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The role of agency for perceived ownership in the virtual hand illusion

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ABSTRACT

The rubber hand illusion shows that people can perceive artificial effectors as part of their own body under suitable conditions, and the virtual hand illusion shows the same for virtual effectors. In this study, we compared a virtual version of the rubber-hand setup with a virtual-hand setup, and manipulated the synchrony between stimulation or movement of a virtual "effector" and stimulation or movement of people's own hand, the similarity between virtual effector and people's own hand, and the degree of agency (the degree to which the virtual effector could be controlled by people's own movements). Synchrony-induced ownership illusion was strongly affected by agency but not similarity, which is inconsistent with top-down modulation approaches but consistent with bottom-up approaches to ownership. However, both agency and similarity induce a general bias towards perceiving an object as part of one's body, suggesting that ownership judgments integrate various sources of information.

1. Introduction

How do we come to experience ourselves as independent individuals? According to Jeannerod (2003), self-perception relies on two ingredients: experiencing oneself as the owner of one's body (ownership) and experiencing oneself as the agent of one's actions (authorship or agency). Recent research on body ownership has made use of the rubber hand illusion (RHI). In the classical RHI study design, a person's real hand is hidden from his or her view and a static rubber hand is being placed in front of his or her—often in close distance to the real hand. Then the real and the rubber hand are synchronously or asynchronously stroked or otherwise stimulated (e.g., Botvinick & Cohen, 1998; Ehrsson, Spence, & Passingham, 2004; Tsakiris, 2010; Tsakiris & Haggard, 2005). After receiving synchronous (but not asynchronous) stimulation for several minutes or even shorter time periods (Kalckert & Ehrsson, 2014; Tsakiris, Prabhu, & Haggard, 2006), participants start to feel the stimulation at the location of the rubber hand, rather than on their real hand, and report perceiving the rubber hand as their own hand (sense of ownership) and as more controllable (sense of agency) (Kalckert & Ehrsson, 2014). More recently, various researchers were able to replicate the RHI in virtual environments by replacing the rubber hand by a virtual hand—which often can be controlled by the participants by means of a data glove (the virtual hand illusion or VHI; see Ma & Hommel, 2013, 2015; Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008). The main question the present study aimed to address was whether the RHI and the VHI are the same. While this might be considered a rather methodological question, we think it relates to two major theoretical issues that are dominating research on

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body ownership: the relevance of bottom-up and top-down factors in creating ownership illusions, like the RHI and the VHI, and the relationship between ownership and agency.

1.1. Bottom-up and top-down factors

With regard to the first question, one can distinguish two general approaches, one assuming that bottom-up information (such as created by synchronous stroking) is sufficient to create the illusion of body ownership and another that assumes an interaction between bottom-up information and top-down-operating schemata representing body characteristics. Botvinick and Cohen (1998) and Armel and Ramachandran (2003) proposed versions of a bottom-up account, that assumes that the processing of spatially and temporally matching multisensory information, such as coming from the seen stroking of a rubber hand and the felt stroking of one's own hand, is sufficient to perceive an object as part of one's body. In support of that assumption, Armel and Ramachandran (2003) provided some preliminary evidence that participants can perceive ownership for a wooden table and feel nervous when they see the table being ''hurt''—even though the experimental design of this study was likely to invite transfer effects. Later research revealed a number of further constraints that seem to limit the impact of bottom-up information, such as the anatomical and postural properties of the artificial hand in relation to one's own hand (De Vignemont, 2011; Haans, IJsselsteijn, & de Kort, 2008; Lloyd, 2007; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2009; Makin, Holmes, & Ehrsson, 2008; Pavani & Zampini, 2007; Tsakiris, 2010; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005; Tsakiris, Schütz-Bosbach, & Gallagher, 2007).

These and other observations have been taken to imply contributions of a relatively permanent body representation that gates the processing of bottom-up information. For instance, Makin et al. (2008; Ehrsson et al., 2004; Maravita, Spence, & Driver, 2003) have suggested that ownership illusions can only be created if the rubber hand is placed in an anatomically and postural plausible (i.e., expected, given the current position of one's real hand) position, and if the synchronous stimulation is presented near to the artificial hand. Another, even more top-down-heavy model was proposed by Tsakiris (2010). He assumes that people possess a relatively permanent model of their own body, which contains information about both the structural aspects of the body in general and about the current states and effector positions. Bottom-up information will consistently be checked for a match with information from the body model and censored in the case of a mismatch (Costantini & Haggard, 2007; Haans et al., 2008; Lloyd, 2007; Tsakiris, 2010; Tsakiris & Haggard, 2005; Tsakiris et al., 2007, 2010). According to this approach, the resemblance between the visible artificial effector and the real hand/body part is a predominant factor for RHI illusions (Tsakiris et al., 2010): Artificial effectors are perceived as body parts only if they are sufficiently similar to the content of the internal body model, which in turn represents the person's actual body. However, in contrast to this prediction, the similarity between real and artificial effectors failed to play a decisive role in several studies. For example, using a rubber hand with a skin color or roughness different from the participant's real hand did not reduce the strength of the ownership illusion (Farmer, Tajadura-Jiménez, & Tsakiris, 2012; Longo et al., 2009; Schütz-Bosbach, Tausche, & Weiss, 2009; White, Davies, Halleen, & Davies, 2010) and even balloons and geometric objects (Ma & Hommel, 2015) or empty spaces (i.e., objects bearing no similarity to people's real effectors) can be incorporated by healthy participants (Guterstam, Gentile, & Ehrsson, 2013). These findings do not support the idea that artificial effectors are accepted as body parts only if they are sufficiently similar to components of internally stored body representations.

1.2. Ownership and agency

While earlier studies tended to consider body ownership and agency as separate components of the self (see Gallagher, 2000; Jeannerod, 2003; Tsakiris et al., 2007), there is increasing evidence that these two factors interact in producing ownership illusions (Burin et al., 2015; Dummer, Picot-Annand, Neal, & Moore, 2009; Kokkinara & Slater, 2014; Ma & Hommel, 2013, 2015; Tsakiris et al., 2006, 2007). However, the relationship between sense of ownership and sense of agency is still not clear: Some studies showed greater sense of illusory ownership with greater sense of agency, some studies showed the opposite relationship between the two senses, and some studies showed no correlation at all.

For example, Burin et al. (2015) found that patients with left upper limb hemiplegia display stronger illusory effects than healthy participants when the affected hand is stimulated but no effects when the unaffected hand is stimulated, and concluded that active movement plays a role for body ownership maintenance. Along the same lines, Kokkinara and Slater (2014) observed higher ownership for a virtual leg in active-movement than visuotactile-stimulation conditions. Caspar et al. (2014) also report a positive correlation between agency and ownership ratings. However, Walsh, Moseley, Taylor, and Gandevia (2011) showed that ratings for passive-stimulation conditions were higher than for active-movement conditions and Dummer et al. (2009) found more pronounced ownership illusions for visuotactile stimulation than for active and passive movement conditions. Lastly, Riemer, Kleinböhl, Hölzl, and Trojan (2013) report equally strong subjective ratings for active-movements and visuotactile-stimulated conditions and both Tsakiris et al. (2006) and Kalckert and Ehrsson (2012, 2014) found no difference in ownership ratings or proprioceptive drift between three conditions that differed in activity. To add to the confusion, Braun, Thorne, Hildebrandt, and Debener (2014) found some associations and some double-dissociations between sense of agency and sense of ownership.

What might be the reason for these confusing, seemingly inconsistent findings? We suggest that terminological confusion may be the main culprit. As discussed elsewhere (Hommel, in press), objective ownership and agency is often confused with the subjective experience of ownership and agency, commonly called the sense of ownership and the sense of agency, respectively (for an example, see Tsakiris et al., 2007). Whereas objective agency refers to the question whether a person was actually producing a particular action, subjective (perceived) agency is about whether this person is actually sensing, experiencing, or reporting to have some sort of authorship. Objective agency may or may not provide the critical information used for subjective agency: While most researchers investigating the sense of agency implicitly assume that it does (so that manipulations of objective agency are assumed to be reflected in subjective agency), some authors have argued that objective and subjective agency rely on different sources of information (e.g., Wegner, 2003). At the same time, objective agency is likely to provide crucial information for subjective ownership: when in doubt whether an object belongs to one's body the most obvious test would be to try moving it intentionally (e.g., when having perceptually "lost" one's hands under the table during intense discussion), and Tsakiris et al. (2006) have indeed considered the possibility that control over an effector determines both sense of agency and sense of ownership. Importantly, however, the previous investigations of the relationship between ownership and agency have not focused on the impact of objective agency on subjective ownership but, rather, on the relationship between subjective agency and subjective ownership.

Among other things, this overlooks the fact that objective agency (subjectively experienced or not) provides a means to create re-afferent multimodal stimulation, which according to bottom-up approaches to ownership should increase the informational basis to make ownership judgments. This suggests that the traditional RHI setup, in which the artificial effector is either completely static (Botvinick & Cohen, 1998) or moves with the real effector in rather limited ways (Dummer et al., 2009; Kalckert & Ehrsson, 2012, 2014; Tsakiris et al., 2006; Walsh et al., 2011), is a particularly conservative, ecologically invalid measure of the perception of ownership—which according to our considerations may be the main reason for the conflicting findings of earlier studies. In contrast, VHI setups, in which the virtual hand can be almost freely moved in sync with the real hand (Ma & Hommel, 2013, 2015; Padilla et al., 2010; Perez-Marcos, Sanchez-Vives, & Slater, 2012; Sanchez-Vives et al., 2010), and which sometimes even include simulated contact with other virtual objects, provide a much richer database. Indeed, continuously moving one's felt hand together with the seen virtual hand and having simulated contact with another object creates hundreds if not thousands of data points that can be correlated to calculate the degree of intermodal matching. Accordingly, it is not surprising that VHI studies provide much more evidence for correlations between measures of body ownership and measures of agency than RHI studies do (e.g., Kokkinara & Slater, 2014; Ma & Hommel, 2013, 2015; Padilla et al., 2010).

1.3. Aim of study

To get back to our original question, we consider RHI setups and VHI setups as basically addressing the same issue but as different with respect to their sensitivity to the influence of (objective) agency. RHI setups create highly artificial situations in which the agent is prevented from using active exploration to find out whether the artificial effector is part of her own body. This drastically restricts the available database for judging ownership, so that this setup can be considered to underestimate the contribution of bottom-up factors in the role of (objective) agency. In contrast, VHI setups permit the agent to actively explore and generate a rich database for ownership judgments. As this is particularly true for cases of objective agency, it makes sense to assume that subjective ownership and subjective agency correlate to the degree that objective agency translates into subjective agency—which again is more likely with VHI setups.

Motivated by these considerations, the present study directly compared a RHI-type setup (i.e., a VHI setup that sought to re-create the classical RHI setup as far as possible) with a VHI setup. With the RHI-type setup, participants passively received visuotactile stimulation, just like in the classical rubber-hand study, which is why we refer to this condition as the "passive condition". In addition to visual tactile stimulation, participants were allowed to actively operate the virtual hand by moving their own hand with the VHI setup, which is why we refer to this as the "active condition". Hence, the major difference between the two conditions was the presence or absence of efferent and re-afferent information about the participant's self-produced movement. Our first prediction was that the latter, which allowed active exploration, would lead to the stronger perception of ownership of the artificial effector than the former, which used passive stimulation. We tested this hypothesis by comparing synchronous stimulation/action conditions with asynchronous stimulation/action conditions. As common in rubber-hand studies, we considered the synchrony effect as an indication of (synchrony-induced) ownership and were interested to see whether our passive/active manipulation would modify this effect in the expected direction.

Our second question was whether the resemblance between the artificial and the real effector would matter. According to top-down approaches of ownership (Makin et al., 2008; Tsakiris, 2010), lesser resemblance should reduce, if not eliminate the illusion of ownership, because bottom-up information would only be accepted if it matches the internal body representation. In contrast to this prediction, in a recent study we obtained significant ownership effects for visual balloons changing in size, and squares changing in size or color, in sync with movements that the participants carried out with their real hand (Ma & Hommel, 2015). In the present study, we thus wanted to see whether these effects are replicable and whether they may interact with the passive/active manipulation.

We used a similar VHI setup as Ma and Hommel (2013, 2015). In a within-participants design, we manipulated (a) the resemblance between the real hand of the participants and a virtual object (henceforth "effector"), which was a virtual hand or a virtual rectangle; (b) the way the participants encountered another virtual object, which they did either passively, by keeping the real hand still and waiting for a virtual object to touch the virtual effector, or actively, by moving their real hand to move the virtual effector to touch the other virtual object; and (c) the synchrony between the movements of the virtual effector and either the stimulation (in the passive condition) or the active movement (in the active condition) of the real hand. We assessed the subjective experience of ownership for the virtual effector in the different conditions by means of an adjusted Botvinick/Cohen-style questionnaire, and for explorative purposes we also included measures of proprioceptive drift and skin conductance responses (SCR). The proprioceptive drift represents the recalibration of proprioceptive information of the real hand towards the visually viewed candidate effector. While various RHI studies have used proprioceptive drift rates as an objective equivalent to the perception of ownership (e.g., Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2014; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Makin et al., 2008; Tsakiris & Haggard, 2005; Tsakiris et al., 2010), the two measures often diverge, which renders their conceptual relationship opaque. Irrespective of this relationship, there is evidence that the drift rates relate to visuo-proprioceptive mismatch between the seen and felt position of the hand (Holmes, Snijders, & Spence, 2006; Rohde, Di Luca, & Ernst, 2011). The SCR measure represents the affective arousal that is elicited by threatening virtual effectors that are perceived as part of one's own body—a measure that sometimes parallels the perception of ownership (Armel & Ramachandran, 2003; Guterstam et al., 2013) and sometimes diverges from it (Ma & Hommel, 2013).

2. Experiment

The experiment adopted the basic VHI setup of Ma and Hommel (2013, 2015: Exp. 2). Participants were facing a horizontally oriented screen on top of a black box, in which they put their real hands (see Fig. 1). In each condition, one of two virtual "effectors" appeared on the screen: either a virtual hand that looked like a human hand or a virtual green[1] rectangle. In the active conditions, the participant could control the movement and orientation of the virtual hand, or the movement, orientation, and size of the virtual rectangle, by moving their right unseen hand by means of a data glove. In the passive conditions, participants did not control characteristics of the virtual effector but were presented with multimodal stimulation, similar to the classical rubber-hand manipulation. A virtual stick (i.e., a virtual object that would interact with the virtual effector) was shown on the screen. It sometimes contacted the virtual effector, which would trigger a vibration of the vibration stimulator on the data glove—so to give participants the impression of real contact. The movements of the real hand (in the active conditions) or the visual contact between the virtual effector and the virtual stick (in both active and passive conditions) were either directly translated into the orientation or size changes of the virtual effector (in the active conditions) or the vibrotactile stimulation (in the active and passive conditions), respectively (the synchronous conditions); or with a considerable temporal delay (the asynchronous conditions). To induce ownership-related affective responses in the SCR, we designed a threat phase, in which participants were shown a virtual knife that would cut the virtual effector (see Ma & Hommel, 2013, 2015).

2.1. Method

2.1.1. Participants

Forty-four participants (10 males; mean age = 24 years, SD = 2.93, range 20–34) were recruited from Leiden University in exchange for course credit or pay. We used the department's standard advertisement system and accepted all volunteers registering in the first wave. Informed consent was obtained from all participants before the experiment, which was approved by the Leiden University Human research ethics committee. Participants were naive with respect to the RHI/VHI.

2.1.2. Design

Participants underwent 8 conditions, presented in counterbalanced order, which emerged from crossing three factors: (1) the virtual effector (a virtual hand, which resembled the participants own real hand, vs. a virtual rectangle that did not); (2) the kind of stimulation/control (active vs. passive); and (3) the degree of synchrony between real hand movements and movements of the virtual effector or between or visual impact on the virtual effector and vibrotactile stimulation (synchronous vs. asynchronous).

2.1.3. Experimental setup

The study was performed in a virtual reality environment (see Ma & Hommel, 2013). The setup consisted of a 3-DOF orientation tracker (InterSense), a data glove (Cyberglove, measurement frequency = 100 Hz, latency = 10 ms), a black box (50 × 24 cm × 38 cm) which the participant put his or her right hand into along the depth axis, so to shield it from view, a cloth placed over the participant's right shoulder to cover the space between the virtual effector and the participant, and virtual reality software (Vizard). The Cyberglove has six vibration stimulators attached, one on each finger and one on the palm; they are programmable to set the vibration time and strength (Vibrational frequency = 0–125 Hz). We designed a virtual hand and a virtual rectangle and imported the two effectors, the tracker and data glove module into Vizard, so the virtual hand or rectangle received the data from the tracker and data glove and was controlled by the participant's hand movement (see Fig. 1).

2.1.4. Procedure

Participants were seated in front of the black box with a computer monitor on its top. They wore the glove on their right hand and the orientation tracker on their right wrist, put their hands inside the box, and looked down on the monitor. The

[1] For interpretation of color in Fig. 1, the reader is referred to the web version of this article.

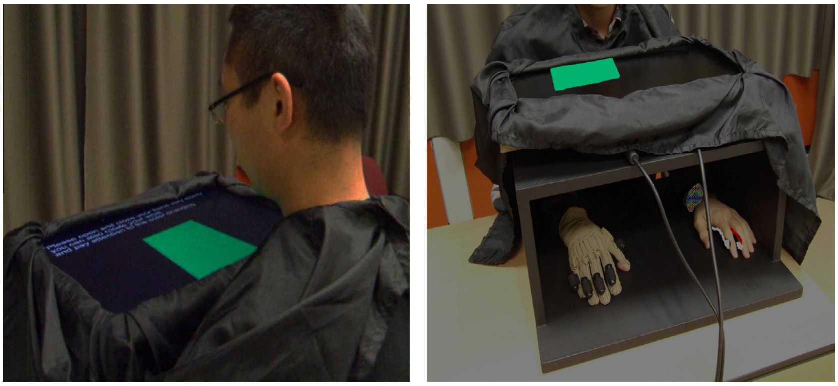

Fig. 1. Experimental setup. Participants wore an orientation tracker and a data glove on their right hand, and SCR remote transmitter on their left hand, the cloth served to cover the area between screen and participants.

computer program generated a virtual effector on the screen and the trial started. Each participant ran through all eight conditions following a sequence that was balanced across participants. The conditions were nested in such a way that: (a) the first four conditions used one virtual effector and the last four conditions the other; (b) the first two conditions within each effector block were all active or all passive, while the last two conditions would be passive or active, respectively; (c) and synchrony would alternate from each condition to the next. Each condition would consist of a pre-measure of proprioceptive hand location (explained below), the actual induction of the illusion for about 90 s, a post-measure of proprioceptive hand location, the presentation of the questionnaire and, after a short break, the threat phase. This threat phase repeated the previous illusion-induction procedure for another 90 s, after which a virtual knife would cut the virtual effector. SCR was measured during the entire threat phase.

During the illusion-induction phase of the synchronous/passive conditions, participants were unable to move the virtual effector and were asked to keep their real hand still while watching the virtual effector. Then a virtual blue stick appeared on the screen and took two seconds to move to contact the viewed effector, which was associated with the onset of the finger vibration stimulator of the glove, and then took another two seconds to return to its original position. This procedure was repeated until 90 s were over. The respective asynchronous conditions were the same except that the felt vibration was delayed by two seconds.

In the illusion-induction phase of synchronous/active conditions, participants were asked to move their fingers and rotate their real hands freely and watch the movement/size changes and orientation changes of the virtual effectors for 90 s, during which the orientation and posture of the virtual hand, or the orientation and size of the virtual rectangle, changed in synchrony with the participant's own hand movements (i.e., the orientation and the opening and closing of the participant's real hand). A virtual blue stick appeared on the screen and participants were asked to freely move their real hands to control the virtual effector so to touch the virtual stick repeatedly with their fingers; and each contact with the stick would lead to a felt vibration on the fingers. The asynchronous conditions were the same except that the seen movements of the virtual effector corresponding to the real hand movement were delayed by five seconds, and the felt vibration did not coincide with the finger's contact with the stick but with a stick position away from the hand.

For the proprioceptive drift measurement, the position of the virtual effector, the real positions, and the felt proprioceptive position of the real hidden hand were measured before and after the first illusion-induction phase of each condition. Participants were exposed to a horizontal array of letters on the screen and were asked to indicate which letter would correspond to the felt position of the real hidden hand middle fingertip; the experimenter also recorded the positions of both the virtual hand's middle fingertip (or the virtual rectangle's midline) and the real hand's middle fingertip with reference to the same array. The sequences of the shown letters were randomly determined and different for each condition, so to avoid response strategies based on the recall of the previous response.

In the threat phase, participants were asked to keep their hand still, so that the virtual effector would not move. A virtual knife appeared on the screen, took four seconds to approach and cut the virtual effector, the cut position was approximately on fingers of the virtual hand or the front part of the virtual rectangle, which was associated with the onset of the finger vibration stimulator of the glove, and then took another four seconds to return to its original position. This procedure was repeated for several times and it was the same for all conditions.

2.1.5. Questionnaire

To assess the extent to which participants experienced the VHI we used an adapted version of the standard RHI questionnaire (Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2014; Kammers et al., 2009; Slater et al., 2008). For each statement, participants responded by choosing a score in a 7-point (1–7) Likert scale, ranging from 1 for 'strongly disagree' to 7 for 'strongly agree'. The statements for virtual hand conditions were:

Q1. I felt as if the hand on the screen were my right hand or part of my body.
Q2. It seemed as if what I were feeling on my right hand was caused by the touch of the blue stick on the hand on the screen that I was seeing.
Q3. I had the sensation that the vibration I felt on my right hand was on the same location where the hand on the screen was touched by the blue stick.
Q4. It seemed my right hand was in the location where the hand on the screen was.
Q5. It seemed like I could not really tell where my right hand was.
Q6. It no longer felt like my right hand belonged to my body.
Q7. It seemed as if I might have a third hand besides my left and right hands.
Q8. The vibration on my right hand and touch on the hand on the screen were at the same time.
Q9. Sometimes I felt as if my right hand were turning virtual.
Q10. The hand on the screen began to resemble my right hand, in terms of shape, skin tone, or some other visual feature.
Q11. It appeared (visually) as if the hand on the screen were drifting towards my right hand.
Q12. It seemed like I could have moved the hand on the screen if I had wanted, as if it were obeying my will (In passive conditions). OR, The movements of the hand on the screen were caused by myself (In active conditions).
Q13. I felt as if my right hand grew longer.

According to Botvinick and Cohen (1998), Slater et al. (2008), and Kalckert and Ehrsson (2014), Q1 directly assesses the ownership illusion, Q1–Q4 are considered ownership-related questions (that are sometimes aggregated to assess ownership, as in Kalckert & Ehrsson, 2014), and Q12 is an agency question. The remaining questions assess more specific (and probably design-dependent) perceptual aspects and correlates of the illusion. For questionnaires in the virtual rectangle conditions, we replaced the reference to virtual hand with the reference to virtual rectangle; Q7 was changed to 'It seemed as if I might have a rectangle-like hand besides my left and right hands'.

2.1.6. Proprioceptive drift measurement

We recorded the three letters in the letter array corresponding to virtual effector position, the real position and the felt position of the real hidden hand before and after the illusion induction process (Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2014; Tsakiris et al., 2006). The computer screen was 48 cm wide. We measured the actual positions of each letter in the letter array shown on the screen. The letters sizes differed depending on their alphabetic shape, with the biggest letter measuring approximately 0.4 cm. Because the real hand positions and virtual effector positions could be different before and after the illusion induction in active conditions, we standardized the six positions in pre- and post-measurements for each condition, so as to relate all measures to the same scale. We calculated the proprioceptive drift by subtracting the participants' felt position at the post-measure from the felt position at the pre-measure, so that positive values imply a drift towards the virtual effector.

2.1.7. Skin conductance response (SCR) measurement

SCR data were recorded with a Biopac MP100 acquisition unit and AcqKnowledge software. The SCR remote transmitter with a strap was worn on the participant's left wrist. We measured SCR during the threat phase and then defined a latency onset window between 1 and 6 s after stimulus/event onset, namely when the virtual knife cut the virtual effector, with the skin conductivity before event onset serving as baseline (see Boucsein, 1992; Figner & Murphy, 2011; Ma & Hommel, 2013, 2015). We then calculated the magnitude of the event-induced SCR by subtracting baseline skin conductivity from the peak amplitude of the SCR during the analyzed time window, and took the log(magnitude + 1) per participant and condition.

2.2. Results

2.2.1. Questionnaire

The 2(effector) × 2(activity) × 2(synchrony) ANOVA analysis of the thirteen questionnaire items and an additional ANOVA of the four aggregated ownership questions (Q1–4) revealed various significant effects; for an overview of ANOVA terms see Table 1.

The main effect of synchrony was significant for almost all questions (except Q5 and Q7). Ratings were higher in synchronous than asynchronous conditions, which indicates that multimodal bottom-up information tempted participants to perceive the virtual effectors as a part of their own body. However, several items showed not only an activity main effect but also a significant interaction between synchrony and activity, due to that synchrony having a stronger effect in the active conditions. This interaction was particularly pronounced in the main ownership question (Q1), two of the other three ownership-related questions (Q3, Q4), and the agency question (Q12). Fig. 2 shows the underlying pattern. Unsurprisingly, the separate ANOVA on the aggregated ownership items (Q1–4) also showed all three main effects being significant, as well as the interaction between synchrony and activity. Two-tailed paired *t*-tests confirmed that synchrony modulated illusion ratings in both passive conditions, $t(43) = 4.576$, $p < 0.001$, $d = 0.535$, and active conditions, $t(43) = 9.853$, $p < 0.001$, $d = 1.147$. Also of interest, synchrony modulated agency (Q12) in both passive conditions, $t(43) = 2.760$, $p = 0.007$, $d = 0.251$, and active conditions, $t(43) = 9.703$, $p < 0.001$, $d = 1.214$.

Table 1
F, P and Partial Eta squared (PES)-values for the effects for all the questionnaire items ratings, with df = 43.

F/P/PES	EFF	ACT	SYN	EFF ∗ ACT	EFF ∗ SYN	ACT ∗ SYN	EFF ∗ ACT ∗ SYN
Q1	11.657	10.112	45.384			10.084	
	0.001	0.003	<0.001			0.003	
	0.213	0.190	0.513			0.190	
Q2		5.372	47.650				
		0.025	<0.001				
		0.111	0.526				
Q3	10.747		41.296			9.810	
	0.002		<0.001			0.003	
	0.200		0.490			0.186	
Q4	12.858	17.165	15.121			10.604	
	0.001	<0.001	<0.001			0.002	
	0.230	0.289	0.260			0.198	
Q1–4	14.848	9.319	48.352			13.676	
	<0.001	0.004	<0.001			0.001	
	0.257	0.178	0.529			0.241	
Q5							
Q6			5.738				
			0.021				
			0.118				
Q7							
Q8			33.707				
			<0.001				
			0.439				
Q9	14.845	18.286	56.872			8.078	
	<0.001	<0.001	<0.001			0.007	
	0.257	0.298	0.569			0.158	
Q10	56.892	7.373	18.090		7.271	12.633	6.536
	<0.001	0.009	<0.001		0.010	0.001	0.014
	0.570	0.146	0.296		0.145	0.227	0.132
Q11	12.393		13.777		5.230		
	0.001		0.001		0.027		
	0.224		0.243		0.108		
Q12	6.940	79.598	54.637			23.357	
	0.012	<0.001	<0.001			<0.001	
	0.139	0.649	0.560			0.371	
Q13			19.362			6.448	
			<0.001			0.015	
			0.310			0.130	

EFF: virtual effector (virtual hand vs. rectangle).
ACT: activity (active exploration vs. passive stimulation).
SYN: synchrony (synchronous vs. asynchronous).

The main effect of effector was also significant for the majority of the items, including three of the four items that directly relate to the ownership illusion. This effect indicates that participants received more ownership for the virtual hand than for the virtual rectangle. This amounts to a resemblance effect, that is, more ownership was experienced for the virtual effector that was more similar to the participant's real hand. Note, however, that there was no indication that the impact of resemblance on ownership depends on, or interacts with synchrony—as top-down approaches to ownership would predict. That is, there was no evidence that resemblance mediates the processing of bottom-up information.

Given the strong connection between synchrony—an important ingredient of the ownership illusion—and activity—the crucial element for agency, we computed one-tailed Spearman correlations between the ownership illusion (as assessed by the aggregation of Q1–4) and the agency question (Q12). These correlations were all positive and significant for all eight conditions, *r*s = .35–.65, *p*s =< .001–.01.

2.2.2. Proprioceptive drift

With the left edge of the computer screen set as zero position, the standardized average position of the virtual effector was 21.6 cm, SD = 1.991 cm, and of the real right hand 32.7 cm, SD = 2.758 cm. And a 2(effector) × 2(activity) × 2(synchrony) ANOVA of the proprioceptive drift rates yielded significant main effects of synchrony, $F(1,43) = 10.335$, $p = 0.002$, $\eta p2 = 0.194$, and of activity, $F(1,43) = 10.403$, $p = 0.002$, $\eta p2 = 0.195$. These effects showed that drift rates were more

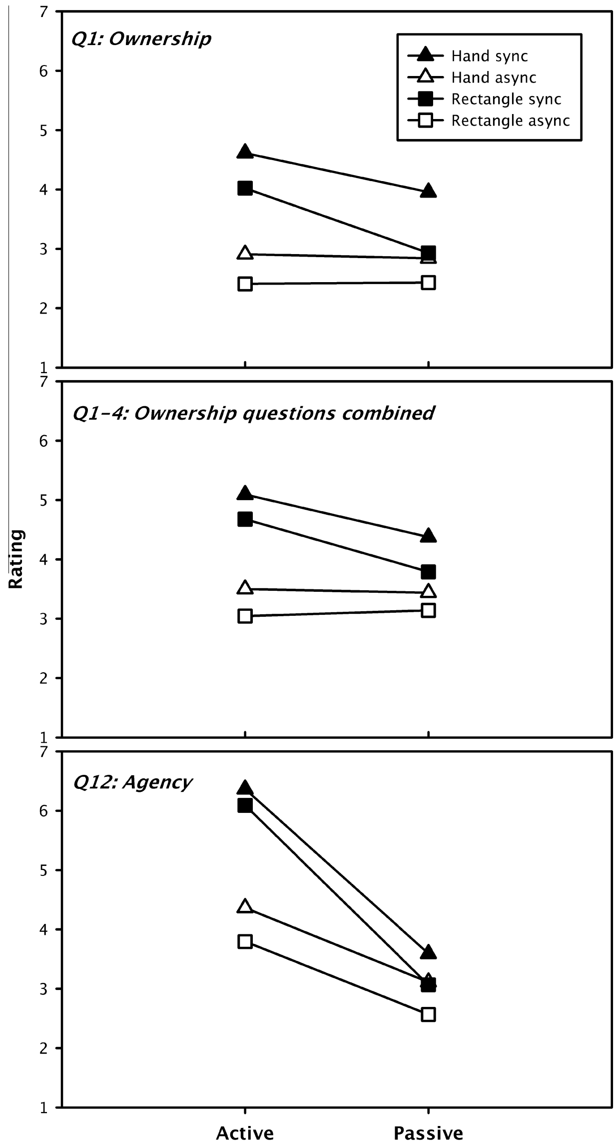

Fig. 2. Ratings for Q1, the mean of Q1–4, and for Q12, as a function of virtual effector, activity, and synchrony.

pronounced and more positive in synchronous than in asynchronous conditions (0.783 cm vs. 0.003 cm) and in active as compared to passive conditions (0.695 cm vs. 0.091 cm). The interaction between effector and activity was also significant, $F(1,43) = 4.738$, $p = 0.035$, $\eta p2 = 0.099$, indicating that activity did not matter for the virtual hand (0.383 cm vs. 0.286 cm for active and passive conditions, respectively) but strongly increased the drift rate for the virtual rectangle (1.007 cm vs. −0.104 cm). No other effects were significant. We directly compared the synchrony difference for virtual hand and rectangle conditions with one-tailed paired *t*-tests, which showed significant effects for the virtual hand, $t(43) = 3.682$, $p < 0.001$, $d = 0.505$; and for the virtual rectangle, $t(43) = 1.762$, $p = 0.041$, $d = 0.249$. The proprioceptive drift results is shown in Fig. 3.

It is interesting to compare these findings to those obtained for Q11, which directly asked participants to judge the illusion-induced proprioceptive drift. It is obvious that the two measures do not converge: while the proprioceptive drift rates show main effects of synchrony and activity, and an effector-by-activity interaction, the judgment main effects of synchrony and effector, and an interaction between effector and synchrony (indicating a stronger synchrony effect for the virtual hand, 3.79 vs. 2.76, than for the virtual rectangle, 2.92 vs. 2.42).

2.2.3. SCR

A 2(effector) × 2(activity) × 2(synchrony) ANOVA of the event-induced SCRs (see Fig. 3) revealed significant main effects of effector, $F(1,43) = 4.202$, $p = 0.046$, $\eta p2 = 0.089$, indicating that skin conductance was stronger in the virtual hand conditions than the virtual rectangle conditions (0.446 vs. 0.375 log(microsiemens − 1)), and of synchrony, $F(1,43) = 6.903$,

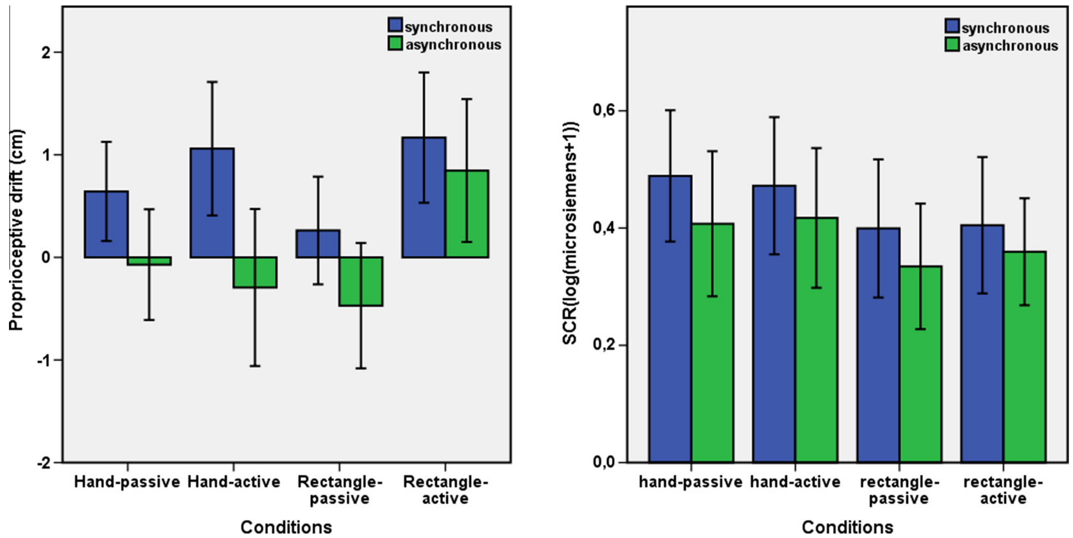

Fig. 3. Results for proprioceptive drift (left panel) and SCR (right panel).

$p = 0.012$, $\eta p2 = 0.138$, indicating stronger skin conductance in synchronous conditions (0.441vs. 0.380 log(microsiemens − 1)). No other effects were significant. We directly compared the synchrony difference for virtual hand and rectangle conditions with one-tailed paired *t*-tests, which showed significant effect for the virtual hand, $t(43) = 1.732$, $p = 0.044$, $d = 0.177$; but not for the virtual rectangle, $t(43) = 1.442$, $p = 0.077$, $d = 0.156$. This pattern may be similar to previous observations that illusory ownership was successfully induced by visuotactile stimulation when the non-corporeal effector was active controlled by participants (Ma & Hommel, 2015) but not when it was a static wooden block (e.g. Tsakiris et al., 2010).

3. Discussion

The main aim of this study was to directly compare ownership illusions evoked by a more RHI-like paradigm and ownership illusions evoked by a more VHI-like paradigm with our virtual reality setup. We were mainly interested in testing whether objective agency would directly contribute to perceived ownership and whether the similarity between people's real hand and the virtual effector would matter. With respect to our first question, the results showed that both setups induced significant synchrony effects, which confirms that they were successful in inducing a rubber-hand-like ownership illusion. However, having the opportunity to actively operate the virtual effector (and thereby obtain additional efferent and re-afferent information) did not only increase perceived agency, but also boosted both the general impression of ownership and the synchrony-induced rubber-hand like ownership illusion. This is rather strong evidence for a substantial contribution of objective agency to perceived body ownership.

The significant effect of activity of the questionnaire results implies that passive and active VHI paradigms induce different kinds of illusion. This suggests that not only the spatiotemporal relationship of the input sensory signals matters for the ownership illusion (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Kalckert & Ehrsson, 2014; Tsakiris, 2010; Tsakiris & Haggard, 2005), but also the amount of sensory information. Indeed, the probably most obvious explanation for the interaction between activity and synchrony, as well as for the correlation between agency and ownership perception, is the fact that active exploration multiplies the amount of information that reveals multimodal correlations. Moving one's real hand systematically leads to hundreds if not thousands of proprioceptive and tactile impressions that can be correlated with the just as many visual impressions created by the synchronously moving virtual effector. As compared to the classical rubber-hand setup, these three more or less continuous informational streams provide a much richer database for the computation of cross-modal contingencies. Given that these computations are considered to represent the main factor that underlies both subjective agency (Burin et al., 2015) and subjective body ownership (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998), one would indeed expect that objective agency increases both subjective agency and synchrony effects. However, while objective agency clearly plays a role for subjective ownership, it is less clear whether subjective agency is relevant for subjective ownership as well. True, objective agency led to stronger subjective agency, as the results for our agency question indicate, and subjective agency correlated with perceived ownership. However, this remains a correlational finding which may merely reflect that subjective ownership and subjective agency rely on the same kind of information—on objective agency, that is, and the richer multimodal database it helps to create.

Our second question was whether resemblance between a novel effector and people's real effectors would matter. Effects of resemblance are directly predicted by top-down models, especially if they assume that bottom-up synchrony information is matched against an internal body image (Tsakiris, 2010). That is, people should accept new, artificial effectors only to the degree that they are similar to effectors that are already part of the body image—even in the presence of synchronous multisensory stimulation. Several aspects of our findings speak against this possibility. First, we were able to find significant ownership illusions for virtual rectangles. As rectangles are unlikely to fit any representation included in a permanent representation of our body, this observation is inconsistent with top-down approaches. Second, even though participants were more tempted to accept hands than rectangles as part of their body overall, the kind of virtual effector had no impact on the synchrony effect for the questionnaire, proprioceptive drift, and SCR. This is inconsistent with the prediction from top-down modulation approaches that the processing of bottom-up information is modulated and gated by internal body representations.

And yet, the main effect of effector does indicate that similarity between a novel effector and longer-term representations and expectations have some role for the experience of one's body. While the lack of an interaction between effector and synchrony in all three relevant measures speaks against the top-down modulation approach, it seems possible to reconcile our observations by considering the reasoning of Synofzik, Vosgerau, and Newen (2008) for the case of perceived agency. These authors have pointed out that under some circumstances bottom-up information may be insufficient for agency judgments, which may lead people to consider other information as well. As a consequence, agency judgments may integrate various sources of information, which may vary in strength depending on the situational circumstances. Along these lines, it is possible that facing a virtual hand creates a more general bias towards perceiving body ownership. While this bias need not interact or censor synchrony-based information, as our findings suggest, it may play a stronger role under conditions in which this kind of information is less reliable, as in traditional RHI design. These considerations would also explain why our participants experienced more agency with the virtual hand than the virtual rectangle. The possibility that facing a virtual hand induces a general bias towards perceived ownership would fit with the argument of Synofzik et al. (2008) that self-related judgments rely on multiple informational sources, and with the assumption that vision tends to dominate tactile and proprioceptive sensory input (Ernst & Banks, 2002).

If ownership judgments are based on the integration of multiple informational sources, it is possible that information from one source can compensate for a lack of information from another. Support for this possibility comes from the observation that proprioceptive drift rates depended on activity with the virtual rectangle but not with the virtual hand. The absence of the activity effect for the virtual hand (i.e., the equivalence of proprioceptive drift in active and passive conditions) is consistent with earlier studies (Kalckert & Ehrsson, 2012, 2014; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Tsakiris et al., 2006). However, the presence of the activity effect for the virtual rectangle implies that objective agency plays a stronger role for less familiar or plausible body parts. If so, it is possible that general expectations or plausibility and objective agency can compensate for each other, so that the impact of objective agency increases the less top-down support a candidate effector receives.

Taken altogether, our account emphasizes bottom-up mechanisms in the generation of subjective ownership without excluding top-down influences. Along the lines of Synofzik et al. (2008), we assume that multiple informational sources contribute to perceived ownership. Hence, internal body representations do not seem to censor bottom-up information (e.g. Tsakiris, 2010) but, rather, emerge from the integration of equally weighted bottom-up and top-down information. However, we have also consider the possibility that one informational source might dominate if another is unreliable or lacking. For example, given that the absence of objective agency reduces the amount and reliability of bottom-up information, it is certainly possible that occasional visuotactile stimulation alone fails to induce illusory ownership without sufficient top-down information to compensate (e.g., Haans et al., 2008; Tsakiris, 2010; Tsakiris & Haggard, 2005; Tsakiris et al., 2010). The presence of objective agency, in turn, would be likely to induce ownership illusions even have top-down information from internal body representations is lacking, as in the case of body-dissimilar effectors like a rectangle (cf., Ma & Hommel, 2015).

There are two more observations that we consider interesting to discuss, in particular with respect to methodology. One refers to the relationship between proprioceptive drift rates and responses to Q11, the subjective counterpart. On the one hand, participants were more likely to perceive the virtual hand moving towards their real hand in synchronous conditions, and more so with a virtual hand than with a virtual rectangle, which is consistent with observations of Tsakiris et al. (2010). But, on the other hand, the different patterns in drift rates and subjective drift ratings suggest that the two measures do not rely on exactly the same information. It may be that conscious self-perception is less reliable than drift rates and/or that self-perception integrates more, or other kinds of information (Ernst & Banks, 2002; Holmes, Snijders, & Spence, 2006; Rohde, Di Luca, & Ernst, 2011).

The other interesting observation is that higher SCR was found for the virtual hand than for the virtual rectangle, but that this effect did not interact with synchrony. This suggests that people generally care more about objects that resemble their own body parts, but this effect is not dependent on the synchrony-induced ownership illusion. This replicates previous findings of Ma and Hommel (2013), who observed that participants were emotionally involved (as assessed by SCR) even if a threat was targeting a virtual hand that they did not perceive as their own. Both findings are consistent with the consideration that we developed above: facing an object that resembles a body part may activate corresponding representations in a body image (Tsakiris, 2010) and thus produce a top-down bias towards perceived ownership. This may not censor bottom-up information, which explains why the object effect did not interact with synchrony, but rather increase the general tendency to perceive an object as part of one's own body.

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