings than the parts that received synchronous stimulation. The two control statements receive low ratings in all conditions as expected and are not considered further. Referral of touch is affirmed in all conditions featuring at least one synchronous stimulation; presumably, this factor was driven by the body part(s) receiving the synchronous stimulation.

4.2. *Experiment 1 - Full-body ownership*

Motivated by an observation made in the pairwise tests (see the Supporting Information, Experiment 1 – Full-Body Ownership: Pairwise Comparisons), which indicated that the subjective illusory full-body ownership percept was not affected by which body part was synchronously stimulated during each of the three conditions involving two synchronously and one asynchronously stimulated body part and each of the three conditions involving one synchronously and two asynchronously stimulated body parts, we concatenated the data such that different configurations for the same number of synchronous and asynchronous stimulations were treated as a single condition. This approach resulted in a single numeric variable (n_sync) reflecting the number of synchronous visuotactile stimulations: zero ($A_{RA}A_TA_{RL}$), one ($S_{RA}A_TA_{RL}$, $A_{RA}S_TA_{RL}$ and $A_{RA}A_TS_{RL}$), two ($S_{RA}S_TA_{RL}$, $S_{RA}A_TS_{RL}$ and $A_{RA}S_TS_{RL}$) and three ($S_{RA}S_TS_{RL}$). Next, a linear mixed effects model was created using the clmm2 function of the ordinal package for R (Christensen, 2019; Taylor et al., 2022) to determine whether the number of

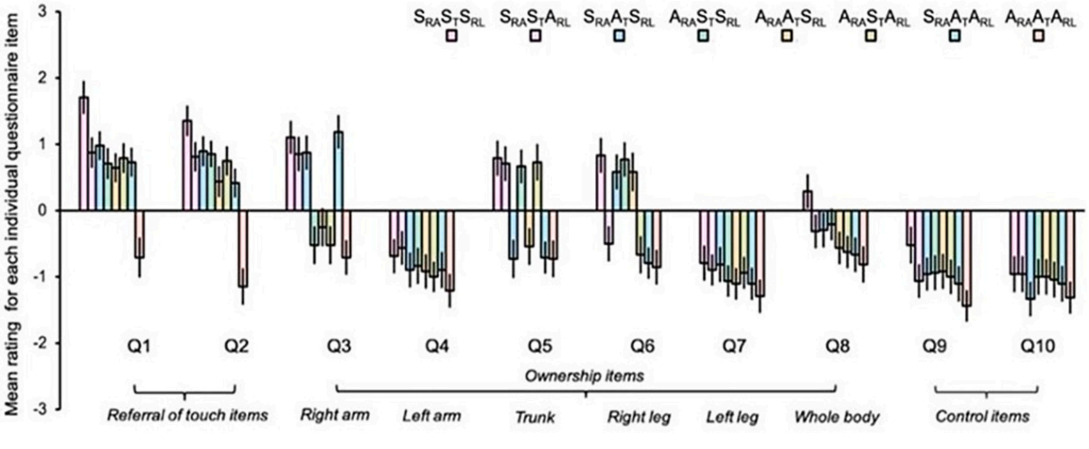

Fig. 2. Mean ratings for each individual questionnaire item (1–10) across the eight experimental conditions. For illustrative purposes and to facilitate comparisons with previous studies (Petkova & Ehrsson, 2008), this figure presents the mean response ($N = 48$) to each questionnaire item (described by the annotations at the bottom of the figure) for conditions involving different ratios of synchronous and asynchronous visuotactile stimulation. Error bars represent the standard error of the mean (SEM). For further descriptive boxplots of the data and individual datapoints, see Supporting Information SI Fig. 4 and SI Fig. 5.

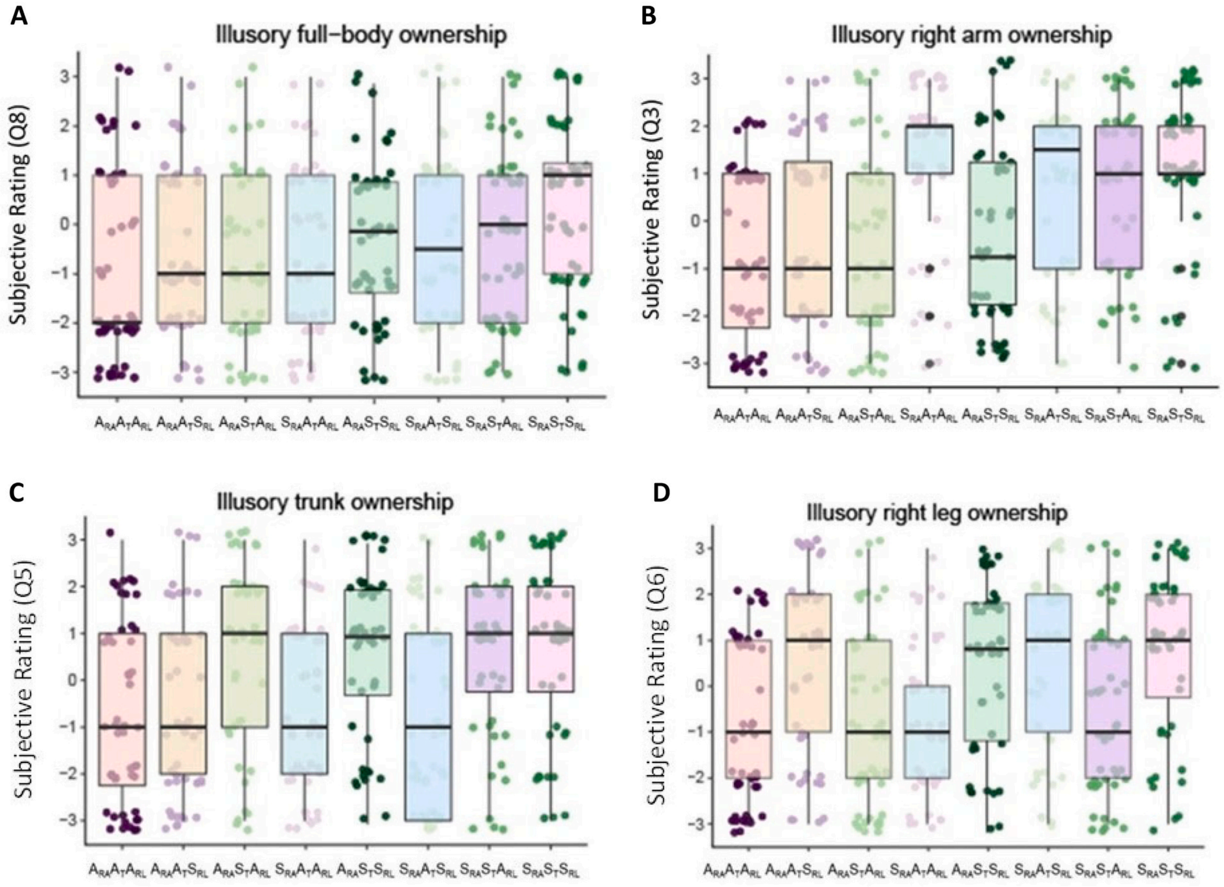

Fig. 3. A-D. Questionnaire results regarding full-body and body part ownership. Boxplots showing the distribution of ratings for illusory full-body ownership (Q8) (A) as well as illusory ownership of the mannequin's right arm (Q3) (B), trunk (Q5) (C) and right leg (Q6) (D) across the eight conditions (N = 48). Illusory full-body ownership increases as more body parts are stimulated synchronously instead of asynchronously (A). Illusory ownership of the mannequin's right arm is higher in experimental conditions in which the right arm is stimulated synchronously compared to when it is stimulated asynchronously (B). Illusory ownership of the mannequin's trunk is higher in experimental conditions in which the trunk is stimulated synchronously relative to asynchronously (C). Illusory ownership of the mannequin's right leg is higher in experimental conditions in which the right leg is stimulated synchronously versus asynchronously (D). Inferential statistics for the corresponding planned comparisons are reported in SI Tables 1–4 (and pairwise comparison lines for Q8 shown in SI Fig. 1). The black lines within each boxplot correspond to the median; for a visualisation of the means, refer to Fig. 2.

synchronous (vs. asynchronous) visuotactile stimulations was predictive of the magnitude of subjective illusory full-body ownership ratings (Illusory full-body ownership rating ~ n_sync, link = logistic). Analysing the data based on a linear mixed effects model offers several advantages; most notably, it allows us to test for a nonlinear relationship between the number of synchronously stimulated parts and the rating of full-body ownership, it replaces the large number of pairwise comparisons with a single model that can be tested (but see the Supporting Information for the complete set of pairwise test results), and it accounts for the random variance introduced by each individual participant (which was included as a random effect).

The gradient of the slope between zero and one synchronous visuotactile stimulation was not significant (β estimate = 0.40, SE = 0.33, z = 1.19, p = .232), suggesting that experimental conditions comprising only one synchronous visuotactile stimulation are just as unlikely to elicit a full-body ownership illusion as the fully asynchronous control condition. In addition, the coefficients for the gradient between one and two synchronous visuotactile stimulations (β estimate = 0.97, SE = 0.34, z = 2.90, p = .004) and two and three synchronous visuotactile stimulations (β estimate = 1.87, SE = 0.42, z = 4.46, p < .001) were both significant. Therefore, the full-body ownership illusion produced by two synchronous visuotactile stimulations (e.g., $A_{RA}S_TS_{RL}$) is significantly greater than that produced by one synchronous visuotactile stimulation (e.g., $S_{RA}A_TA_{RL}$) with an average difference of +0.97 rating units, and the illusory full-body ownership illusion produced by three synchronous visuotactile stimulations (i.e., $S_{RA}S_TS_{RL}$) is significantly greater than that produced by two synchronous visuotactile stimulations (e.g., $A_{RA}S_TS_{RL}$) with an average difference of +1.87 rating units. These results are visualised in Fig. 4.

These findings were also supported by pairwise comparisons (22 tests), which were corrected for multiple comparisons using the Benjamini Hochberg False Discovery Rate procedure and complemented by Bayes factors (see the Supporting Information, Experiment 1 – Full-Body Ownership: Pairwise Comparisons for details). These tests recapitulated the essence of the model described above, showing that fully synchronous stimulation elicited the strongest full-body ownership illusion and confirming that full-body ownership illusion ratings were significantly higher in the conditions containing two synchronously and one asynchronously stimulated body part than in the fully asynchronous condition. With regard to conditions featuring one synchronously and two asynchronously stimulated body parts, the pairwise tests supported the claim that this configuration of stimulations is unable to elicit a full-body ownership illusion that is greater than the illusion elicited in the fully asynchronous condition.

4.3. *Experiment 1 – Body part ownership for stimulated body parts*

Wilcoxon signed ranks tests (two-tailed) were used to investigate

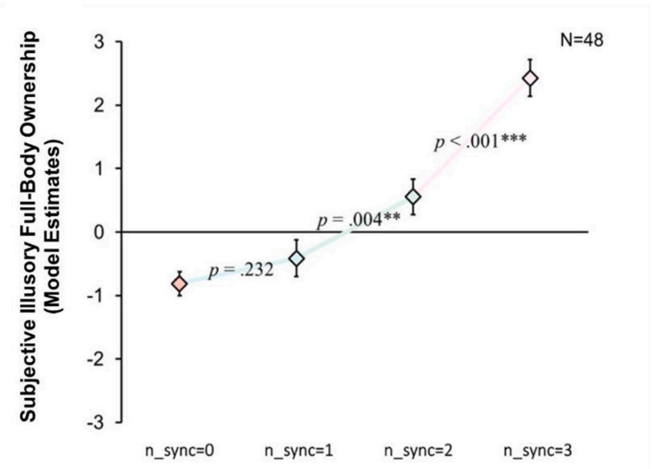

Fig. 4. The nonlinear relationship between illusory full-body ownership ratings and the number of synchronous visuotactile stimulations revealed based on cumulative link mixed effects modelling. $N = 48$. Illusory full-body ownership ratings do not differ significantly between the fully asynchronous (control) condition (n_sync = 0) and the conditions comprising only one synchronous visuotactile stimulation (n_sync = 1; illusory full-body ownership ratings averaged across $S_{RA}A_{T}A_{RL}$, $A_{RA}S_{T}A_{RL}$ and $A_{RA}A_{T}S_{RL}$). However, illusory full-body ownership ratings increase significantly (gradient slope, $p = .008$) between conditions comprising only one synchronous visuotactile stimulation (n_sync = 1) and conditions comprising two synchronous visuotactile stimulations (n_sync = 2; illusory full-body ownership ratings averaged across $S_{RA}S_{T}A_{RL}$, $S_{RA}A_{T}S_{RL}$ and $A_{RA}S_{T}S_{RL}$). Likewise, illusory full-body ownership ratings increase significantly (gradient slope $p < .001$) between conditions comprising two synchronous visuotactile stimulations (n_sync = 2) and those comprising three synchronous visuotactile stimulations (n_sync = 3, the fully synchronous condition $S_{RA}S_{T}S_{RL}$). Model estimates are plotted with error bars denoting the standard error. For details concerning the model, see the text.

whether questionnaire ratings related to body part ownership for the stimulated body parts (Q3, Q5, Q6) exhibited significant differences across our eight experimental conditions. The results are summarised in the Supporting Information, Tables 2, 3, and 4. When a particular body part received synchronous stimulation, it was always associated with significantly ($p < 0.05_{FDR}$) higher body part ownership ratings than were observed when the same part received asynchronous stimulation. This difference was always present, irrespective of the total number of synchronously stimulated body parts, i.e., regardless of the context of the full-body ownership illusion. This finding shows that visuotactile synchrony is a strong driver of body part ownership, in line with our expectations.

4.4. Experiment 1 – Body part ownership for nonstimulated body parts

Although the left body parts were never directly stimulated in this study, illusory ownership ratings for the mannequin's left arm (Q4) and leg (Q7) were significantly higher for $S_{RA}S_{T}S_{RL}$ than for $A_{RA}A_{T}A_{RL}$, in line with our hypothesis that synchronous stimulation has an illusory ownership effect that is inclusive of mannequin's whole body (Q4: $S_{RA}S_{T}S_{RL} - A_{RA}A_{T}A_{RL}$: $Z = 5.04$, $p = .017$, $p_{FDR} = 0.018$, $r = 0.73$, $BF_{10} = 3.22$, %error $= 1.29e^{-6}$; Q7: $S_{RA}S_{T}S_{RL} - A_{RA}A_{T}A_{RL}$: $Z = 2.38$, $p = .018$, $p_{FDR} = 0.018$, $r = 0.34$, $BF_{10} = 2.91$, %error $= 1.41e^{-6}$). To test the hypothesis that the illusory ownership of nonstimulated body parts is also influenced by the number of synchronous versus asynchronous visuotactile stimulations, a linear mixed effects model was specified using the same method as employed for the illusory full-body ownership ratings; however, illusory body part ownership ratings averaged between the left arm (Q4) and the left leg (Q7) instead supplied the dependent variable (Q4 + Q7/2). These averaged left limb ratings were assessed for the fully synchronous (n_sync = 3) and asynchronous (n_sync = 0) conditions as well as for the three conditions comprising two synchronous and one asynchronous visuotactile stimulation (concatenated to n_sync = 2) and the three conditions comprising one synchronous and two asynchronous stimulation (concatenated to n_sync = 1). We confirmed that no significant differences were observed in the averaged nonstimulated left limb ratings based on *which* body parts received synchronous or asynchronous stimulation and that illusory left arm ownership (Q4) was comparable to illusory left leg ownership (Q7) across the eight experimental conditions (see Supplemental Information - Confirming Comparable Left Limb Ownership Ratings for Mixed Effects Modelling in Experiments 1, 2 & Pooled Analysis), thereby supporting the averaging of these questionnaire items in the mixed effects model (illusory ownership rating for nonstimulated body parts ~ n_sync, link = logistic).

The gradient of the slope between zero and one synchronous visuotactile stimulation was marginally statistically significant (β estimate = 0.71, SE = 0.35, $z = 2.02$, $p = .043$), and the coefficients for the gradient between one and two synchronous visuotactile stimulations (β estimate = 0.93, SE = 0.35, $z = 2.64$, $p = .008$) and two and three synchronous visuotactile stimulations (β estimate = 1.15, SE = 0.43, $z = 2.67$, $p = .007$) were clearly significant. Therefore, it is inconclusive whether experimental conditions comprising only one synchronous visuotactile stimulation are slightly more likely than the fully asynchronous control condition (i.e., $A_{RA}A_{T}A_{RL}$) to increase ownership ratings for the nonstimulated left body parts (see the pooled analysis for clarity). The illusory body part ownership ratings for the nonstimulated left arm and leg produced by two synchronous visuotactile stimulations (e.g., $A_{RA}S_{T}S_{RL}$) are significantly greater than those produced by one synchronous visuotactile stimulation (e.g., $S_{RA}A_{T}A_{RL}$) with an average difference of +0.93 rating units. In turn, the nonstimulated body part illusory ownership ratings produced by three synchronous visuotactile stimulations ($S_{RA}S_{T}S_{RL}$) are significantly greater than those produced by two synchronous visuotactile stimulations (e.g., $A_{RA}S_{T}S_{RL}$) with an average difference of +1.15 rating units. This predictive relationship is somewhat similar to that observed for illusory full-body ownership (compare with Fig. 4) and is visualised in Fig. 5 below.

In light of these findings, we developed an additional post hoc mixed effects model, once again using the averaged illusory ownership ratings for the nonstimulated left limbs (Q4 + Q7/2) as the dependent variable; however, in this context, illusory full-body ownership ratings (Q8) supplied the independent variable of full-body ownership, and averaged stimulated body part ownership ratings (Q3 + Q5 + Q6/3) supplied the independent variable of body part ownership (individual subject modelled as a random effect, as in all the models). This model (Illusory ownership rating for nonstimulated body parts ~ Q8 + Averaged stimulated body part illusory ownership rating + Q8*Averaged stimulated body part illusory ownership rating, link = logistic) allows us to corroborate in further detail the claim that full-body ownership influences the ratings of the nonstimulated body parts over and above an effect that can be ascribed to the sum of body part ownership for the stimulated body parts. Illusory ownership of the left nonstimulated limbs could be predicted by both the magnitude of illusory full-body ownership ratings (Q8: β estimate = 0.51, SE = 0.14, $z = 3.64$, $p < .001$) and stimulated body part ownership ratings (averaged over the right arm, trunk, and right leg) (β estimate = 0.80, SE = 0.16, $z = 5.09$, $p < .001$), although no evidence of a significant interaction between these two factors was found (β estimate = −0.02, SE = 0.06, $z = -0.28$, $p = .776$).

4.5. Experiment 1 – Summary and interim discussion

In the first experiment, we quantified body part and full-body ownership across eight experimental conditions, during which we manipulated the temporal congruence of visual and tactile stimuli (synchronous or asynchronous) delivered simultaneously to three body parts (right arm, trunk, right leg) of a mannequin in a full-body illusion

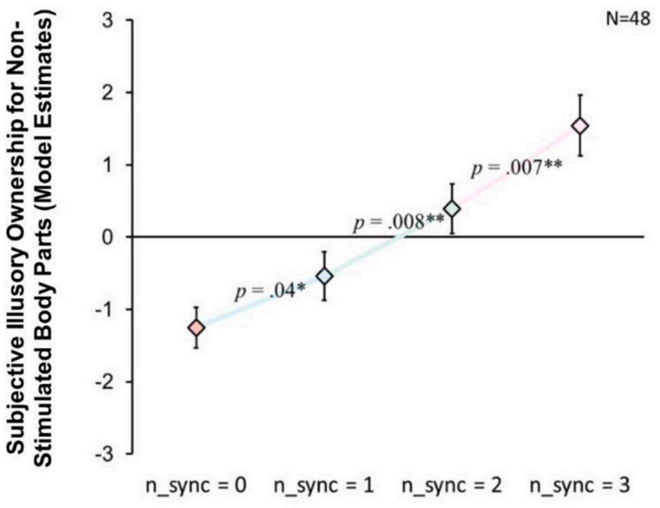

Fig. 5. The relationship between illusory ownership ratings for the left-side nonstimulated body parts and the number of synchronous visuotactile stimulations revealed by cumulative link mixed effects modelling. $N = 48$. The gradient of slope between n_sync = 0 and n_sync = 1 was significant ($p = .043$), indicating that illusory body part ownership ratings for nonstimulated body parts (averaged ratings for the left arm and left leg; [Q4 + Q7]/2) differ significantly between the fully asynchronous (control) condition of zero synchronous stimulations and conditions comprising only one synchronous visuotactile stimulation (averaged illusory body part ownership ratings averaged across $S_{RA}A_{T}A_{RL}$, $A_{RA}S_{T}A_{RL}$ and $A_{RA}A_{T}S_{RL}$). The gradient of the slope between n_sync = 1 and n_sync = 2 was significant ($p = .008$), indicating that body part ownership ratings increase significantly between conditions comprising only one synchronous visuotactile stimulation and conditions comprising two synchronous visuotactile stimulations (averaged illusory body part ownership ratings averaged across $S_{RA}S_{T}A_{RL}$, $S_{RA}A_{T}S_{RL}$ and $A_{RA}S_{T}S_{RL}$). Likewise, the gradient of the slope between n_sync = 2 and n_sync = 3 was significant ($p = .007$); thus, illusory body part ownership ratings for the nonstimulated body parts increase significantly between conditions comprising two synchronous visuotactile stimulations and those comprising three synchronous visuotactile stimulations (fully synchronous (illusion) condition, $S_{RA}S_{T}S_{RL}$). Model estimates are plotted with error bars denoting the standard error. For details concerning-the model, see text.

paradigm. We were particularly interested in clarifying the relationship between the number of illusory owned body parts and the resulting full-body illusory percept and investigating whether body part ownership and full-body ownership could be dissociated.

This experiment revealed three main findings. First, full-body ownership reports (Q8) exhibited a significant relationship to the number of synchronously versus asynchronously stimulated body parts; that is, the more illusorily owned parts there were, the stronger the illusory full-body ownership sensation. However, critically, this relationship was nonlinear, such that stimulating one body part synchronously made little difference above zero, i.e., the fully asynchronous control condition, whereas stimulating two or three synchronously led to significant increases in full-body ownership ratings, and the fully synchronous condition generated the strongest illusion overall. This relationship was evident in both the pairwise comparisons among the conditions and a linear mixed effects model developed using data from all conditions. Thus, full-body ownership seems to be triggered when the overall pattern of multisensory evidence from all parts speaks in favour of the whole body being one's own, and the illusory full-body ownership experience does not appear to reflect a simple summation of illusory body part ownership. This finding supports our hypothesis that full-body ownership involves a different and more complex multisensory integration process than body part ownership.

Second, body part ownership was driven mainly by congruent multisensory signals from the individual limb in question. For every stimulated part – the right arm, the trunk, and the right leg – synchronous visuotactile stimulation was associated with significantly higher body part ownership reports for body part in question than was asynchronous visuotactile stimulation of the same body part, a finding that was further confirmed by high Bayes factors (all $BF_{10} > 40$) in the pairwise tests (Supporting Information, Tables SI 2, SI 3 and SI 4). This observation held true irrespective of how the other body parts were stimulated and the degree of illusory full-body ownership. Importantly, when only one of the three stimulated body parts received asynchronous visuotactile stimulation, as was the case for the right arm, trunk and right leg in the $A_{RA}S_{T}S_{RL}$, $S_{RA}A_{T}S_{RL}$ and $S_{RA}S_{T}A_{RL}$ conditions, respectively, illusory body part ownership ratings for these respective parts were not significantly different from the rating observed for the fully asynchronous condition, a null finding that was further confirmed by low Bayes factors (all $BF_{10} < 1$) in the pairwise tests (Supporting Information, Tables SI 2, SI 3 and SI 4). Thus, although participants experienced a certain degree of full-body ownership when two other body parts received synchronous stimulation, they did not experience the singularly asynchronously stimulated part as their own. In contrast, when only one part received synchronous stimulation and two other body parts were also asynchronously stimulated ($S_{RA}A_{T}A_{RL}$, $A_{RA}S_{T}A_{RL}$ and $A_{RA}A_{T}S_{RL}$), the body part ownership ratings for the singularly synchronously stimulated part were not significantly different from the body part ownership ratings observed when this body part received synchronous stimulation in the fully synchronous condition ($S_{RA}S_{T}S_{RL}$) (all $BF_{10} < 1$) (Supporting Information, Tables SI 2, SI 3 and SI 4). That is, participants could experience illusory ownership of one body part even when they did not experience full-body ownership, and conversely, they could experience a lack of ownership of one part even when they experienced a significant increase in full-body ownership. These observations suggest that body part and full-body ownership can be dissociated, a finding which is in line with our hypothesis that body part ownership and full-body ownership are produced by different multisensory integration processes.

The third main observation is related to the "spread of ownership" phenomenon that has been noted in previous studies (Petkova et al., 2011a; Gentile et al., 2015; O'Kane & Ehrsson, 2021), i.e., the observation that ownership measures tend to be influenced even for body parts that do not receive any synchronous visuotactile stimulation when a full-body illusion is elicited (by stimulating other parts synchronously). In our mixed effects linear model, we found that the magnitude of illusory ownership ratings for the nonstimulated body parts (the left arm and left leg) could be predicted by the number of synchronously stimulated body parts and that the relationship seemed to exhibit a similar nonlinear pattern (albeit less pronounced and on the negative side of the questionnaire scale) to the pattern that we found to characterise the relationship between full-body ownership and the number of synchronously stimulated body parts (see also pooled analysis below, which corroborates this nonlinearity based on additional data). Furthermore, mixed linear modelling showed that full-body ownership ratings predicted ownership ratings for the nonstimulated parts. Therefore, our observations suggest that the stronger the full-body experience is, the greater the influence of full-body ownership on illusory body part ownership for the nonstimulated parts. This finding supports the claim that these small but significant relative increases in the subjective magnitude of illusory ownership of nonstimulated body parts are driven, at least partly, by the illusory full-body experience, in line with our hypothesis.

We did not find that the trunk played a more important role than the arm or leg in the full-body ownership illusion, and all post hoc Bayes factors comparing stimulated body part types supported the null hypothesis (all $BF_{01} > 5$) in the pairwise tests (Supporting Information, Experiment 1 - Full-Body Ownership: Pairwise Comparisons). Instead, the relevant factor was the number of synchronously stimulated body parts, irrespective of which particular combination of body parts was stimulated. Thus, these observations do not support the hypothesis that the trunk might play a particularly important role in body ownership and full-body illusions (Blanke et al., 2015; Park & Blanke, 2019) but are nevertheless consistent with the results of previous studies that have shown that a similarly strong full-body ownership illusion can be elicited by stimulating different body parts (Carey et al., 2019; Gentile et al., 2015; O'Kane & Ehrsson, 2021; Petkova et al., 2011a; Petkova & Ehrsson, 2008). Thus, it appears that the total information conveyed by the multisensory correlations across different parts are relevant to triggering the current full-body illusion rather than anatomy or relative position in the visuospatial body plan. It is still possible that the trunk plays a dominant role in other illusion paradigms that were not examined in the current study, such as cases in which a virtual body is viewed at a distance from the third-person perspective (Lenggenhager, Tadi, Metzinger, & Blanke, 2007) and illusions pertaining to self-location and self-orientation (Blanke et al., 2015; Guterstam et al., 2015; Preuss, Brynjarsdóttir, & Ehrsson, 2018; Preuss Mattsson et al., 2022).

In summary, the questionnaire results found in Experiment 1 revealed several new findings concerning the relationships between body part ownership and full-body ownership by introducing a novel experimental paradigm, in which multiple simultaneously stimulated body parts received synchronous or asynchronous stimulation in all possible combinations. The two main observations regarding a) the nonlinear relationship between body part and full-body ownership and b) the fact that body part ownership and full-body ownership can be dissociated are conceptually the most important findings of this experiment and served as a starting point for the design of the remaining two experiments.

5. Experiment 2 - Aims and rationale

To investigate in further detail the relationship between body part and full body ownership, we simplified our experimental design to include only a smaller set of informative conditions. We were particularly interested in re-examining the hypothesis that body part ownership can be experienced in the absence of full-body ownership and the nonlinear relationship between the number of synchronously stimulated parts and full-body ownership ratings. Therefore, four of the previous eight experimental conditions ($S_{RA}S_TS_{RL}$, $A_{RA}S_TS_{RL}$, $S_{RA}A_TA_{RL}$, $A_{RA}A_TA_{RL}$) were replicated among a new cohort of participants ($N = 48$) using a simplified 2 (visuotactile stimulation: synchronous/asynchronous) x 2 (stimulation configuration: whole body/body part) design. This simplified design was also considered to be suitable for the SCR experiment that we were planning to conduct later (Experiment 3). Since several previous full-body illusion studies have stimulated the right arm (Gentile et al., 2015; O'Kane & Ehrsson, 2021; Petkova et al., 2011a) and the arm is the limb that has been investigated in the rubber hand illusion literature, we chose to focus on the relationship between right arm ownership and full-body ownership.

Given that the conditions used in Experiment 2 were also included in Experiment 1, we took advantage of the fact that we could pool the data from the two experiments to conduct complementary analyses based on 96 participants, thus increasing the power and examining the robustness of the results obtained at N = 48 versus $N = 96$.

6. Experiment 2 – Methods & materials

6.1. Experiment 2 – Participants

Forty-eight healthy adults (25 females, 23 males; average age: 26.7 ± 4.4 years; age range: 18–37 years; all self-reported right-handed individuals) were recruited via online and poster advertisements to participate in Experiment 2, which lasted approximately 20 min; these participants were compensated with one cinema ticket. The sample size was based on Experiment 1 and a previous study (O'Kane & Ehrsson, 2021) and was predetermined before data collection commenced. Furthermore, based on post hoc power calculations, which suggested that the full-body ownership differences between one and two synchronously stimulated body parts were underpowered at N = 48 but would exhibit sufficient power at N = 96, we also conducted several analyses by pooling data from the relevant conditions across Experiments 1 and 2 (see further details below). All recruits were naïve to the full-body ownership illusion (e.g., none had taken part in Experiment 1 or participated in any similar illusion involving a mannequin's whole body), and they provided written informed consent upon arrival. The study was approved by the Swedish Ethical Review Authority.

6.2. Experiment 2 – Experimental conditions

As noted, for Experiment 2, we selected four experimental conditions from Experiment 1 (Fig. 6) to investigate the effect of combining synchronous and asynchronous visuotactile stimulation on both illusory full-body ownership and body part ownership in further detail using a 2 (visuotactile stimulation: synchronous/asynchronous) x 2 (stimulation configuration: whole body/body part) experimental design. These conditions featured synchronous stimulation of the right arm, trunk, and right leg ($S_{RA}S_TS_{RL}$); synchronous stimulation of the trunk and right leg plus asynchronous stimulation of the right arm ($A_{RA}S_TS_{RL}$); synchronous stimulation of the right arm plus asynchronous stimulation of the trunk and right leg ($S_{RA}A_TA_{RL}$); and asynchronous stimulation of the right arm, trunk and right leg ($A_{RA}A_TA_{RL}$).

6.3. Experiment 2 – Questionnaire

After completing each experimental condition, participants completed a questionnaire that was identical to the one used in Experiment 1, with the exception that we omitted the referral of touch items (Q1, Q2). This exclusion was due to their ambiguity in conditions that contained both synchronous and asynchronous visuotactile stimulation and because they were not important to the current study's objectives. Items relating to full-body ownership (Q6) and ownership of individual body parts (Q1-Q5) were presented identically to Experiment 1, and the

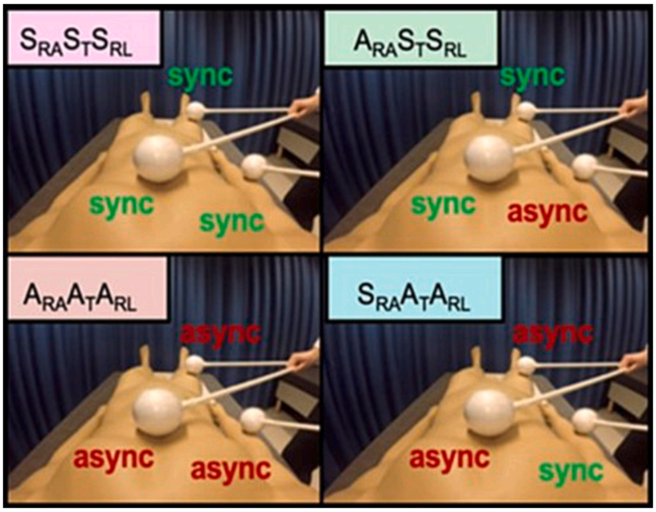

Fig. 6. Four experimental conditions used for Experiment 2. The visual stimulation was identical across each experimental condition and identical to the visual stimuli used in Experiment 1 (see Fig. 1 for details). The tactile stimulation applied to the right arm, trunk, and right leg of participants' real bodies was either synchronous or asynchronous. $S_{RA}S_TS_{RL}$ represents the delivery of all three synchronous stimuli, $A_{RA}S_TS_{RL}$ represents the delivery of two synchronous and one asynchronous stimulus, $S_{RA}A_TA_{RL}$ represents the delivery of one synchronous and two asynchronous stimuli and $A_{RA}A_TA_{RL}$ represents the delivery of zero synchronous and three asynchronous stimuli. Stimulus onset asynchrony (SOA) during asynchronous visuotactile stimulation (visual event always preceding tactile stimulation) was 2 s.

same two control statements were used again (Q7, Q8). The items were rearranged in a novel order upon each presentation, just as in Experiment 1. Responses were scored on a 7–point Likert scale, in which −3 indicated 'strongly disagree' and + 3 indicated 'strongly agree', as in Experiment 1.

6.4. *Experiment 2 – Procedure*

For Experiment 2, participants provided written informed consent and were instructed in an identical manner to that used in Experiment 1 (see Experiment 1: Procedure for details). The only differences were that fewer conditions were included in Experiment 2 and that it employed the shortened 8-item questionnaire (Table 2), as described above.

6.5. *Experiment 2 – Statistical analysis and data availability*

Despite the existence of a priori hypotheses generated from the observations resulting from Experiment 1, we continued to employ two-tailed hypothesis testing for consistency. The following six contrasts comprised our planned comparisons, which were analysed using a series of Wilcoxon's signed ranks tests ($S_{RA}S_TS_{RL}$ – $A_{RA}S_TS_{RL}$, $S_{RA}S_TS_{RL}$ – $S_{RA}A_TA_{RL}$, $S_{RA}S_TS_{RL}$ – $A_{RA}A_TA_{RL}$, $A_{RA}S_TS_{RL}$ – $S_{RA}A_TA_{RL}$, $A_{RA}S_TS_{RL}$ – $A_{RA}A_TA_{RL}$ and $S_{RA}A_TA_{RL}$ – $A_{RA}A_TA_{RL}$) for full-body ownership ratings (Q6) and for body part ownership ratings with regard to the mannequin's right arm (Q1). FDR correction and Bayesian analyses were employed in the same manner as in Experiment 1 (see above). We conducted the same statistical analyses in Experiment 2 as in Experiment 1, with the only difference being the addition of one mixed linear model (see below). For clarity, details regarding the mixed linear models used in some of the analyses are presented in the corresponding results sections below. All questionnaire data are publicly available: https://osf.io/nxpvy/?view_only=e70f00a9354d4331b7c9e58bf0ddc235.

In the post hoc complementary analyses, where we pooled the data from Experiments 1 and 2 to increase statistical power (see further below). In this combined dataset, we replicated the main statistical analyses conducted for Experiments 1 and 2.

7. Experiment 2 – Results

See the Supporting Information for the complete results concerning the data collected for Experiment 2 ($N = 48$), as we focus on the results of the pooled analysis ($N = 96$) in the main text.

7.1. *Experiment 2 – Descriptive overview of questionnaire results*

Mean ratings for each individual questionnaire item across the four experimental conditions are presented in Fig. 7A (N = 48) and Fig. 7B (N = 96). N = 48 refers to the results obtained for Experiment 2; N = 96 refers to the results obtained after the data for Experiment 2 and the data pertaining to the identical conditions from Experiment 1 were pooled together for analysis. Boxplots for each individual questionnaire item across conditions for both N = 48 and N = 96 are presented in the Supporting Information – Fig. S2. As shown in Fig. 7A, synchrony affected body part ownership ratings for the right hand, trunk, and right leg, with positive mean scores occurring when the body part in question received synchronous stimulation and negative mean scores occurring when asynchronous stimulation was provided, regardless of the experimental condition. Full-body ownership (Q6) received the highest mean illusion score in the fully synchronous condition, a relatively lower score when only the right arm was asynchronously stimulated, and even lower scores when two or three body parts received asynchronous stimulation. As in Experiment 1, the control statements (Q7, Q8) received low scores as expected and are thus not considered further. The pooled analyses (Fig. 7B) indicate a similar pattern of results.

Table 2
Questionnaire statements used for the full-body ownership illusion.

Item	Statement	Purpose
Q1	I felt as though the mannequin's right arm were my arm	Body part ownership
Q2	I felt as though the mannequin's left arm were my arm	Body part ownership
Q3	I felt as though the mannequin's trunk were my trunk	Body part ownership
Q4	I felt as though the mannequin's right leg were my leg	Body part ownership
Q5	I felt as though the mannequin's left leg were my leg	Body part ownership
Q6	I felt as though the mannequin's whole body were my own body	Full-body ownership
Q7	I felt as though my real body were turning into a plastic body	Control
Q8	I felt naked	Control

Note. The reduced 8-item questionnaire used for Experiment 2, which omitted the first two items assessing referral of touch.

7.2. *Experiment 2 – Full-body ownership*

With regard to illusory full-body ownership ratings (Q6), we found that $S_{RA}S_TS_{RL}$ led to significantly greater illusory ownership ratings than did $A_{RA}S_TS_{RL}$ ($Z = 2.716$, $p = .007$, $p_{FDR} = 0.014$, $r = 0.39$, $BF_{10} = 4.884$, %error = $8.62\ e^{-7}$), $S_{RA}A_TA_R$ ($Z = 3.530$, $p < .001$, $p_{FDR} = 0.003$, $r = 0.51$, $BF_{10} = 109.707$, % error = $1.36\ e^{-8}$) and $A_{RA}A_TA_{RL}$ ($Z = 3.490$, $p < .001$, $p_{FDR} = 0.003$, $r = 0.40$, $BF_{10} = 80.032$, % error = $2.33e^{-8}$). $A_{RA}S_TS_{RL}$ did not lead to significantly greater illusory full-body ownership ratings than did $S_{RA}A_TA_R$ ($Z = 1.736$, $p = .083$, $p_{FDR} = 0.51$, $r = 0.25$, $BF_{10} = 0.602$, % error = $4.55e^{-6}$) or $A_{RA}A_TA_{RL}$ ($Z = 1.925$, $p = .054$, $p_{FDR} = 0.081$, $r = 0.28$, $BF_{10} = 0.994$, % error = $3.33e^{-6}$) (but see the results at N = 96), and $S_{RA}A_TA_R$ did not lead to significantly greater illusory full-body ownership ratings than did $A_{RA}A_TA_{RL}$ ($Z = 0.798$, $p = .425$, $p_{FDR} = 0.425$, $r = 0.12$, $BF_{10} = 0.177$, % error = $7.12e^{-6}$). These results are shown in Fig. 8A.

The mixed effect modelling analysis confirmed a nonlinear relationship between full-body ownership ratings and the number of synchronously versus asynchronously stimulated body parts (Fig. 9). As in Experiment 1, we investigated illusory full-body ownership ratings as a function of the number of synchronously stimulated body parts using the linear mixed effects model with the categorical predictor "Condition" since only four conditions were investigated and each condition differed in terms of how many body parts received synchronous (vs. asynchronous) stimulation (zero, one, two or three). We found that for our fixed effect, the number of synchronous relative to asynchronous visuotactile stimulations, the coefficient for the gradient of the slope between zero ($A_{RA}A_TA_{RL}$) and one synchronous stimulation ($S_{RA}A_TA_{RL}$) was not significant (β estimate = 0.22, SE = 0.40, $z = 0.55$, $p = .583$), suggesting that these conditions are similarly unlikely to elicit a full-body ownership illusion. Meanwhile, the coefficients for the gradients between one ($S_{RA}A_TA_{RL}$) and two ($A_{RA}S_TS_{RL}$) synchronous stimulations (β estimate = 0.83, SE = 0.41, $z = 2.04$, $p = .042$) and between two ($A_{RA}S_TS_{RL}$) and three ($S_{RA}S_TS_{RL}$) synchronous stimulations were significant (β estimate = 1.68, SE = 0.42, $z = 3.96$, $p < .001$). Therefore, the illusory full-body ownership illusion produced by two synchronous visuotactile stimulations ($A_{RA}S_TS_{RL}$) is significantly greater than that produced by one synchronous visuotactile stimulation ($S_{RA}A_TA_{RL}$) with an average difference of +0.83 rating units, and the illusory full-body ownership illusion produced by three synchronous visuotactile stimulations ($S_{RA}S_TS_{RL}$) is significantly greater than that produced by two ($A_{RA}S_TS_{RL}$) with an average difference of +1.68 rating units. In the main text, a visualisation of these results is displayed in Fig. 9A, while Fig. 9B shows the pooled results.

To investigate the effect of full-body ownership in the data in further detail, a second mixed effects model was constructed for illusory full-body ownership ratings, in which conditions in which a greater ratio of synchronous stimulations were applied were coded as 1 ($S_{RA}S_TS_{RL}$ and

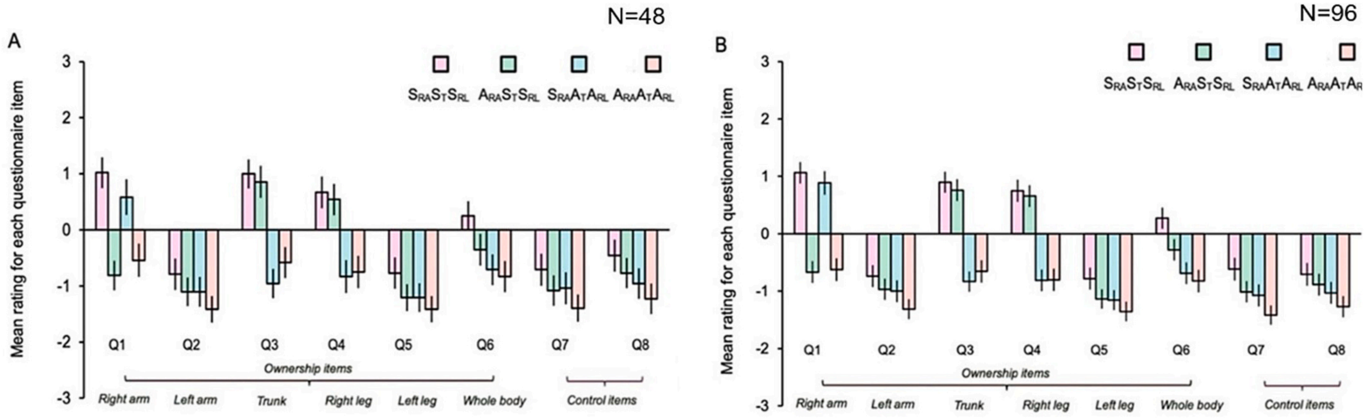

Fig. 7. A-B. Mean ratings and SEM for each individual questionnaire item (Q1 – Q8) across the four experimental conditions for both N = 48 (Panel A) and N = 96 (Panel B). Mean response to each questionnaire item, as described by annotations within the figure, for $S_{RA}S_TS_{RL}$, $A_{RA}S_TS_{RL}$, $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$. (see Fig. 6 for condition abbreviations) Error bars represent the standard error of the mean (SEM). This figure is presented for illustrative purposes and to facilitate comparisons with previous studies. See Supporting Information SI Fig. 6 for a detailed descriptive presentation of the data, including boxplots and individual data points.

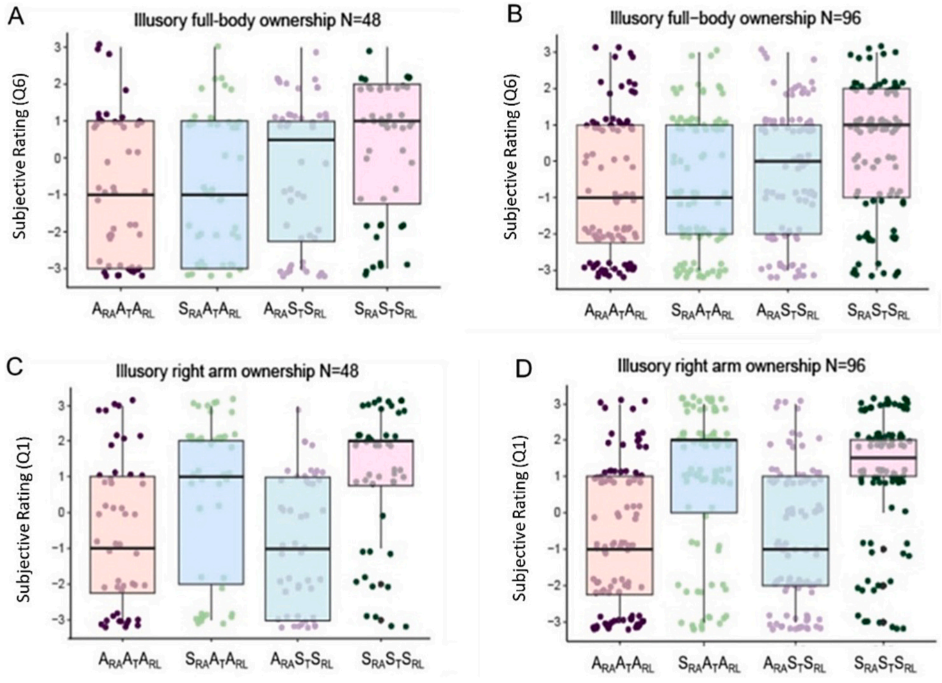

Fig. 8. A-D. Boxplots of the questionnaire responses representing illusory full-body ownership (top) and illusory ownership of the mannequin's right arm (bottom) at N = 48 (Panel A, C) and N = 96 (Panel B, D). Illusory full-body ownership increases when two or three body parts are stimulated synchronously rather than asynchronously ($A_{RA}S_TS_{RL}$ and $S_{RA}S_TS_{RL}$), with the highest ratings observed in the fully synchronous condition (Panel A, B). Illusory body part ownership ratings for the mannequin's right arm depended upon whether this body part received synchronous or asynchronous visuotactile stimulation. Both conditions that included synchronous visuotactile stimulation to the right arm ($S_{RA}A_TA_R$ and $S_{RA}S_TS_R$) were associated with significant reports of right-hand ownership, while both conditions in which this right extremity was stimulated asynchronously were associated with very low rating scores ($A_{RA}S_TS_{RL}$ and $A_{RA}A_TA_{RL}$). Pooling data across Experiment 1 and Experiment 2 had little effect on body part ownership results, but for illusory full-body ownership, the difference between $S_{RA}A_TA_{RL}$ and $A_{RA}S_TS_{RL}$ was significant only at $N = 96$ due to the increased experimental power. For statistical results, see text, and for pairwise comparison lines, see Supporting Information SI Fig. 2 and SI Fig. 3.

$A_{RA}S_TS_{RL}$), while conditions in which a greater ratio of asynchronous stimulations were applied were coded as 0 ($S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$), thus creating one variable, i.e., a (theoretical) illusory full-body ownership predictor. Conditions were additionally coded based on whether they applied synchronous stimulation to the mannequin's right arm (1 = $S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$) or not (0 = $A_{RA}S_TS_{RL}$ and $A_{RA}A_TA_{RL}$) to establish a second (theoretical) illusory body part ownership predictor based upon the stimulation synchronicity of the right arm specifically. Then, the question of whether illusory full-body ownership ratings could be predicted by the illusory full-body ownership predictor, the illusory body part (right arm) ownership predictor, or by an interaction between the two stimulations was investigated. We found that the illusory full-body ownership predictor was significant (β estimate = 0.83, SE = 0.41, $z = 2.04$, $p = .042$), but the estimates for the illusory body part ownership predictor (β estimate = 0.22, SE = 0.40, $z = 0.55$, $p = .583$) and the interaction term (β estimate = 0.62, SE = 0.56, $z = 1.11$, $p = .266$) were not significant. Thus, this second mixed linear model further corroborates our main conclusion regarding the relationship between full-body ownership and the conditions in which two or all three body parts received synchronous (vs. asynchronous) stimulation.

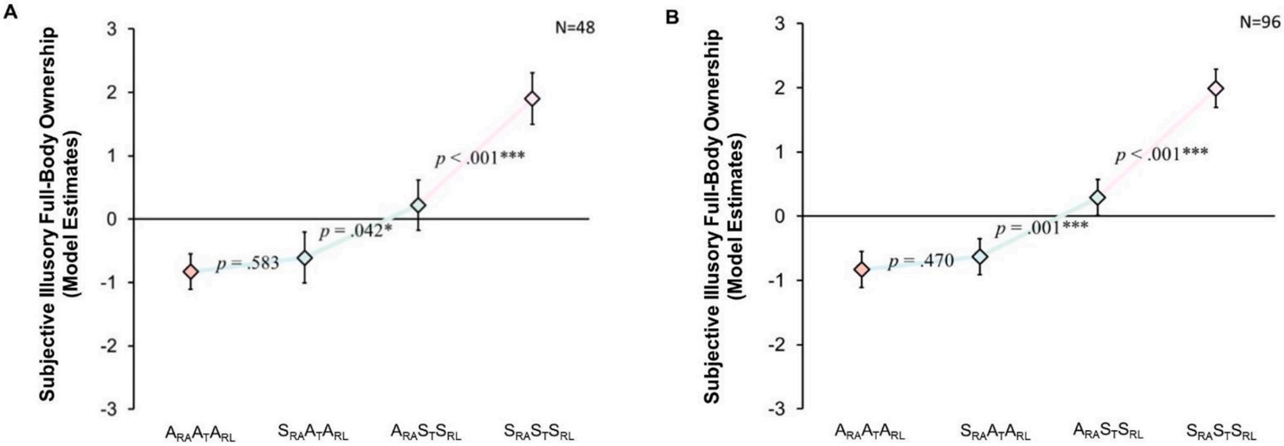

Fig. 9. A-B. The nonlinear relationship between illusory full-body ownership ratings and the number of synchronous (vs. asynchronous) visuotactile stimulations revealed by cumulative link mixed effects modelling at N = 48 (Panel A) and $N = 96$ (Panel B). The coefficient for the gradient of the slope between $A_{RA}A_TA_{RL}$ and $S_{RA}A_TA_{RL}$ was not statistically significant ($p = .583$), while the coefficients for the gradient of the slopes between $S_{RA}A_TA_{RL}$ and $A_{RA}S_TS_{RL}$ and between $A_{RA}S_TS_{RL}$ and $S_{RA}S_TS_{RL}$ were statistically significant ($p = .042$ and $p < .001$, respectively), albeit only marginally so for the slope between $S_{RA}A_TA_{RL}$ and $A_{RA}S_TS_{RL}$ (Experiment 2's data, N=48, Panel A). This finding is comparable to Panel B for the pooled data, $N = 96$, where the coefficient for the gradient of the slope between $A_{RA}A_TA_{RL}$ and $S_{RA}A_TA_{RL}$ was not found to be statistically significant ($p = .470$), while the coefficients for the gradient of the slopes between $S_{RA}A_TA_{RL}$ and $A_{RA}S_TS_{RL}$ and between $A_{RA}S_TS_{RL}$ and $S_{RA}S_TS_{RL}$ were statistically significant ($p = .001$ and $p < .001$, respectively). Both results are also comparable to those of Experiment 1 (Fig. 4). Model estimates are plotted with error bars denoting the standard error. For details concerning the model, see the text.

7.3. Experiment 2 – Body part ownership

With regard to the illusory body part ownership ratings pertaining to the mannequin's right arm (Q1), we found that $S_{RA}S_TS_{RL}$ led to significantly greater illusory ownership ratings than did $A_{RA}S_TS_{RL}$ ($Z = 4.369$, $p < .001$, $p_{FDR} = 0.002$, $r = 0.63$, $BF_{10} = 18{,}682.010$, %error = $3.11e^{-8}$), and $A_{RA}A_TA_{RL}$ ($Z = 3.750$, $p < .001$, $p_{FDR} = 0.002$, $r = 0.54$, $BF_{10} = 201.015$, %error = $4.21e^{-9}$). Similarly, $S_{RA}A_TA_R$ led to significantly greater illusory ownership ratings for the mannequin's right arm than did $A_{RA}S_TS_{RL}$ ($Z = 3.757$, $p < .001$, $p_{FDR} = 0.002$, $r = 0.54$, $BF_{10} = 355.691$, %error = $1.03\ e^{-9}$) and $A_{RA}A_TA_{RL}$ ($Z = 2.921$, $p = .003$, $p_{FDR} = 0.0045$, $r = 0.42$, $BF_{10} = 10.342$, %error = $3.85e^{-7}$). The ratings associated with $S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_R$ were not significantly different from one another ($Z = 1.561$, $p = .119$, $p_{FDR} = 0.3636$, $r = 0.23$, $BF_{10} = 0.638$, %error = $4.40e^{-6}$). Therefore, $S_{RA}A_TA_R$ elicited an illusory ownership percept with regard to the mannequin's right arm, even in the absence of a full-body ownership illusion. As the right arm was stimulated asynchronously in condition $A_{RA}S_TS_{RL}$, this condition did not elicit an illusory ownership percept that was significantly different from $A_{RA}A_TA_{RL}$ ($Z = 1.031$, $p = .303$, $p_{FDR} = 0.303$, $r = 0.15$, $BF_{10} = 0.288$, %error = $6.35e^{-6}$). These data are presented in Fig. 8C. For the results of a mixed effects modelling analysis, which emphasises the independence of illusory body part ownership from illusory full-body ownership, please refer to the Supporting Information section – Experiment 2 – Mixed-Effects Modelling – Stimulated Body Part Ownership. Below, we proceed by presenting the results of the pooled analysis.

8. Pooled analysis

8.1. Pooled analysis – Full-body ownership

We repeated the analysis using data from Experiment 2 pooled with data drawn from the identical experimental conditions in Experiment 1 ($S_{RA}S_TS_{RL}$, $A_{RA}S_TS_{RL}$, $S_{RA}A_TA_R$ and $A_{RA}A_TA_{RL}$), which we reasoned would be of particular benefit with regard to the comparison between $A_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$. At $N = 48$, while the effect size for the contrast $S_{RA}S_TS_{RL}$ – $A_{RA}A_TA_{RL}$ was associated with an estimated 75% power, the mixed synchronicity contrast $A_{RA}S_TS_{RL}$ – $S_{RA}A_TA_{RL}$ was associated with an estimated 38% power. Therefore, a pooled data analysis ($N = 96$) could help us overcome this limitation in terms of power. Partly for this reason, we also judged that the pooled dataset would be advantageous for the mixed linear modelling for full-body ownership as well as for investigations of illusory ownership of the nonstimulated left body parts.

Pairwise comparisons at N = 96 revealed that $S_{RA}S_TS_{RL}$ led to significantly higher illusory full-body ownership ratings than did $A_{RA}S_TS_{RL}$ ($Z = 3.354$, $p = .001$, $p_{FDR} = 0.0015$, $r = 0.34$, $BF_{10} = 34.866$, %error = $4.050e^{-7}$), $S_{RA}A_TA_{RL}$ ($Z = 4.857$, $p < .001$, $p_{FDR} = 0.0015$, $r = 0.50$, $BF_{10} > 100$, %error = $6.078e^{-11}$) and $A_{RA}A_TA_{RL}$ ($Z = 5.126$, $p < .001$, $p_{FDR} = 0.0015$, $r = 0.52$, $BF_{10} > 100$, %error = $1.943\ e^{-11}$). In this analysis, the $A_{RA}S_TS_{RL}$ condition also led to significantly greater illusory ownership ratings than did $S_{RA}A_TA_R$ ($Z = 3.408$, $p = .001$, $p_{FDR} = 0.0015$, $r = 0.35$, $BF_{10} = 5.229$, %error = $3.002e^{-6}$) and $A_{RA}A_TA_{RL}$ ($Z = 2.784$, $p = .005$, $p_{FDR} = 0.008$, $r = 0.28$, $BF_{10} = 25.908$, %error = $5.577e^{-7}$). As in the analysis at $N = 48$, at N = 96, the experimental condition $S_{RA}A_TA_{RL}$ was not found to lead to significantly greater illusory full-body ownership ratings than $A_{RA}A_TA_{RL}$ ($Z = 1.040$, $p = .298$, $p_{FDR} = 0.298$, $r = 0.11$, $BF_{10} = 0.162$, %error = $9.103e^{-5}$). Therefore, visuotactile stimulation in condition $S_{RA}A_TA_{RL}$ does not evoke a full-body ownership illusion. These data are presented in Fig. 8B.

Analogous to Experiments 1 and 2 (N = 48), we once again investigated illusory full-body ownership ratings as a function of the number of synchronously stimulated body parts using the linear mixed effects model with the categorical predictor "Condition" at N = 96 (Illusory full-body ownership rating ∼ n_sync, link = logistic). Consistent with the results of Experiments 1 and 2, we found that our fixed effect, namely, the number of synchronous (vs. asynchronous) visuotactile stimulations, did not significantly influence the gradient slope's location coefficient between $A_{RA}A_TA_{RL}$ and $S_{RA}A_TA_{RL}$ were not significant (β estimate = 0.20, SE = 0.28, $z = 0.72$, $p = .470$). This suggests that these conditions are similarly unlikely to increase ratings of full-body ownership. Furthermore, the location coefficients for the gradient of the slopes between $S_{RA}A_TA_{RL}$ and $A_{RA}S_TS_{RL}$ (β estimate = 0.92, SE = 0.28, $z = 3.27$, $p = .001$) and between $A_{RA}S_TS_{RL}$ and $S_{RA}S_TS_{RL}$ were significant (β estimate = 1.70, SE = 0.30, $z = 5.76$, $p < .001$). Hence, the enhancement in perceived full-body ownership due to two synchronous visuotactile stimulations ($A_{RA}S_TS_{RL}$) is significantly greater than that produced by one synchronous visuotactile stimulation ($S_{RA}A_TA_{RL}$), with an average increase of +0.92 rating units. Similarly, the illusion of full-body ownership generated by three synchronous visuotactile stimulations ($S_{RA}S_TS_{RL}$) significantly exceeds that produced by two synchronous stimulations ($A_{RA}S_TS_{RL}$), in this case, with an average increase of +1.70 rating units. A visualisation of these results is displayed in Fig. 9B ($N = 48$ in Fig. 9A).

Finally, we examined whether a mixed effects model that used a category coding approach to specify the main effect of illusory full-body ownership-inducing stimulation, which was achieved by assigning a value of '1' for conditions $S_{RA}S_TS_{RL}$ and $A_{RA}S_TS_{RL}$ and a value of '0' for conditions $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$, and the main effect of illusory body part ownership-inducing stimulation, which was achieved by assigning a value of '1' for conditions $S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$ and a value of '0' for conditions $A_{RA}S_TS_{RL}$ and $A_{RA}A_TA_{RL}$ as well as their mutual interaction (full-body ownership * body part ownership), could predict ratings for full-body ownership (Q6). This mixed linear model (Illusory full-body ownership rating ~ FBO + BPO + FBO*BPO, link = logistic) revealed a significant effect for the full-body ownership-inducing stimulation factor (β estimate = 0.92, SE = 0.28, $z = 3.27$, $p = .001$) but no significant effect for the illusory body part ownership-inducing stimulation factor (β estimate = 0.20, SE = 0.28, $z = 0.72$, $p = .470$) or the illusory full-body ownership-inducing stimulation * illusory body part ownership-inducing stimulation interaction (β estimate = 0.58, SE = 0.39, $z = 1.47$, $p = .142$). Thus, in line with our hypothesis and the results obtained when the data collected for Experiment 2 were analysed in isolation (see above), this analysis confirmed that illusory full-body ownership ratings were driven primarily by the full-body ownership-inducing factor ($S_{RA}S_TS_{RL}$, $A_{RA}S_TS_{RL}$) rather than by the body part ownership-inducing factor ($S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$).

8.2. Pooled analysis – Body part ownership for stimulated body parts

With regard to illusory body part ownership ratings specific to the mannequin's right arm, both $S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_R$ led to significantly greater illusory ownership ratings than did $A_{RA}S_TS_{RL}$ ($Z = 5.958$, $p < .001$, $p_{FDR} = 0.0015$, $r = 0.61$, $BF_{10} > 100$, %error = $2.895e^{-14}$; $Z = 5.750$, $p < .001$, $p_{FDR} = 0.0015$, $r = 0.59$, $BF_{10} > 100$, %error = $1.344e^{-13}$) and $A_{RA}A_TA_{RL}$ ($Z = 5.969$, $p < .001$, $p_{FDR} = 0.0015$, $r = 0.61$, $BF_{10} > 100$, %error = $8.315e^{-14}$; $Z = 5.368$, $p < .001$, $p_{FDR} = 0.0015$, $r = 0.55$, $BF_{10} > 100$, %error = $1.191e^{-12}$). As above ($N = 48$), the illusory body part ownership for the mannequin's right arm produced by $S_{RA}S_TS_{RL}$ was not significantly different from that produced by $S_{RA}A_TA_{RL}$ ($Z = 1.003$, $p = .316$, $p_{FDR} = 0.3792$, $r = 0.10$, $BF_{10} = 0.213$, %error = $7.055e^{-5}$), confirming that $S_{RA}A_TA_R$ elicited an illusory ownership percept for the mannequin's right arm, irrespective of full-body ownership. In contrast, $A_{RA}S_TS_{RL}$ did not elicit an illusory body part ownership percept that was significantly different from that elicited by $A_{RA}A_TA_{RL}$ ($Z = 0.296$, $p = .767$, $p_{FDR} = 0.767$, $r = 0.03$, $BF_{10} = 0.116$, % error = $1.238e^{-4}$), despite being associated with a full-body ownership illusion that was significantly greater than those elicited by $S_{RA}A_TA_{RL}$ or $A_{RA}A_TA_{RL}$ (see above). These results data are presented in Fig. 8D and replicate the findings of Experiments 1 and 2 mentioned above.

Using the pooled dataset, we also inspected the mixed effects model results when illusory body part ownership ratings for the mannequin's right arm supplied the dependent variable and the model posited an illusory full-body ownership-inducing factor (1 = $S_{RA}S_TS_{RL}$ and $A_{RA}S_TS_{RL}$; 0 = $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$) and an illusory body part ownership-inducing factor for the right arm (1 = $S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$; 0 = $A_{RA}S_TS_{RL}$ and $A_{RA}A_TA_{RL}$) (Illusory body part ownership rating ~ FBO + BPO + FBO*BPO, link = logistic). Only the illusory body part ownership-inducing factor was significant (illusory body part ownership-inducing stimulation: β estimate = 1.98, SE = 0.29, $z = 6.80$, $p < .001$; illusory full-body ownership-inducing stimulation: β estimate = 0.01, SE = 0.27, $z = 0.03$, $p = .974$; illusory body part ownership-inducing stimulation * illusory full-body ownership-inducing stimulation interaction: β estimate = 0.11, SE = 0.38, $z = 0.30$, $p = .764$). Therefore, we replicated the finding indicating that illusory right arm ownership ratings were driven exclusively by the factor body part ownership ($S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$) rather than by the full-body ownership factor ($S_{RA}S_TS_{RL}$, $A_{RA}S_TS_{RL}$) or their mutual interaction.

8.3. Pooled analysis – Body part ownership for nonstimulated body parts

Similar to Experiment 1, the nonstimulated body parts (averaged between the left arm and left leg, Q2 + Q5/2) were predicted in a nonlinear fashion by the number of synchronously stimulated body parts using the categorical predictor "Condition" in a cumulative mixed effect model at $N = 96$ (Illusory ownership rating for nonstimulated parts ~ n_sync, link = logistic). The results here mirror, albeit on a reduced and negative scale, the data pertaining to illusory full-body ownership; the gradient of the slope between zero and one synchronous visuotactile stimulation (between $A_{RA}A_TA_{RL}$ and $S_{RA}A_TA_{RL}$) was not significant, β estimate = 0.47, SE = 0.29, $z = 1.63$, $p = .103$; the slope's gradient between one and two synchronous visuotactile stimulations (the interval between $S_{RA}A_TA_{RL}$ and $A_{RA}S_TS_{RL}$) was significant, β estimate = 0.58, SE = 0.28, $z = 2.05$, $p = .040$; and the slope's gradient between two and three synchronous visuotactile stimulations (between $A_{RA}S_TS_{RL}$ and $S_{RA}S_TS_{RL}$) was significant, β estimate = 0.97, SE = 0.29, $z = 3.32$, $p = .001$. These results are displayed in Fig. 10B. Fig. 10A presents the results obtained by applying the cumulative mixed effect model exclusively to the data from Experiment 2 ($N = 48$; for details, see Supporting Information section Experiment 2 – Mixed-Effects Modelling – Body Part Ownership for Nonstimulated Body Parts at N = 48).

Similar to the analysis of the full-body ownership illusion data presented above, we also examined whether a mixed effects model that specified the main effects of illusory full-body ownership-inducing stimulation (1 = $S_{RA}S_TS_{RL}$ and $A_{RA}S_TS_{RL}$; 0 = $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$) and illusory body part ownership-inducing stimulation (1 = $S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$; 0 = $A_{RA}S_TS_{RL}$ and $A_{RA}A_TA_{RL}$) and their interaction (illusory full-body ownership-inducing stimulation * illusory body part ownership-inducing stimulation) could predict ratings for nonstimulated parts (N = 96) (Illusory ownership rating for nonstimulated parts ~ FBO + BPO + FBO*BPO, link = logistic). The results showed that for nonstimulated body parts (averaged between the left arm and left leg), only the main effect of full-body ownership was significant: illusory full-body ownership, β estimate = 0.58, SE = 0.28, $z = 2.05$, $p = .040$; illusory body part ownership, β estimate = 0.47, SE = 0.29, $z = 1.63$, $p = .103$; illusory full-body ownership* illusory body part ownership interaction, β estimate = −0.08, SE = 0.40, $z = -0.19$, $p = .846$. Therefore, only the illusory full-body ownership factor was significantly predictive of the subjective magnitude of illusory ownership ratings with regard to the nonstimulated body parts, thereby corroborating the results of Experiment 1.

8.4. Experiment 2 and pooled analysis – Summary and interim discussion

In Experiment 2, we replicated four of the eight experimental conditions included in Experiment 1 ($S_{RA}S_TS_{RL}$, $A_{RA}S_TS_{RL}$, $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$) using a simplified 2 × 2 design that focused on the dissociation between body part (right arm) and full-body ownership in the context of the current bodily illusion paradigm. The results were consistent with the findings of Experiment 1: ownership of the right arm was driven by the visuotactile synchrony of the stimuli applied to the right arm, whereas full-body ownership was related to the number of synchronously stimulated parts, with the strongest illusion occurring in the fully synchronous condition. Notably, when considering the pairwise comparisons, we found that illusory ownership of the mannequin's right arm could be experienced either with ($S_{RA}S_TS_{RL}$) or without ($S_{RA}A_TA_{RL}$) a significant illusory full-body ownership experience of the entire mannequin. Furthermore, a mixed effects linear model revealed a significant nonlinear relationship between the number of synchronously stimulated body parts and the resulting full-body ownership illusory percept (both at $N = 48$ and N = 96), thereby

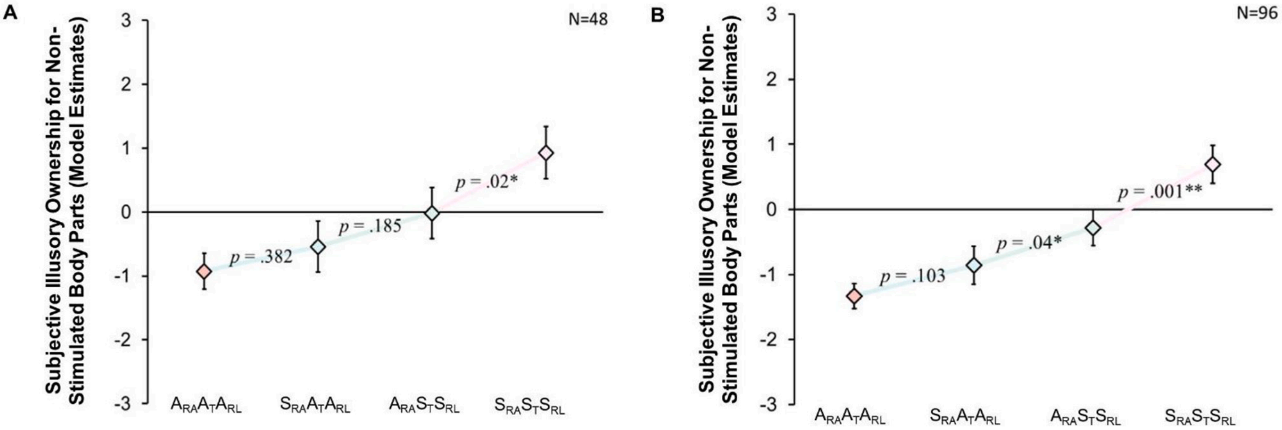

Fig. 10. A-B. The nonlinear relationship between illusory ownership ratings for the left nonstimulated body parts and the number of synchronous visuotactile stimulations revealed by cumulative link mixed effects modelling at N = 48 (Panel A) and N = 96 (Panel B). For purposes of visualisation and comparison, the results at N = 48 are shown in Panel A and the results for N = 96 are shown in Panel B. In Panel A, a nonlinear relationship is depicted that is particularly notable for the fully synchronous stimulation condition where the gradient slope between $A_{RA}S_{T}S_{RL}$ (n_sync = 2) and $S_{RA}S_{T}S_{RL}$ (n_sync = 3) is significant. In Panel B, the results for the pooled analysis look similar, again illustrating a non-linear relationship. In this analysis, the gradient of the slope between $A_{RA}A_{T}A_{RL}$ (n_sync = 0) and $S_{RA}A_{T}A_{RL}$ (n_sync = 1) was not significant, while the gradients of the slopes between $S_{RA}A_{T}A_{RL}$ (n_sync = 1) and $A_{RA}S_{T}S_{RL}$ (n_sync = 2) and between $A_{RA}S_{T}S_{RL}$ (n_sync = 2) and $S_{RA}S_{T}S_{RL}$ (n_sync = 3) are significant. Model estimates are plotted with error bars denoting the standard error. For details concerning the model, see the text.

replicating Experiment 1's findings. Specifically, the mixed effects modelling revealed little overall change in participants' illusory full-body ownership ratings between $A_{RA}A_{T}A_{RL}$ and $S_{RA}A_{T}A_{RL}$, while significant increases were observed between $S_{RA}A_{T}A_{RL}$ and $A_{RA}S_{T}S_{RL}$ and between $A_{RA}S_{T}S_{RL}$ and $S_{RA}S_{T}S_{RL}$, thereby replicating this principal observation from Experiment 1. Moreover, a mixed linear model featuring a 2 × 2 factorial analysis revealed a significant main effect of a full-body ownership-inducing stimulation ($S_{RA}S_{T}S_{RL}$, $A_{RA}S_{T}S_{RL}$) on full-body ownership ratings but did not provide any evidence of a significant interaction between full-body ownership-inducing stimulation and body part ownership inducing stimulation. These observations corroborate the conclusions of Experiment 1, although some of the pairwise comparisons, especially between conditions in which one or two body parts received synchronous stimulation, did not reach statistical significance; however, a power analysis indicated the statistical methods used were underpowered at $N = 48$.

By using the pooled dataset regarding these four conditions in both Experiments 1 and 2 to increase statistical power (N = 96), we obtained more robust and statistically significant differences for all relevant comparisons: $S_{RA}S_{T}S_{RL}$ produced both illusory full-body ownership and illusory body part ownership for the mannequin's right arm; $A_{RA}S_{T}S_{RL}$ produced an intermediary illusory full-body ownership percept (that was significantly greater than those produced by both $S_{RA}A_{T}A_{RL}$ and $A_{RA}A_{T}A_{RL}$) in the absence of illusory body part ownership for the mannequin's right arm (statistically comparable to $A_{RA}A_{T}A_{RL}$); $S_{RA}A_{T}A_{RL}$ produced an illusory body part ownership percept for the mannequin's right arm (statistically comparable to that produced by $S_{RA}S_{T}S_{RL}$) in the absence of an illusory ownership percept for the mannequin's entire body (statistically comparable to $A_{RA}A_{T}A_{RL}$); and $A_{RA}A_{T}A_{RL}$ produced the lowest body part and full-body ownership ratings, which, were statistically comparable to $A_{RA}S_{T}S_{RL}$ and $S_{RA}A_{T}A_{RL}$ for illusory right arm ownership ratings and illusory full-body ownership ratings, respectively. Furthermore, the mixed linear models using the pooled dataset revealed a significant main effect of a full-body ownership-inducing stimulation ($S_{RA}S_{T}S_{RL}$, $A_{RA}S_{T}S_{RL}$) on full-body ownership ratings and a significant main effect of body part ownership-inducing stimulation ($S_{RA}S_{T}S_{RL}$, $S_{RA}A_{T}A_{RL}$) on illusory right arm ownership ratings, in each case without any evidence of a significant interaction between full-body ownership-inducing stimulation and body part ownership-inducing stimulation. Consequently, these observations bolstered the conclusion that body-part ownership and full-body ownership can be dissociated.

With respect to the question of the "spread of ownership" to the nonstimulated left limbs in the pooled data, mixed linear modelling indicated a significant main effect of full-body ownership-inducing stimulation ($p < .05$), but not a significant main effect of body part ownership-inducing stimulation ($p = .103$); furthermore, no interaction was indicated between the two factors ($p = .806$). These findings further support the claim that the increases in ownership ratings observed with regard to the nonstimulated body parts were driven primarily by illusory full-body ownership; however, see the evidence concerning a marginally significant interaction in the model for Experiment 2 (N = 48) in the Supporting Information. A further crucial point was that the pooled analysis revealed that the increased ownership ratings pertaining to the nonstimulated body parts (the left arm and left leg) could be predicted by the number of synchronously stimulated body parts based on a nonlinear relationship that was similar to the pattern we observed in the case of illusory full-body ownership. These findings reinforce the conclusion that the illusory ownership of nonstimulated body parts is influenced, at least partially, by increases in illusory full-body ownership.

Thus, collectively, the findings of Experiment 2 and the pooled analysis support the conclusion that body part ownership and full-body ownership can be dissociated at the level of subjective reports, which is in line with our observations in Experiment 1, and our hypotheses that body part ownership is related to a local multisensory integration process and that full-body ownership is related to a more global multisensory integration process. We conclude that subjective experiences of illusory body part ownership and illusory full-body ownership are supported by different processes but that these phenomena are functionally related in a hierarchical structure; namely, depending on the configuration of synchronous and asynchronous multisensory stimulation applied to multiple body parts simultaneously, local synchrony drives body part ownership, while the weighted combination of the outputs of local body part processes drive full-body ownership.

9. Experiment 3 - Aims and rationale

After conducting two questionnaire experiments, we wanted to obtain more objective evidence regarding the illusion-related effects described in the subjective psychometric data. The questionnaire results suggested that condition $S_{RA}A_{T}A_{RL}$ did not elicit a full-body ownership illusion that was significantly greater than that elicited by $A_{RA}A_{T}A_{RL}$

despite being conducive to an illusory body part ownership percept for the mannequin's right arm. In contrast, in condition $A_{RA}S_TS_{RL}$, participants denied ownership of the mannequin's right arm despite the fact that their illusory full-body ownership ratings were significantly enhanced when compared to those associated with $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$. Therefore, Experiment 3 was designed to provide more objective physiological evidence regarding the dissociation between body part and full-body ownership by registering electrodermal activity in response to threats specifically targeting the mannequin's right arm. We tested the following hypotheses: (i) illusory arm ownership is sufficient to elicit skin conductance responses (SCR) following the presentation of knife threats to the mannequin's right arm, even when the full-body ownership illusion is weak, and (ii) the asynchronous stimulation provided in condition $A_{RA}S_TS_{RL}$ is sufficient to reduce or eliminate the threat-evoked SCR to the mannequin's right arm, even when the full-body ownership illusion is moderately enhanced. Thus, in Experiment 3, threat-evoked SCRs triggered by moving a knife close to the mannequin's right arm (over the dorsal surface of its hand) were collected during the same four experimental conditions as were used in Experiment 2. We reasoned that since threat-evoked SCR has been used both to probe body part ownership in rubber hand illusion studies (Armel & Ramachandran, 2003; Fan et al., 2021; Petkova & Ehrsson, 2009) and as an index of full-body ownership illusions (Petkova & Ehrsson 2008; O'Kane & Ehrsson, 2021), this 2 × 2 factorial design would allow us to test the contributions of body part and full-body ownership as well as that of their potential interaction using a single experimental design.

10. Experiment 3 - Methods & materials

10.1. Experiment 3 - Participants

Forty-eight healthy adults (28 females, 20 males; average age: 27.6 ± 4.8 years; age range: 18–36 years; all self-reported right-handed individuals) were recruited via online and poster advertisements to participate in the experiment, which lasted approximately 45 min; these participants were compensated with one cinema ticket. The sample size was based on a previous study (O'Kane & Ehrsson, 2021) and was predetermined before data collection commenced. All participants were naïve to the full-body ownership illusion (e.g., none had taken part in Experiments 1 or 2 or participated in any other experiment involving a full-body illusion); they provided written informed consent upon arrival. The study was approved by the Ethical Review Board at the Karolinska Institutet, Stockholm, Sweden.

10.2. Experiment 3 - Visual threat stimulus and skin conductance response (SCR)

We used a Biopac MP150 (Biopac Systems Inc., Goleta, USA) to record continuous electrodermal activity (μS) with the goal of collecting threat-evoked skin conductance responses (SCRs), which were registered in the associated software (AcqKnowledge 5.0). After applying conductive electrode gel (Biopac Systems Inc., Goleta, USA) to the bottom surface of the third phalange of the index and middle finger of the participant's left hand, two recording electrodes were attached (Biopac Systems Inc., Goleta, USA). We recorded electrodermal activity (i.e., skin conductance) from participants' left hand, and the raw tonic signal was collected at a sample rate of 100 Hz. The data were stored and analysed on a computer using AcqKnowledge 5.0 software (Biopac Systems Inc., Goleta, USA).

The visual stimulation used in Experiment 3 was identical to that used in Experiment 2 but with the addition of a threat stimulus. At the end of visuotactile stimulation, a knife entered the field of view from the upper right quadrant and contacts the mannequin's right hand in a threatening-looking stabbing motion (Fig. 11). This approach enabled us to collect threat-evoked SCRs (μS), as a physiological measure of illusory body part ownership (Guterstam, Petkova, & Ehrsson, 2011) with regard to the mannequin's right arm. The knife threat appeared at predetermined time points, which ranged from early to middle to late with respect to the onset of visuotactile stimulation. Specifically, this threat appeared after 14, 16 or 18 visuotactile stimulations, although the participants received no information about this manipulation to avoid anticipatory reactions. The knife remained in this position for 5 s before being removed from view, leaving a still image of the mannequin's body displayed via the HMD for 10 s; the duration of this still image ensured that we captured the peak of the SCR response, which is known to vary in terms of latency across participants, during a period in which no tactile stimulation was provided, which could otherwise influence the SCR (Etzi, Carta, & Gallace, 2018) before ending the data collection for that experimental condition. The video clip featuring the knife stimulus was filmed in a separate session to the filming of the original movies. Using video editing software, the transition to this clip at the end of the visuotactile stimulation was gradual and unnoticed by participants (as assessed by verbal report in pilot experiments). The frequency of the visuotactile stimulations delivered was also different in Experiment 3 in that it was fixed and slightly higher, onsetting every 6 s (intertrial interval = 5 s).

Fig. 11. Knife stimulus eliciting threat-evoked skin conductance responses. Following each condition's visuotactile stimulation, and on every repetition, a knife appeared to target the hand region of the mannequin's right arm in a stabbing motion and remained on the screen for 5 s before being removed from view. We registered the changes in skin conductance evoked by this threat stimulus as physiological evidence of bodily illusion.

10.3. Experiment 3 - Procedure

The experimental procedure used for Experiment 3 was identical to that used for Experiment 2, with the exceptions of the changes described herein. To collect threat-evoked SCRs, we conducted three repetitions of each of the four experimental conditions to determine an average threat-evoked SCR (μS) for each experimental condition for each subject. Each of the three repetitions of each of the four experimental conditions contained a single knife threat to minimise habituation effects. Each repetition contained the same prerecorded movie clip containing the presentation of a knife as described above, which onset after 14 (total duration: 30 s), 16 (total duration: 45 s) or 18 (total duration: 60 s) visuotactile stimulations. The order of the 12 experimental blocks was pseudorandomised to produce 48 possible sequences, once again motivating our desired sample size of 48. The sequence of experimental conditions was counterbalanced across participants. Before the experiment began, the participant wore the recording electrodes for approximately five minutes to ensure a steady signal before the experiment began. Between each experimental condition, participants removed the HMD, then observed and moved their real body to break the illusion, minimise the risk of carry-over effects and ensure that the procedure was similar to the questionnaire experiment (during which participants moved when completing the questionnaire) before preparing to continue to the next trial. As in Experiments 1 and 2, participants were reminded to look at and spread their attention equally across the mannequin's body during the experiment, relax and avoid movement, breathe normally, and not remove the HMD until the end screen appeared.

10.4. Experiment 3 - Statistical analyses and data availability

Of the 48 individuals who participated in Experiment 3, the datasets from 5 individuals were removed, as two-thirds or more of the twelve trials in these cases did not exceed the threshold criteria for inclusion, i.e., 0.02 µS (Braithwaite, Watson, Jones, & Rowe, 2013); therefore, for this analysis, $N = 43$. As the data were nonnormally distributed, we first used Friedman tests to show that no significant differences in SCR (µS) magnitude (see below) occurred due to repeat/trial number, which we varied with regard to when the knife was presented in relation to the visuotactile stimulation (relatively early: after 14 stimulations: in the middle: after 16 stimulations; and relatively late: after 18 stimulations) separately for each of the four experimental conditions ($S_{RA}S_TS_{RL}$: $X^2(2, N = 43) = 0.854$, $p = .653$, $A_{RA}S_TS_{RL}$: $X^2(2, N = 43) = 3.488$, $p = .175$; $S_{RA}A_TA_{RL}$: $X^2(2, N = 43) = 0.573$, $p = .751$; $A_{RA}A_TA_{RL}$: $X^2(2, N = 43) = 3.520$, $p = .172$).

We analysed the SCR data using a manual extraction protocol similar to that used in previous studies (O'Kane & Ehrsson, 2021; Petkova & Ehrsson, 2008). We transformed the raw tonic signal to a phasic signal using Acknowledge 5.0, which automatically baseline corrects the data, before manually extracting the amplitude of threat-evoked SCRs (µS) and determining averages for the three repetitions of each of the four experimental conditions including null responses, thereby computing the magnitude of the SCR (Braithwaite, Watson, Jones, & Rowe, 2013; Dawson, Schell, & Filion, 2000; Petkova & Ehrsson, 2008). The planned comparisons were $S_{RA}S_TS_{RL} – A_{RA}S_TS_{RL}$, $S_{RA}S_TS_{RL} – S_{RA}A_TA_{RL}$, $S_{RA}S_TS_{RL} – A_{RA}A_TA_{RL}$, $A_{RA}S_TS_{RL} – S_{RA}A_TA_{RL}$, $A_{RA}S_TS_{RL} – A_{RA}A_TA_{RL}$ and $S_{RA}A_TA_{RL} – A_{RA}A_TA_{RL}$ (the same as in Experiment 2); we used Wilcoxon's signed rank tests to account for nonnormality in the dataset.

We also employed a mixed effects model similar to that used in Experiments 1 and 2 with regard to the questionnaire data. We were interested in analysing the effects of body part and full-body ownership across all four conditions using a 2 × 2 factorial design; accordingly, we specified a main effect of illusory full-body ownership-inducing stimulation by assigning a value of '1' for conditions $S_{RA}S_TS_{RL}$ and $A_{RA}S_TS_{RL}$ and a value of '0' for conditions $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$ as well as a main effect of illusory body part ownership-inducing stimulation by assigning a value of '1' for conditions $S_{RA}S_TS_{RL}$ and $S_{RA}A_TA_{RL}$ and a value of '0' for conditions $A_{RA}S_TS_{RL}$ and $A_{RA}A_TA_{RL}$ as well as their mutual interaction (illusory full-body ownership-inducing stimulation * illusory body part ownership-inducing stimulation). This approach allowed us to test whether any of these factors could predict the magnitude of the SCRs (µS) recorded in the experiment. The preprocessed threat-evoked magnitude SCR data are publicly available: https://osf.io/nxpvy/?view_only=e70f00a9354d4331b7c9e58bf0ddc235.

11. Experiment 3 - Results

11.1. Experiment 3 - Threat-evoked skin conductance responses (SCRs)

Fully synchronous visuotactile stimulation, $S_{RA}S_TS_{RL}$, produced significantly greater threat-evoked SCRs (µS) than did $A_{RA}S_TS_{RL}$ ($Z = 3.345$, $p < .001$, $p_{FDR} = 0.003$, $r = 0.51$, $BF_{10} = 1.352$, %error $= 1.84e^{-6}$), $S_{RA}A_TA_{RL}$ ($Z = 3.526$, $p < .001$, $p_{FDR} = 0.003$, $r = 0.54$, $BF_{10} = 17.862$, %error $= 5.145e^{-9}$) and $A_{RA}A_TA_{RL}$ ($Z = 2.632$, $p = .008$, $p_{FDR} = 0.016$, $r = 0.40$, $BF_{10} = 2.465$, %error $= 8.07e^{-7}$). No significant differences were observed between any other pair of experimental conditions: $A_{RA}S_TS_{RL} – A_{RA}A_TA_{RL}$, $Z = 0.791$, $p = .429$, $p_{FDR} = 0.6435$, $r = 0.12$, $BF_{10} = 0.175$, %error $= 1.34e^{-5}$; $A_{RA}S_TS_{RL} – S_{RA}A_TA_{RL}$, $Z = 0.314$, $p = .754$, $p_{FDR} = 0.754$, $r = 0.05$, $BF_{10} = 0.168$, %error $= 1.38e^{-5}$) or $S_{RA}A_TA_{RL} – A_{RA}A_TA_{RL}$ ($Z = 0.326$, $p = .744$, $p_{FDR} = 0.754$, $r = 0.05$, $BF_{10} = 0.196$, %error $= 1.34e^{-5}$). These results are shown in Fig. 12 below.

Next, we used lmer linear mixed effects modelling (Threat-evoked SCR ~ FBO + BPO + FBO*BPO) to investigate whether the magnitude of SCRs was related to body part ownership, full-body ownership, or a significant interaction between illusory part- and full-body ownership. Interestingly, the mixed effects model revealed that only the interaction between illusory full-body ownership and body part ownership with regard to the threat-targeted body part was significant with respect to predicting the magnitude of threat-evoked SCRs: illusory full-body ownership*illusory body part ownership, β estimate = 0.20, SE = 0.09, $t = 2.33$, $p = .02$. Unexpectedly, neither illusory full-body ownership (β estimate = −0.02, SE = 0.06, $t = −0.32$, $p = .747$) nor illusory body part ownership (β estimate = −0.03, SE = 0.06, $t = −0.50$, $p = .614$) were significant. This finding suggests that only when both the illusory full-body ownership-inducing factor *and* the illusory body part ownership-inducing factor with regard to the mannequin's right arm are present does the magnitude of participants' threat-evoked SCRs (µS) significantly increase.

11.2. Experiment 3 - Summary and interim discussion

The threat-evoked SCRs were significantly the strongest in the fully synchronous condition ($S_{RA}S_TS_{RL}$) compared to the three other experimental conditions ($A_{RA}S_TS_{RL}$, $S_{RA}A_TA_{RL}$ and $A_{RA}A_TA_{RL}$). Therefore, while the asynchronous visuotactile stimulation of the right arm in condition $A_{RA}S_TS_{RL}$ successfully reduced the threat-evoked SCRs compared to condition $S_{RA}S_TS_{RL}$ in line with our hypothesis, the synchronous stimulation of only the right arm in condition $S_{RA}A_TA_{RL}$ was not sufficient to elicit a significantly greater threat-evoked SCRs than that elicited in the fully asynchronous condition $A_{RA}A_TA_{RL}$, as we had

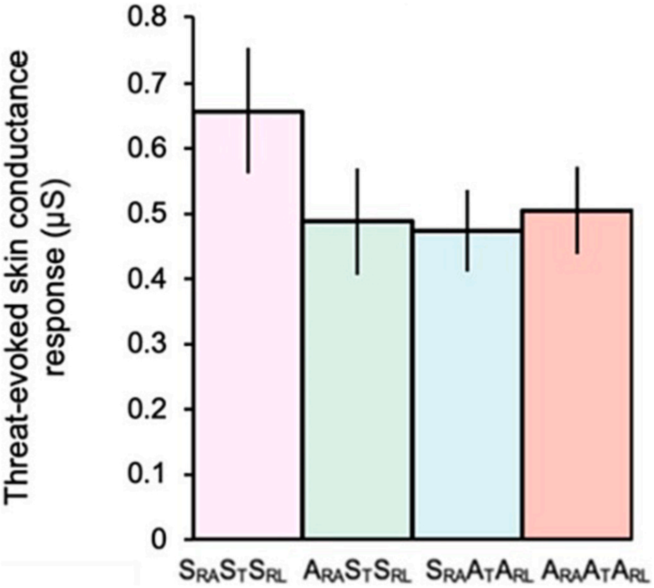

Fig. 12. Mean SCR magnitude (µS) associated with the visual threat stimulus presented near the mannequin's right arm across the four experimental conditions in Experiment 3 (N = 43) (error bars show SEM). Condition $S_{RA}S_TS_{RL}$ elicited significantly greater threat-evoked SCR magnitude than each of the other three conditions ($p < .005$ and $p_{FDR} < 0.05$ in all pairwise comparisons). See the Supporting Information concerning individual datapoints and pairwise comparison lines for these data (SI Fig. 7).

hypothesised. Since we also found a significant interaction between illusory body part ownership-inducing stimulation and illusory full-body ownership-inducing stimulation in the mixed effects linear model but no significant main effect of body part ownership-inducing stimulation itself, the results of Experiment 3 provide evidence of a crossover interaction, in which context the effect of one independent variable depends critically on the value of the other independent variable; here, this finding implies that illusory body part ownership interacts with illusory full-body ownership to produce emotional autonomic reactions when an illusorily owned body part is threatened. Thus, a limb must feel like one's own and be experienced as part of a whole body that is also one's own to evoke significant emotional defence reactions at the autonomic physiological level; neither factor in isolation appears to be sufficient.

Thus, the dissociation between part and whole, as observed at the subjective level in Experiments 1 and 2, was not present in the threat-evoked SCR data. Thus, it could be that threat-evoked SCRs are sensitive to the integration of an illusorily owned body part into a full-body ownership percept rather than perceived ownership of that body part per se. This view is consistent with the results of a study that reported significantly reduced threat-evoked SCRs in response to an illusorily owned virtual hand that was visibly disconnected from the rest of the body (Tieri, Tidoni, Pavone, & Aglioti, 2015); it is also consistent with the fMRI findings reported by Petkova et al. (2011a), who showed that synchronous versus asynchronous stimulation of a mannequin's arm presented in isolation (without being connected to a mannequin) did not produce body-ownership related activation in frontoparietal areas that would be indicative of a subjective body ownership illusion (Petkova et al., 2011a). In addition, note that the current SCR results are not inconsistent with the rubber hand illusion literature, since when people experience the rubber hand as their own, they also perceive it to be an anatomically integrated part of their own real body (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008), much of which they can see and obviously experience as their own.

However, the fact that the subjective questionnaire results, which supported the claim that part- and full-body ownership percepts can be dissociated, diverged from the results of the threat-evoked SCR experiment deserves further consideration. It could be that subjective ownership and autonomic emotional embodiment involve different processes (Ehrsson, 2012), with the latter involving changes in emotional processing, threat monitoring and preparation for defensive action (Ehrsson et al., 2007) that may result from the multisensory illusion and that may operate under constraints and principles other than those associated with multisensory perception of body parts and whole bodies. The psychometric data pertaining to condition $S_{RA}A_TA_{RL}$ provide abundant evidence to support participants' subjective illusory experience of owning only a "perceptually disconnected" synchronously stimulated right arm in isolation without ownership of the rest of the visible body due to the asynchronous visuotactile stimulation of the trunk and right leg. It may be that in this unusual perceptual state, illusory arm ownership leads to a weaker updating of bodily related emotional representations than would otherwise be observed in rubber hand illusion experiments, for example. However, one should also bear in mind the fact that since we used different cohorts of participants for each experiment in the current study, it is difficult to compare the ownership ratings for the mannequin's right arm with the magnitude of threat-evoked SCRs directly. Neither has the literature formally clarified the degree to which illusory ownership ratings for body parts versus those for whole bodies are correlated with the magnitude of threat-evoked SCRs; sometimes small but significant changes in subjective ownership ratings have been noted, which are nevertheless not reflected as significant changes in threat-evoked SCR (O'Kane & Ehrsson, 2021; Preuss Mattsson et al., 2022). However, comparing a condition featuring a strong ownership illusion to a condition in which the illusion is abolished typically leads to significant differences in threat-evoked SCR (Gentile et al., 2013; Petkova & Ehrsson, 2008, 2009; Preston et al., 2015; van der Hoort et al., 2011). It could be that to capture fine-grained changes in body part and full-body ownership with the threat-evoked SCR method requires a specifically optimised paradigm. Such a paradigm would presumably necessitate many more trials of threat stimuli presentation than we used in the current study.

We should also consider an alternative interpretation of the SCR findings, namely, that the significantly increased threat-evoked SCR in the fully synchronous condition could reflect the fact that participants experienced the strongest full-body illusion in this condition. Indeed, in both Experiments 1 and 2, the subjective full-body ownership ratings were the strongest in the $S_{RA}S_TS_{RL}$ condition, in which context these ratings were significantly stronger than all other conditions, and $S_{RA}S_TS_{RL}$ was the only condition that received positive affirmative mean ratings with regard to the full-body ownership statement (Q8 in Experiment 1 and Q6 in Experiment 2). Therefore, the enhanced threat-evoked SCR response observed in the fully synchronous condition could reflect the fact that the full-body ownership illusion was strongest in this condition. However, the mixed effects model applied to the SCR data revealed only a significant the interaction between body part and full-body ownership predictors, rather than a main effect of body part ownership or full-body ownership. Furthermore, the interpretation that a strong full-body ownership experience is the main driving factor does not fit well with previous studies that have documented changes in threat-evoked SCR that are related to changes in illusory hand ownership in various versions of the rubber hand illusion paradigm (Fan et al., 2021; Gentile et al., 2013; Guterstam et al., 2011; Petkova & Ehrsson, 2009). Therefore, we believe that an interaction between body part and full-body ownership offers a more plausible explanation overall.

In summary, the SCR results provide indirect physiological evidence indicating that a full-body illusion was elicited in the fully synchronous condition and suggest that the threat-evoked SCR response triggered by a threatening stimulus targeting a limb arises as a result of the interaction between illusory body part ownership and illusory full-body ownership.

12. A Bayesian hierarchical model of part and full-body ownership

Finally, we asked whether it would be possible to develop a theoretical model that could explain the relationship between body part and full-body ownership ratings we had observed in Experiments 1 and 2. In particular, we wanted to translate the notion of local and global multisensory processes supporting part and full-body ownership, respectively, to probabilistic models of multisensory perception (Körding et al., 2007; Sato et al., 2007). Recently, Bayesian causal inference models have been formalized to explain the rubber hand illusion and the sense of limb ownership (Chancel et al., 2022a; Chancel & Ehrsson, 2023; Kilteni et al., 2015; Samad et al., 2015). Within this Bayesian framework, body ownership corresponds to the outcome of a probabilistic computational process that determines whether sensory inputs should be combined or segregated when building a coherent multisensory percept of one's own body parts (Ehrsson & Chancel, 2019). More specifically, when processing two sensory signals from two different sensory modalities, the brain's perceptual systems use an inference process following the Bayesian principle to decide whether the two signals are more likely to originate from a common cause or more likely to originate from two separate causes (Shams & Beierholm, 2022). This probabilistic causal inference process uses both top-down and bottom-up information, such as the spatial proximity, simultaneity, and temporal correlation of the sensory signals, their relative uncertainty, and prior knowledge extracted from contextual cues in the environment (and, in our case, from the body) and previous experience. The outcome of this probabilistic inference process determines whether the sensory signals should be combined or segregated and the extent of this combination or segregation. This Bayesian causal inference framework has successfully been applied to various multisensory paradigms related to perception of events and objects in the external environment (Aller & Noppeney, 2019; Kayser & Shams, 2015; Rohe et al., 2019), as well as to the rubber hand illusion, as said (Bertoni et al., 2023; Chancel & Ehrsson, 2023; Chancel et al., 2022a; Chancel et al., 2022b; Kilteni et al., 2015; Samad et al., 2015). A causal inference model of body ownership has also recently been proposed to explain full-body ownership in a variant of the current full-body illusion paradigm based on correlated visual, tactile, and vestibular information (Preuss Mattsson et al., 2022); however, without addressing the relationship between part and full-body ownership. Building upon this previous theoretical and empirical work, we here aimed to extend the Bayesian causal inference framework of body ownership to explain the dynamic interplay between body part (local processes) and full-body ownership (global process). Thus, we outline a theoretical hierarchical model that specifies the processing relationships between parts and whole (Fig. 13).

Let us start by first considering how likely it is for each of the mannequin's body parts to belong to the participant's own body: initially, and before any dynamic visuotactile stimulation, due to the degree of visual resemblance (degree of humanoid shape), the degree of spatial incongruence between the location and posture of the mannequin's body parts and limbs (in view) and the participant's real limbs and body parts (out of view) set an a priori probability for a common cause for visual, tactile and proprioceptive signals for each body part. As we will describe below, these priors are also influenced by contextual information related to the sense of full-body ownership. When receiving the visuotactile stimulation, a posterior probability of a common cause is inferred according to the Bayesian causal inference framework, which takes into account the sensory signals' temporal correlation, the degree of temporal asynchrony, relative uncertainty (for formal description, see Chancel et al., 2022a). Hence, synchronous visuotactile stimulation will lead to a high posterior probability of a common cause of visual and tactile information at the local level. This means that these signals will be combined, and body-part ownership will be experienced for the body part in question. In contrast, asynchronous visuo-tactile stimulation will lead to a low posterior probability of a common cause for vision and touch (Fig. 14, lower left box) and, therefore, weak, or abolished body part ownership perception. These local body ownership experiences can be represented as distributions in response to visuotactile stimulation (dashed curves in Fig. 15). The degree of the spatial incongruence of visual and proprioceptive information also contributes to body part ownership through a parallel causal inference process that gives a posterior probability of visuoproprioceptive combination and a resulting visuoproprioceptive estimate (Fig. 14, right lower box) (see Samad et al., 2015). The visuotactile and visuoproprioceptive estimates are combined (linearly averaged or through reliability-weighed combination; Chancel & Ehrsson, 2023; Samad et al., 2015) to obtain a single body ownership estimate that captures the probability of the body part as one's own (corresponding to the strength of the subjective body-part ownership illusion). In the current model, such local Bayesian causal inference processes thus give us a local body ownership distribution for each of the stimulated and non-stimulated body parts (Fig. 13–14). Note that in the current study, we did not manipulate the degree of visuoproprioceptive incongruence; thus, for the stimulated body parts, the information linked to the visuotactile stimulation predominantly determines the body ownership distributions.

Critically, these local body part ownership distributions are then combined into a global full body ownership distribution that specifies the probability of the mannequin's body as a complete whole to be one's own (Fig. 15). The participants' subjective reports of full-body ownership experience are extracted from this a posteriori full-body ownership distribution (Fig. 15). We posit that a higher rating of illusion strength corresponds to a higher probability of experiencing the illusion (human experiment in Fang et al., 2019; Samad et al., 2015). Critically, we propose that in this combination of the local estimates into a global estimate, the local estimates are weighted according to their relative reliability (Preuss Mattsson et al., 2022), rather than being averaged (linear averaging). This reliability-weighed optimal

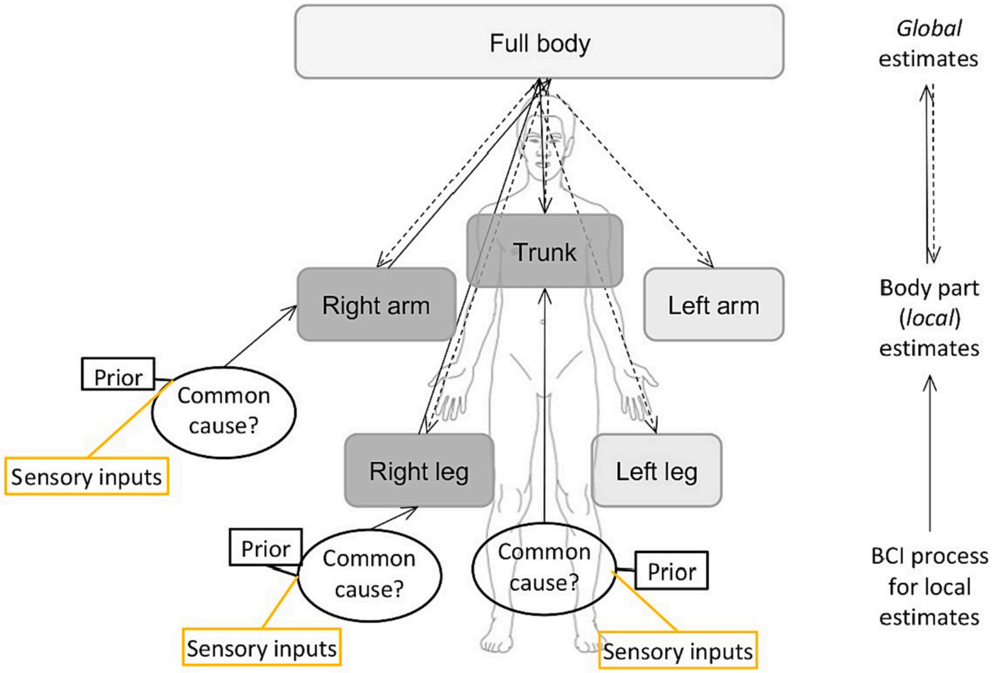

Fig. 13. A hierarchical Bayesian model for body part and full-body ownership. Sensory inputs delivered to the different body parts and a priori probabilities (prior) for the body parts to belong to the participant are integrated according to the Bayesian causal inference (BCI) principle (common cause; only shown for stimulated parts in this figure; see Fig. 14 for details). The output of this process is an a posteriori body part ownership distribution for each body part, which reflects the sense of body part ownership. These local distributions are merged into a full-body ownership distribution (black arrows and lines) according to optimal integration principles (i.e., the local estimates are averaged and weighted according to the inverse of their relative uncertainty), which leads to the full-body ownership percept. The global full-body distribution, in turn, influences the local distributions in a feedback loop (dashed arrows and lines), influencing the prior probability of body part ownership.

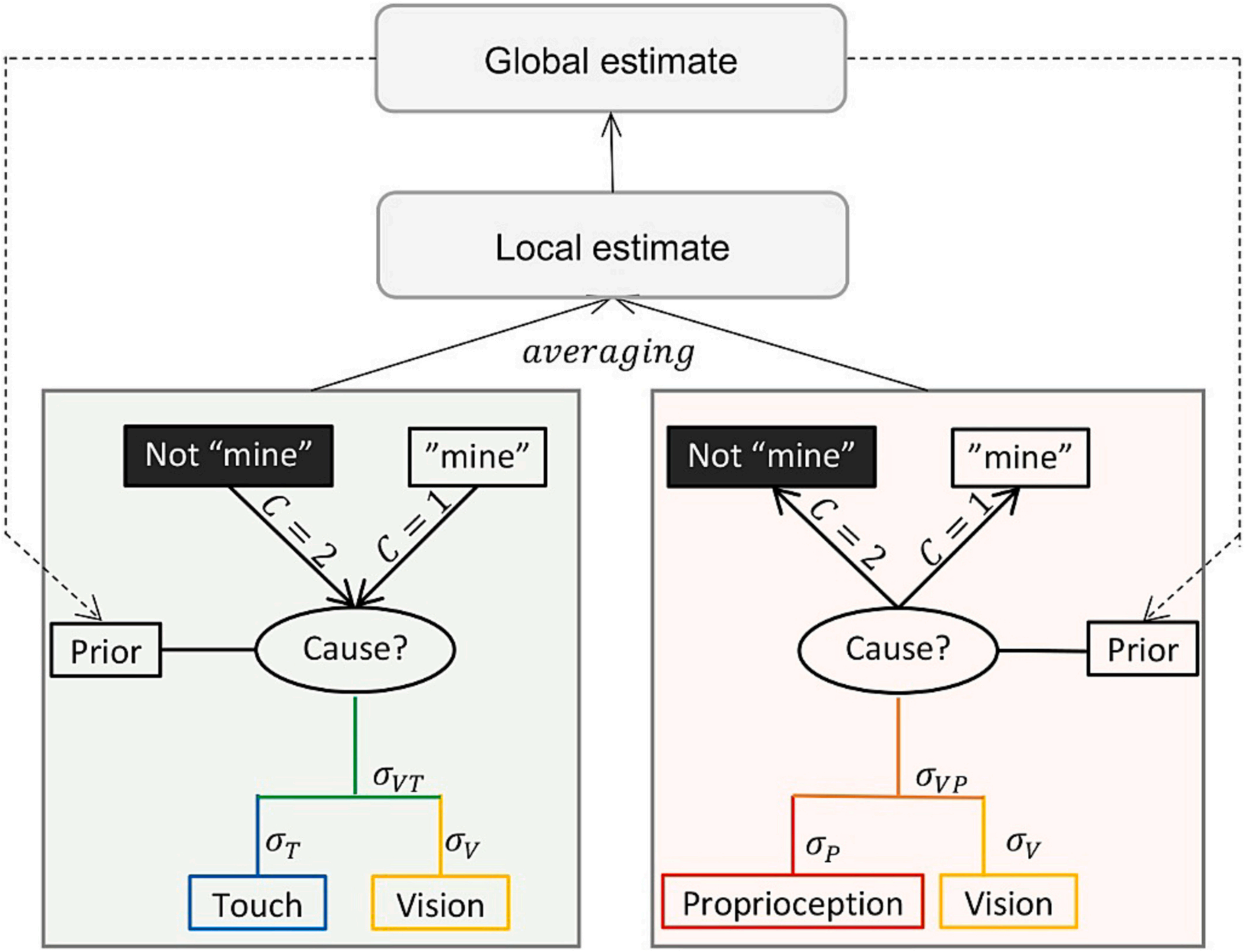

Fig. 14. Contribution of visual, tactile, and proprioceptive signals to a local body part ownership distribution and global full-body ownership distribution. The most likely causal structure (common cause C = 1 or different causes C = 2) for the visual and tactile signals (left box), as well as for the visual and proprioceptive signals (right box) is inferred from the priors, the sensory signals, and the corresponding sensory uncertainty (σ_{VT}, σ_{VP}, resulting from the combination of unisensory noise $\sigma_{V,}$ $\sigma_{T,}$ *and* σ_P). The resulting a posteriori distributions (from which the local estimate is sampled) can account for both temporal and spatial aspects and influence each other via a modulation of their respective priors. From this Bayesian causal inference process, the participant will perceive the stimulated body part as theirs or not, depending on whether a common cause is inferred or not; and the higher the posterior probability of a common cause, the higher the participants will rate the body-part ownership illusion. Such computational principles fit with previous findings of studies based on the rubber hand illusion (Chancel et al., 2022a, Samad et al., 2015). The local body part ownership distributions are then merged into a global full-body ownership distribution as described in detail in Fig. 15. Additionally, we propose that the full body ownership distribution (from which the global estimate is sampled) also influences the local (body part) distributions via modulation of the priors in the local causal inference process.

combination (multiplying the local distributions) ensures a non-linear relationship between the number of synchronously stimulated body parts and full-body ownership (confirmed in simulations) that matches our questionnaire results (see above) and encapsulates the concept of probabilistic inference. Consequently, the perception of full-body ownership is reflective of the integrated probability of the entire body being one's own, a probability that is derived from the individual probabilities of each body part being experienced as one's own.

In turn, the a posteriori full-body ownership distribution influences the causal inference processes for body parts at the local level through a "feedback" mechanism that affects the prior probability of a common cause for visuotactile and visuoproprioceptive combination (as shown in Fig. 14). Thus, the state of full-body ownership influences the causal inference processes related to body part ownership; if you feel the entire body as your own, you are more likely to experience the individual parts as your own as well (Figs. 13–14). This "feedback" influence would explain the "spread of ownership" effect that was described in the previous literature (see introduction), i.e., the increase in sensed ownership for non-stimulated limbs when the full body ownership is at the highest, despite these body parts not receiving any dynamic visuo-tactile stimulation. The mechanism would be a change in the prior probability of a common cause for the visual and proprioceptive information, thereby slightly enhancing the body part ownership reports (Chancel & Ehrsson, 2023). The fact that such modulation is not seen for synchronously stimulated body parts reflects, according to the model, that the a posteriori body part ownership distribution in these cases is determined predominately by information from the visual and tactile sensory signals (and, therefore, the effect of full-body ownership modulating the priors has little effect on the body part ownership estimate). Collectively, this probabilistic and hierarchical conceptualisation of body part ownership and full-body ownership based on the Bayesian theory of multisensory perception captures our key idea that full-body ownership is more than the sum of ownership of the parts and can explain our key questionnaire findings

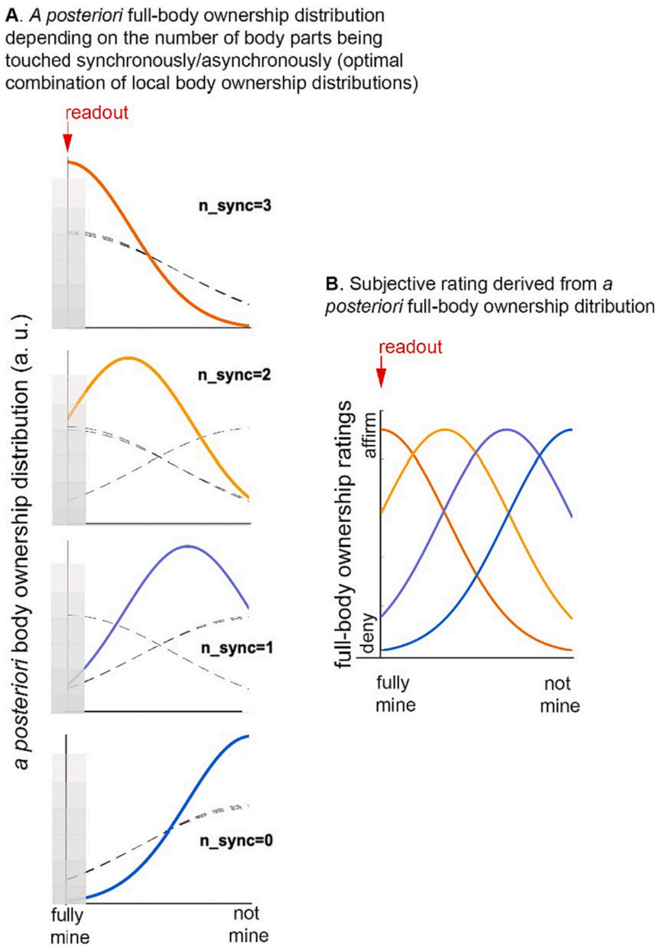

Fig. 15. Theoretical model for full-body ownership based on the combination of body-part ownership distributions into a full-body ownership distribution. The visuotactile stimulation of each body part leads to body part ownership distribution (dashed gray curves in panel A, three curves for the three stimulated body parts) that are combined in an optimal manner (maximum likelihood estimation principle, see, for example, Ernst and Banks 2002) to extract the a posteriori full-body distribution (distribution representing how likely the body is to belong to the participant, colored curves in panel A & B). The four plots to the left show local body part ownership distributions and the associated full-body ownership distributions for four conditions when the number of synchronously stimulated body parts is systematically varied from three to zero (n_sync = 3 to n_sync = 0). The subjective full-body ownership experience rated by the participants (Likert scale from +3 to −3) is derived from this underlying full-body ownership distribution (readout illustrated by the gray-zones overlayed with the y-axis and in panel B). The higher the posterior probability for full-body ownership, the more likely it is that participants affirm experiencing the illusion and reporting a high illusion rating (+1 to +3). This figure presents the simulated results of such optimal combinations of the local distributions (dashed curves, custom script running on Matlab) for different conditions when 3 (orange), 2 (yellow), 1 (purple), or 0 (blue) body parts receive a synchronous visuotactile stimulation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(see above). Although our model is mainly conceptual and not a complete formal model, we think it serves as a good starting point for future computational studies on full-body ownership.

13. General discussion

Previous studies suggest that congruent multisensory signals drive the illusory ownership of both body parts and the whole body, but without an experimental paradigm capable of manipulating illusory full-body ownership independently of body part ownership and vice versa, it has been difficult to investigate how full-body ownership sensations and body part ownership sensations are related to one another. To address this issue, we developed a variant of a full-body illusion paradigm based on using a set of HMDs to view a mannequin's body from the 1PP while the mannequin received either synchronous or asynchronous visuotactile stimulation to three different body parts concurrently while recording subjective reports of body part ownership and full-body ownership (Experiments 1 and 2) as well as threat-evoked SCR as an indirect physiological index (Experiment 3). Our analyses of the data collected through these subjective reports suggest that body part ownership and full-body ownership are supported by different multisensory processes – local versus global – which can be experimentally dissociated. Moreover, a dynamic and nonlinear relationship was observed between body part ownership and full-body ownership, thus suggesting a hierarchical structure according to which full-body ownership (global process) is based on information drawn from body part ownership (local processes), and this global process, in turn, influences local processes. From a broader perspective, the current findings advance our theoretical understanding of how parts and whole are related in the multisensory experience of one's own body and inform us about the cognitive architecture and processing principles that determine how a unitary sense of owning a single body emerges from the multisensory experiences of its parts.

13.1. *Subjective full-body ownership*

Our study's findings not only extend but also enrich our understanding of full-body ownership, presenting several advancements over previous literature. Firstly, unlike prior work, which has emphasised the similarities between the rubber hand illusion and illusions involving ownership of a mannequin or virtual body in terms of multisensory processing and perceptual constraints (temporal, spatial and object identity) (e.g., Maselli & Slater, 2013; Petkova & Ehrsson, 2008), the findings of the present research highlight differences in processing and the ways in which these two factors are functionally related. Specifically, we found that body part ownership and full-body ownership can be dissociated, which supports the hypothesis that different processes underlie these phenomena. This allows participants to experience illusory ownership of one part of the body in view without necessarily experiencing ownership of the body as a whole; conversely, they can also experience that the body at which they were looking felt like their own that but a single part of that body did not. Secondly, and crucially, the relationship between subjective full-body ownership and the number of body parts receiving synchronous (vs. asynchronous) visuotactile stimulation was nonlinear, with the sense of full-body ownership intensifying progressively as more body parts were synchronously stimulated and perceived as one's own. Once again, these findings cannot easily be explained simply by assuming that body part ownership and full-body ownership involve the same multisensory process. Instead, our findings fit better a hierarchical model according to which local multisensory processes determine body part ownership, and the outcomes of these processes are combined in a global process to determine full-body ownership. The emergence of a holistic full-body experience that cannot be derived solely from a linear summation of its component parts is in line with the conceptualisation of ownership of the entire body as a "full-body perceptual gestalt", in accordance with gestalt principles of perceptual organisation and the idea that the whole is something other than the sum of its parts (Gentile et al., 2015; O'Kane & Ehrsson, 2021; Wagemans et al., 2012). The nonlinear relationship between part and whole is also generally consistent with the previously expressed view that full-body ownership is phenomenologically "all-or-nothing" (Noel et al., 2019; O'Kane & Ehrsson, 2021; Swinkels, Veling, Dijksterhuis, & van Schie, 2021) but nevertheless serve to explain why this situation comes to be and reveal that the emergence of this complex perceptual experience is based on a graded nonlinear function rather than a binary perceptual switch (such as binocular rivalry). In situations with sufficient local sensory evidence favouring the multisensory combination of bodily signals from numerous individual body parts, rather than their segregation, this scenario guides a global multisensory decision process into leading the individual to perceive the entire fake body in view as their own, culminating in an illusory full-body ownership experience. These conclusions are relevant to theories in the field of cognitive neuroscience regarding full-body ownership, which have suggested that the key mechanism is multisensory integration across multiple bodily segments. This integration is thought to occur through neuronal populations with large visual and somatosensory receptive fields covering multiple bodily segments (Blanke et al., 2015; Ehrsson, 2020; Petkova et al., 2011a). Although our data are not inconsistent with such theories, they cannot fully account for the nonlinear relationship between part and whole that we observed in the current experiments. Previous investigations into bodily mereology in the fields of philosophy and cognitive science have focused on how a whole can be subdivided into parts (Bermúdez, 2011, 2017, 2018; de Vignemont et al., 2005, de Vignemont et al., 2009; Miller et al., 2022; Munro, 2021) and how body part ownership presupposes full-body ownership (Bermúdez, 2017). However, the current study poses different questions, exploring whether the experience of full-body ownership is something different from or more than the sum of its parts and how the ownership of body parts contributes to a sense of full-body ownership.

13.2. Subjective body part ownership

With regard to synchronously stimulated body parts, illusory body part ownership was found to occur relatively independently of illusory full-body ownership. This finding demonstrates that it is possible to isolate illusory body part ownership from illusory full-body ownership by using combinations of synchronous and asynchronous visuotactile stimulation on different parts in the full-body ownership illusion paradigm. As such, the observation that synchronous versus asynchronous visuotactile stimulation is an important factor in determining the illusory ownership of a single body part is consistent with the extensive literature on the rubber hand illusion (see the introduction) and similar "real hand disownership paradigms" using mixed-reality technology (Gentile et al., 2013; Newport & Gilpin, 2011; Reader & Ehrsson, 2019; Roel Lesur, Weijs, Simon, Kannape, & Lenggenhager, 2020); however, the current paradigm extends this principle to the case when the body part in question is part of an entire body in view under varying degrees of full-body ownership. Thus, the results of the current research provide more direct evidence to support the claim that subjective body part ownership is determined primarily by local multisensory integration processes operating on the part in question rather than a more general multisensory process that encompasses the parts and whole alike.

The finding that the people in our experiments could experience ownership of a single body part without experiencing full-body ownership of the rest of the body in view (e.g., $S_{RA}A_TA_{RL}$) may seem to be counterintuitive and in direct contradiction with mereological principles that define parts as subdivisions of a whole. However, the current study views the relationships between parts and the whole from the perspectives of bodily perception, gestalt principles of perception, and multisensory integration. According to gestalt principles, one can experience parts without perceiving the whole, and the whole can emerge as a global pattern from the parts. In multisensory perception, one can experience unisensory events in isolation from the more complex multisensory perceptions to which the same unisensory cues can sometimes give rise when paired with certain other sensory cues. Thus, from these perspectives, it makes sense that one can experience vivid ownership of a single body part even when the experience of full-body ownership is weak. However, it should be noted that, to our knowledge, no neurological cases have been described that correspond to an experience of the ownership of a single body part while disowning the rest of the body. Although ownership of a single body part without full-body ownership is a very unusual experience, perhaps only producible in the laboratory under certain experimental conditions, it is a highly significant observation. This is because it underscores the notion that the processes governing body part and full-body ownership are separate. It also reinforces that the relationship between parts and the whole in bodily awareness is best understood within a hierarchical model. Understanding this separation and hierarchy can stimulate research on possible similar dissociations in neurological and neuropsychiatric conditions.

Importantly, in addition to illusory body part and whole-body dissociation, our experimental paradigms also revealed interactions between body part and full-body ownership, indicating that body part ownership is influenced by the context of full-body ownership experience. First, for nonstimulated body parts, an influence of full-body ownership was observed, such that as full-body ownership ratings increased, the nonstimulated left leg and left arm exhibited a similar pattern of increasing body part ownership ratings (albeit from low absolute scores). This observation deepens the understanding of the mechanism whereby full-body ownership modulates body part ownership provided in the extant literature (Gentile et al., 2015; O'Kane & Ehrsson, 2021; Petkova et al., 2011a). Instead of an effect that can be explained solely in terms of the influence of the stimulated body part on the nonstimulated body parts or an ambiguous concept such as "the spread of ownership" that does not distinguish between the effects of body part and full-body ownership, the findings of the current research suggest that full-body ownership enhances the ownership experience for nonstimulated body parts. This enhancement, as we interpret it, reflects a contextual top-down influence of full-body ownership on body part ownership. This is particularly notable for the nonstimulated parts, contrasting with the stimulated body parts where ownership is predominantly governed by the bottom-up effect of local visuotactile synchrony.

13.3. A Hierarchical Probabilistic Model of Subjective Body Part and Full-Body Ownership

To relate the results of the current research to leading probabilistic models of multisensory perception (Körding et al., 2007; Sato et al., 2007) and body ownership (Bertoni et al., 2023; Chancel, Ehrsson et al., 2022; Chancel & Ehrsson, 2023; human experiment in Fang et al., 2019; Kilteni et al., 2015; Samad et al., 2015) and obtain an understanding of the possible computational mechanisms involved, we developed a hierarchical Bayesian model (see Figs. 13–15). This model includes a lower level at which local processes determine body part ownership and a higher level at which a global process determines full-body ownership based on a combination of inputs from the lower level. In this model, body part ownership is determined by local casual inference processes that operate independently for each body part. These processes infer a common cause of the visual, tactile and proprioceptive sensory signals, taking into account the temporal and spatial congruence of the sensory signals, the relative reliability of these signals and prior probabilities of a common cause based on information obtained from previous experience and contextual information (Chancel et al. 2022a; Chancel et al., 2022b; Kilteni et al., 2015; Samad et al., 2015). Critically, the probability distributions resulting from the local causal inference processes are combined to obtain a global full-body distribution that specifies the likelihood that the entire body is one's own. The participant's report of experiencing a subjective sense of full-body ownership is extracted from this a posteriori full-body ownership distribution. This model captures the principles of probabilistic perceptual inference in a hierarchical processing structure and can explain the nonlinearity observed in full-body ownership ratings when one, two, or three body parts are stimulated synchronously as opposed to asynchronously (see Fig. 15). Our model also explains how full-body ownership influences body part ownership, which corresponds to a feedback mechanism according to which the global full-body ownership estimate influences the local causal inference processes by changing the prior probability of a common cause, i.e., by increasing the prior probabilities that the body parts are one's own. This impact boosts the visuoproprioceptive combination of sensory signals from the nonstimulated body parts and thereby slightly enhances body part ownership (Chancel & Ehrsson, 2023). The strength of the current Bayesian model lies in the fact that it outlines a computational explanation for how sensory information and prior knowledge are processed in a hierarchical structure featuring dynamic interactions, thus giving rise to both body part ownership and full-body ownership.

This hierarchical and probabilistic conceptualisation of part and whole in the context of body ownership may provide a new perspective for analysing neurological cases of disturbances in body ownership. If full-body ownership is based on a global probabilistic process that is computed based on a combination of multiple inputs from local probabilistic processes, then it is logical to assume that if a single local process is temporarily or permanently impaired due to structural brain damage of physiological dysfunction, the global process that infers full-body ownership may be relatively unaffected, in line with the neurological literature on asomatognosia and somatoparaphrenia (Feinberg & Venneri, 2014; Vallar & Ronchi, 2009). However, if several of these local processes become impaired, then it should be more likely for a person to experience disturbances in the ownership experience over their entire body, although disturbances in full-body ownership selectively have rarely been reported in the neurological and psychiatric literature (Brugger, 2006; Heydrich, Dieguez, Grunwald, Seeck, & Blanke, 2010; Hunter et al., 2003; Smit, Van Stralen, Van den Munckhof, Snijders, & Dijkerman, 2019). In contrast, disturbances in the sense of limb ownership may be regarded as fairly common poststroke, particularly during the acute phase, with a prevalence of 61% (Ocklenburg & Güntürkün, 2018). Speculatively, the global full-body ownership process is more robust than the local processes that determine single-limb ownership due to its reliance on estimates resulting from multiple body parts (i.e., more redundancy in terms of sensory information processing). However, if the global process becomes impaired, it should precipitate disturbances in the sense of full-body ownership; speculatively, these disturbances could include those described in cases of a more psychiatric origin, including depersonalisation-derealisation disorder (Heydrich et al., 2010; Hunter et al., 2003; Sierra & Berrios, 1998), posttraumatic stress disorder (Ataria, 2016) and schizophrenia (Kean, 2009; Klaver and Dijkerman, 2016; Szczotka & Majchrowicz, 2018).

13.4. *Psychophysiological emotional defence reactions*

The SCR results showed that when a visual physical threat was presented to the mannequin's right arm, a significant increase in SCR was observed in cases featuring illusory ownership of the artificial arm as well as illusory ownership of the whole body to which the arm is visibly connected. This finding suggests that at the physiological level, bodily emotional defence reactions depend on both body part and full-body ownership, thus offering another example of the interaction between local and global processes. Increases in threat-evoked SCR responses during body-ownership illusions are believed to reflect the emotional embodiment of the fake limb or body, whereby the brain's emotional system (including the insular cortex and anterior cingulate cortex) starts to monitor the physiological "well-being" of the rubber limb and to react to potential physical threats directed towards that fake limb (Ehrsson et al., 2007; Gentile et al., 2013; Guterstam et al., 2015). Although threat-evoked SCR has often been used as an objective physiological measure of body ownership illusions (Ehrsson, 2012, 2020), the mechanisms whereby information related to multisensory awareness is translated into changes in emotional threat monitoring are unclear. The results of the present research suggest that both body part ownership and full-body ownership contribute to emotional embodiment at the level of changes in autonomic system arousal and highlight the combined effect of these two processes with regard to driving threat-evoked SCR responses. One interpretation of this finding is that ownership of a limb that is not perceived to be part of one's own whole body does not indicate an object that requires protection and emotional defence since it is "detached" from the rest of the bodily self. The same claim applies to a "disowned limb" that is only visually attached to one's own body but does not somatically feel like one's own in terms of subjective body part ownership. Only a limb that both feels like one's own and is experienced as connected to one's own whole body leads to the significant engagement of autonomic emotional defence reactions. This finding makes sense, we think, as emotional and motoric defensive reactions typically involve multiple body parts or the whole body (Bastos et al., 2016). This finding is in line with de Vignemont's (2017) bodyguard hypothesis, which suggests that the sense of body ownership serves to promote our survival and safety. Therefore, when an illusorily owned body part within the whole is under threat, affective representations pertaining to multiple body parts and the whole are activated to facilitate appropriate emotional and potential defensive motor actions.

While somewhat speculative, some intriguing yet tentative connections between the current SCR findings and the clinical neuroscience literature are worth mentioning. For individuals with somatoparaphrenia who experience arm disownership, when a noxious stimulus is presented to the affected limb, typically a left arm, threat-evoked SCRs have been found to exhibit significant reductions in magnitude compared to the SCRs produced when the same stimulus is presented to the ipsilesional (nonaffected) limb (Romano, Gandola, Bottini, & Maravita, 2014). Similarly, in cases of body integrity dysphoria or xenomelia, a neuropsychiatric condition that is associated with feelings of disownership for one of the individual's own real body parts (Romano et al., 2015), SCRs have been reported to exhibit significant reductions when a threatening object approaches the affected limb (Romano et al., 2015). Although traditionally, these findings are interpreted as reduced ownership of the affected limb; our findings suggest another possibility: impairments in integrating part- and full-body ownership may also contribute to altered threat-evoked SCR responses in these neurological and neuropsychiatric groups. Moreover, Dewe, Watson, Kessler, and Braithwaite (2018) showed that SCRs evoked by threats targeting healthy individuals' arms were modulated by trait depersonalisation, which is related to changes in various aspects of bodily awareness, including its coherence. Thus, we tentatively propose a potential link between threat-evoked SCR and a coherent and integrated sense of body part ownership and full-body ownership, warranting further consideration in cognitive neurology and neuropsychiatric research.

13.5. *Limitations*

The current study has certain limitations that are worth discussing. First, our main conclusions are based on results obtained by analysing subjective questionnaire ratings. Questionnaire ratings capture participants' conscious subjective experiences and have often been used in bodily illusion research (e.g., Longo et al., 2008) and psychological science more broadly. However, subjective reports of perceptual phenomena can be influenced by postperceptual cognitive factors and by individual differences in cognitive processing (Costantini et al., 2016; Eshkevari, Rieger, Longo, Haggard, & Treasure, 2012; Marotta et al., 2016; Slater & Ehrsson, 2022). For example, individuals who score high on trait suggestibility tend to provide higher affirmative ratings in response to illusion-related questionnaire statements and control statements in both synchronous and asynchronous conditions in rubber hand illusion studies (Lush et al., 2020; Marotta et al., 2016; Slater & Ehrsson, 2022). However, the main findings of the current study cannot be explained by trait suggestibility because we used a within-subject design and focused our analyses on changes in illusion ratings between conditions within individuals, whereas importantly, trait suggestibility does not correlate with such condition-specific differences in illusion ratings (Ehrsson et al., 2022; Lush et al., 2020; Slater & Ehrsson, 2022) Second, it is important to note that the current study was not designed to test the hierarchical Bayesian model that we developed; such an investigation requires future experiments that can test the model's predictions against large behavioural datasets collected from individual participants to allow for proper model fitting and model comparison at the individual level (Chancel et al., 2022a). Third, the questionnaire results and the SCR did not indicate the same relationship between part and whole; threat-evoked SCR was significantly enhanced only in the fully synchronous condition when both body part ownership and full-body ownership were present. However, based on the previous literature, it is unclear how well the threat-evoked SCR captures smaller changes in the degree of subjectively experienced full-body illusions (O'Kane & Ehrsson, 2021; Preuss Mattsson et al., 2022); thus, the current SCR data could not be used to assess the finding drawn from the questionnaire concerning a graded nonlinear relationship between body part and full-body ownership. A related point is that the finding concerning body part ownership without full-body ownership was supported only by the results of the questionnaire; thus, future studies should re-examine this finding based on objective measures, including functional neuroimaging. Fourth, in this study, we stimulated only three body parts. Therefore, our conclusion that full-body ownership is determined by relative evidence should be further tested in future experiments based on varying numbers of stimulated parts. If more body parts are stimulated than in the current study (for example, five), then more body parts should also need to be stimulated synchronously (probably at least three if five are being tested) to elicit a vivid full-body ownership illusion. Fifth, our study focused on visuotactile integration; thus, future studies are needed to examine whether the current findings also hold true in the context of other types of full-body illusion paradigms that involve the manipulation of sensory information in different modalities, for example, when body part ownership and full-body ownership are induced by correlated limb movement and visual feedback (Kalckert & Ehrsson, 2012; Maselli & Slater, 2013; Slater, 2009).

14. Conclusions

The present study investigated the relationship between part- and full-body ownership within a mannequin-based bodily illusion paradigm. We found that under different combinations of synchronous and asynchronous visuotactile stimulation applied to different combinations of body parts, participants experienced illusory full-body ownership in the absence of body part ownership, body part ownership in the absence of full-body ownership, as well as either both or neither illusory percept. These observations suggest that the processes driving body part ownership and full-body ownership are distinct. Importantly, however, these processes are also interconnected because we found that the number of body parts that were experienced as one's own predicted the experience of full-body ownership, and crucially so, in a nonlinear manner. This finding suggests a hierarchical and dynamic relationship between ownership perception of individual body parts and the whole body, where body part ownership involves local processes that inform a global process corresponding to full-body ownership. Collectively, our findings align well with a hierarchical Bayesian model, where part- and full-body ownership are seen as different levels of probabilistic inferential processes. These insights may have significant implications for future research in behavioural neuroscience, neuroimaging, neuropsychological, and cognitive psychiatric research, particularly in understanding how the brain integrates perceptions of body parts into a unified bodily self, both in health and disease.

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CRediT authorship contribution statement

Sophie H. O'Kane: Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Marie Chancel:** Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review & editing. **H. Henrik Ehrsson:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare no competing interests.

Data availability

Link available to data in OSF: https://osf.io/nxpvy/?view_only=e70f00a9354d4331b7c9e58bf0ddc235

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Appendix A. Supplementary data

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