The body beyond the body: expectation of a sensory event is enough to induce ownership over a fake hand

Francesca Ferri¹, Antonio Maria Chiarelli², Arcangelo Merla², Vittorio Gallese¹ and Marcello Costantini²

More than 100 papers have been published on the rubber hand illusion since its discovery 14 years ago. The illusion has been proposed as a demonstration that the body is distinguished from other objects by its participation in specific forms of intermodal perceptual correlation. Here, we radically challenge this view by claiming that perceptual correlation is not necessary to produce the experience of this body as mine. Each of 15 participants was seated with his/her right arm resting upon a table just below another smaller table. Thus, the real hand was hidden from the participant's view and a life-sized rubber model of a right hand was placed on the small table in front of the participant. The participant observed the experimenter’s hand while approaching—without touching—the rubber hand. Phenomenology of the illusion was measured by means of skin conductance response and questionnaire. Both measures indicated that participants experienced the illusion that the experimenter’s hand was about to touch their hidden hand rather than the rubber hand, as if the latter replaced their own hand. This did not occur when the rubber hand was rotated by 180° or replaced by a piece of wood. This illusion indicates that our brain does not build a sense of self in a merely reactive way, via perceptual correlations; rather it generates predictions on what may or may not belong to itself.

1. Introduction

Usually, we do not question the experience of the body as a part of the self. ‘Body ownership’ is an epistemic definition of the common experience that ‘my body’ belongs to me [1,2], and it is fundamental to self-consciousness [3]. The sense of ownership (SO) is thought to rely on the integration of sensory signals from different modalities [1,4,5]. Illusions manipulating SO, such as the rubber hand illusion (RHI), provide a powerful experimental tool to investigate the individual’s bodily self-perception. In the RHI, watching a rubber hand being stroked synchronously with one’s own unseen hand causes the rubber hand to be attributed to one’s own body, to ‘feel like it is my hand’. This illusion does not occur when the rubber hand is rotated by 180° or replaced by a piece of wood. This illusion indicates that our brain does not build a sense of self in a merely reactive way, via perceptual correlations; rather it generates predictions on what may or may not belong to itself.

Botvinick & Cohen [5] were the first to show that, after synchronous visuo-tactile stimulation of the rubber hand and the participant’s hand, intermanual reaches were displaced towards the rubber hand. In other words, participants perceived the position of their hand to be closer to the rubber hand than it really was. The manipulation of SO with the RHI has been largely confirmed by more than 100 studies (for reviews, see [6,7]). These studies all shared a key research question focused on the necessary and sufficient conditions for inducing a SO. Botvinick & Cohen [5] initially suggested that visuo-tactile integration is both necessary and sufficient for self-attrition of the rubber hand, and that the illusion mainly represents tolerance to discrepancies between the seen and the felt positions of the hand. A more radical proposal then came

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1Department of Neuroscience, Section of Physiology, University of Parma, Via Volturno 39, Parma 43100, Italy
2Department of Neuroscience and Imaging, University ‘G. d’Annunzio’ & ITAB, Institute for Advanced Biomedical Technologies, Foundation University ‘G. d’Annunzio’, Via dei Vestini 33, Chieti 66100, Italy

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Authors for correspondence:
Francesca Ferri
e-mail: francesca.ferri@nemo.unipr.it
Marcello Costantini
e-mail: marcello.costantini@unich.it

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from Armel & Ramachandran [8], who claimed that, in the RHI, the seen and the felt touch are bound because of their temporal synchrony on the basis of a Bayesian principle of perceptual learning. According to this view, in principle any object could be experienced as part of one’s body as a result of a purely bottom-up mechanism. This view was questioned by Tsakiris & Haggard [9], leading to the hypothesis that the brain maintains a coherent sense of one’s body by a test-for-fit process, which enables the distinction between corporeal and non-corporeal objects [10]. Indeed, this process would be in charge of comparing the viewed object with a reference model of the body, which contains a reference description of the visual, anatomical and structural properties of one’s own body [9–11].

In general, there is now plenty of evidence that intermodal matching is not sufficient for RHI induction and SO [7]. Both, instead, seem to be modulated by visual form [9,12] and anatomical [9,13] and postural [9,11,13–15] congruency between the viewed object and the felt body part. Overall, these findings support the hypothesis that perception of one’s body does not only consist of the mere registration of sensory input and SO does not simply rely on stimulus-driven processing. Rather, active processing is also involved, in which top-down influences, originating from the representation of one’s own body, play important roles. This hypothesis is in line with more recent approaches to general perception [16]. Differently from classical theories, which look at the brain as a passive device, new approaches emphasize the constructive and active nature of sensory processing. Indeed, there is ample evidence that the processing of perceptual stimuli is controlled by top-down influences that constantly create predictions about forthcoming sensory events and might lead to states of ‘expectancy’ [16]. Expectations about upcoming sensory events can be used to prepare sensory cortices by instantiating a neural context that allows for enhanced processing of the forthcoming event [16]. Specifically, the sight of objects moving towards one’s body can originate expectation of a tactile event. Accordingly, bimodal neurons both responsive to tactile stimuli applied to a given body part and selective for the sight of objects moving towards the same body part have been recorded in different macaque monkeys brain regions, such as premotor area F4 [17], posterior parietal [18–20] and temporal cortices [21].

Starting from this evidence, we intend to study whether expectation of touch experience arising at the sight of a human hand approaching a rubber hand is enough to induce an SO over the same rubber hand, that is, even if no physical tactile stimulation is delivered on either the rubber hand or on the real hand.

2. Material and methods

(a) Experiment 1: tactile expectation and rubber hand illusion

(i) Participants
Fifteen right-handed healthy naive participants (mean age 22.5, 13 females), with normal or corrected to normal vision, took part in this study after having provided their written informed consent. The study was approved by the Ethics committee of the ‘G. d’Annunzio’ University, Chieti and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.
during the experiment. The consistency of movement direction and speed across trials was monitored by four pairs of switches fixed onto two vertical rods 70 cm in height, enabling the recording of the experimenter’s movements, speed and position. Four switches were positioned on each rod at 60, 45, 30 and 15 cm from the object, respectively. A further switch was positioned at the starting point (70 cm). Each switch fed a signal to the PowerLab (ADInstruments) by means of which participants’ skin conductance response (SCR) was recorded, thus allowing time-locking of experimenter’s hand movements with SCR.

The experiment consisted of four blocks, one for each of the four experimental conditions, whose presentation order was counterbalanced between participants. Each block lasted 2 min, during which four approaching movements were performed. At the beginning of the experimental session, participants were instructed to pay attention to the experimenter’s hand moving towards either a rubber hand or a piece of wood placed in front of them. After receiving instructions, participants wore earphones through which white noise was delivered for the entire duration of each block. After each block, participants took off their earphones and were required to complete the RHI questionnaire.

(iv) Rubber hand illusion questionnaire
We adopted a total of 21 questions from Longo et al. [22]. The questions referred to four different components of the experience of embodiment during the RHI paradigm: (i) 10 statements referring to the embodiment of rubber hand. These comprised items relating to the feelings that: the rubber hand belonged to the participant, the participant had control over the rubber hand, the rubber hand and real hand were in the same location, and the rubber hand had taken on features of the actual hand. (ii) Five statements referring to the experience of loss of one’s hand. These comprised items relating to the feelings of: being unable to move one’s hand, one’s hand disappearing and one’s hand being out of one’s control. (iii) Three statements referring to the feeling of movement. These comprised items relating to perceived motion of one’s own hand, and to movement of the rubber hand. (iv) Three statements referring to affect. These comprised items relating to the appeal and enjoyment of the experienced, and the expected touch being pleasant. Participants completed four versions of the questionnaire, one for each experimental condition. Participants answered each statement by choosing a number from a 7-point Likert Scale, from −3 being strongly in disagreement’ to ‘+3 being strongly in agreement’.

The questions appeared in random order.

(v) Skin conductance response
The SCR reflects the activation of the autonomic nervous system. We used SCR as a proxy of the illusion. SCR was recorded using the ADInstruments PowerLab 16/30 system, following standard published guidelines. Silver electrodes were taped to the palmar surface of the participant’s left hand II and IV fingers. Recordings of experimenter’s hand kinematic and SCR were triggered. The participants wore the electrodes for a few minutes before the recording was initiated to achieve signal stabilization and individual calibration. Data were registered at 1 KHz sample-rate and processed with a Matlab (The Mathworks Inc.) custom program.

(b) Experiment 2: comparing the effects of tactile expectation and only vision of the rubber hand on the rubber hand illusion
One may question whether or not mere exposure to a rubber hand in experiment 1 could have been enough to induce embodiment of the rubber hand [13,23–25]. In this experiment, we compared the contribution of tactile expectation with that of visual exposure with a rubber hand in the RHI.

(i) Participants, experimental design and procedure
Thirty right-handed healthy naive participants (mean age 22.2, 27 females), with normal or corrected to normal vision, took part in this study after having provided their written informed consent. None of them had previously participated in a RHI study and they were naive to the purpose of the study.

Experimental design and procedure were the same as in experiment 1 except for the measured dependent variables. In fact, we did not record SCR and the RHI was assessed only by means of statements referring to the embodiment of the rubber hand. Participants were divided in two groups. The first group was asked to perform the tactile expectation paradigm, as in experiment 1. The second group was asked to perform the vision only paradigm, that is, they were exposed to the same experimental conditions, but in none of them was there an approaching hand.

3. Results

(a) Experiment 1: tactile expectation and rubber hand illusion

(i) Introspective evidence
As described in §2a(iv), participants answered a total of 21 questions for each experimental condition, referring to four different components of the experience of embodiment during the RHI paradigm: (i) embodiment, (ii) loss of one’s own hand, (iii) movement, and (iv) affect. The mean ratings for each component of the experience of embodiment were submitted to a 2 × 2 ANOVA with the viewed object (rubber hand versus piece of wood) and the position of the viewed object (congruent versus incongruent) as main factors.

(ii) Embodiment questions
The main effect of the viewed object was significant ($F_{1,14} = 70.4, p < 0.001; \eta_p^2 = 0.83$). The main effect of position of the viewed object was significant ($F_{1,14} = 176.2, p < 0.001; \eta_p^2 = 0.93$). The interaction between the two factors was also significant ($F_{1,14} = 19.7, p < 0.001 \eta_p^2 = 0.58$). Post hoc comparisons with Bonferroni correction showed higher mean rating for the hand congruent (2.1) condition when compared with all the other conditions (−1.4, −0.6 and −1.6 for hand incongruent, wood congruent, and wood incongruent, respectively; all $p$-values < 0.001; figure 2). None of the other comparisons reached significance (all $p$-values > 0.18).

(iii) Loss of one’s hand questions
The main effect of the viewed object was significant ($F_{1,14} = 8.8, p < 0.05; \eta_p^2 = 0.38$). The main effect of position of the viewed object was significant ($F_{1,14} = 5.8, p < 0.05; \eta_p^2 = 0.29$). The interaction between the two factors was also significant ($F_{1,14} = 5.2, p < 0.05; \eta_p^2 = 0.27$). Post hoc comparisons with Bonferroni correction showed higher mean rating for the hand congruent (0.49) condition when compared with all the other conditions (−0.56, −0.55 and −0.67 for hand incongruent, wood congruent, and wood incongruent, respectively; all $p$-values < 0.05; figure 2). None of the other comparisons reached significance (all $p$-values ≥ 0.9).
(iv) Movement questions
The main effect of the viewed object was significant \( (F_{1,14} = 5.5, p < 0.01; \eta^2 = 0.80) \). The main effect was explained by higher mean rating for the rubber hand \((-1.3)\) condition when compared with the wood condition \((-2.1)\). The position of the viewed object and its interaction were not significant (figure 2).

(v) Affect questions
The main effect of the viewed object was significant \( (F_{1,14} = 10.6, p < 0.01; \eta^2 = 0.43) \). The main effect of viewed object was explained by higher mean rating for the rubber hand \((1.2)\) condition when compared with the wood condition \((0.5)\; \text{figure 2}\). The main effect of position of the viewed object was significant \( (F_{1,14} = 14.6, p < 0.01; \eta^2 = 0.51) \). This was explained by higher mean rating for the congruent \((1.2)\) condition when compared with incongruent condition \((0.5)\). The interaction between the two factors was not significant \( (F_{1,14} = 0.15, p = 0.7) \).

(vi) Skin conductance response
The raw data were down-sampled by a factor of 100. The down-sampled raw data were bandpass filtered \((0.01\text{–}0.5 \text{ Hz})\) with a Chebyshev type 2 digital filter in order to cut down slow signal variations and high-frequency noise.

A principal component analysis (PCA) was performed for each of the four distances from the object in each block. This was done in order to find a common timecourse in the four trials of each block, thus lowering the signal noise while extracting signal features related to the approaching movements. We always found that the first PCA component explained most of the variability of the signal \( (\text{mean } 60\%, \text{ s.d. } = 3\%) \) for both the viewed object and distance. Thus, we decided to perform the statistical analysis on the first PCA component over the four trials as this component could be roughly considered the best descriptor of SCR to the approaching movements for each condition.

For further statistical analysis, we considered the maximum value of the first component of the PCA in a 10 s time-interval after each switch onset activated by the experimenter’s hand movement (PCA SCR value).

The PCA SCR values in all experimental conditions were submitted to a \( 2 \times 2 \times 4 \) ANOVA with the viewed object \( (\text{rubber hand versus piece of wood}) \), the position of the viewed object \( (\text{congruent versus incongruent}) \) and distance \( (60 \text{ versus } 45 \text{ versus } 30 \text{ versus } 15 \text{ cm}) \) as main factors. The main effect of the viewed object was significant \( (F_{1,14} = 11.5, p < 0.01; \eta^2 = 0.45) \). The main effect of the position of the viewed object was significant \( (F_{1,14} = 18.6, p < 0.01; \eta^2 = 0.57) \). The main effect of distance was significant \( (F_{3,42} = 5.1, p < 0.01; \eta^2 = 0.27) \). Strikingly, the three-way interaction was significant \( (F_{3,42} = 3.6, p < 0.05; \eta^2 = 0.21) \). The interaction was explained by the concomitant higher SCR values—when compared with all the other experimental conditions—while observing the experimenter’s hand approaching the rubber hand in the congruent position at the distance of 30 and 15 cm \((p\text{-values} < 0.01 \text{ for both distances}; \text{figure 3})\). For detailed values, see table 1.

(vii) Correlations between introspective evidence and skin conductance response
We performed Pearson’s correlations between the mean scores on embodiment and loss of one’s hand questions and the mean SCR change recorded, while observing the experimenter’s hand approaching the rubber hand in the congruent position at the distance of 15 cm. Correlations were
computed only on embodiment and loss of one’s hand questions because those were the only questions revealing the illusion. SCR change was computed by subtracting SCR recorded at the beginning of the trial (i.e. 70 cm) from the SCR at 15 cm. According to the number of comparisons performed, p-value was set at 0.025 (Bonferroni correction). Interestingly, the higher the SCR change, the greater the likelihood of experiencing embodiment of the rubber hand. More precisely, we observed a significant positive correlation between the reported strength of embodiment and the mean SCR change (r = 0.58, n = 15, p = 0.024, two–tailed; figure 4), whereas there was no correlation with the reported experience of loss of one’s hand and the mean SCR change (r = 0.434, n = 15, p = 0.106, two-tailed).

(b) Experiment 2: comparing tactile expectation and just vision of the rubber hand on the rubber hand illusion

The mean ratings for the experience of embodiment were submitted to a 2 x 2 x 2 ANOVA with group (tactile expectation versus just vision) as between-subject factor, the viewed object (rubber hand versus piece of wood) and the position of the viewed object (congruent versus incongruent) as within subject factors.

The main effects of viewed object (F1,28 = 46.6, p < 0.001; ɳ² = 0.61) and position of the viewed object (F1,28 = 104.6, p < 0.001; ɳ² = 0.79), as well as their interaction (F1,28 = 18.1, p < 0.01; ɳ² = 0.39) were significant. Strikingly, the three-way interaction was also significant (F1,28 = 8.5, p < 0.01; ɳ² = 0.23). Post hoc comparisons showed higher mean rating, in both groups, for the hand congruent condition when compared with all the other conditions (table 2). Importantly, post hoc comparisons also showed higher mean rating for the hand congruent condition (1.7) in the tactile expectation group when compared with the just vision group (0.3; p < 0.01). The other conditions did not differ between groups.

### Table 1. Mean SCR (microsiemens, μS) ± standard errors across viewed objects and distances.

<table>
<thead>
<tr>
<th>distance (cm)</th>
<th>rubber hand</th>
<th>wood</th>
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<tbody>
<tr>
<td></td>
<td>congruent</td>
<td>incongruent</td>
</tr>
<tr>
<td>60</td>
<td>0.41 (± 0.12)</td>
<td>0.28 (± 0.07)</td>
</tr>
<tr>
<td>45</td>
<td>0.46 (± 0.09)</td>
<td>0.24 (± 0.06)</td>
</tr>
<tr>
<td>30</td>
<td>0.64 (± 0.13)</td>
<td>0.26 (± 0.06)</td>
</tr>
<tr>
<td>15</td>
<td>0.88 (± 0.20)</td>
<td>0.26 (± 0.07)</td>
</tr>
</tbody>
</table>

A possibility is to look at predictive processing in perception [28]. Broadly speaking, predictive processing refers to any type of psychological or neural process that uses or generates not only information about the past or the present, but also expectations about future states of the body or the environment. Conceptualizations of predictive processing are mainly grounded on Bayesian statistical inference (for reviews, see [29,30]). This method of inference can be used to determine the probability of a certain outcome, given a predetermined assumption, which can then be subsequently updated according to the actual outcome. Concerning the specific domain of perception, assumptions can be either expectations based on previous experiences, or ‘innate’ priors [30]. Both will act as top-down modulators of bottom-up sensory input.

Strikingly, expectation is not bounded within the psychological domain, as it effects the neural level as well. In particular, in sensory cortices, predictive processing has been associated with a reduction in activation thresholds and increase in signal-to-noise ratio, which facilitates subsequent stimulus processing [29,31]. fMRI investigation revealed that anticipation of a sensory stimulus and processing of the
somatosensory stimulus itself (i.e. tickling) engage a similar network of activation and deactivation [32]. Moreover, magnetoencephalography investigation showed that expectation of a tactile event involves a pre-stimulus modulation of neuronal oscillations in somatosensory cortex [33].

Here, we demonstrate that expectation of an upcoming sensory event is sufficient to induce SO over a rubber hand, even if no physical tactile stimulation is delivered on either the rubber hand or on the real hand. This finding is in line with theories claiming that predictive processing reflects one of the core principles of brain functioning. According to this view, a fundamental function of the brain is to constantly generate predictions that help to interpret the sensory environment in the most efficient manner, rather than waiting to be activated by incoming stimuli. Such predictions facilitate interactions with external stimuli, conserve effort and ultimately increase the chances of survival. Useful predictions typically do not arise de novo; rather they take advantage of past experiences [30]. Our behavioural and physiological results extend this view from the perception of external environment to the SO. Indeed, they support the hypothesis that our brain does not build a sense of bodily self in a merely reactive way, via perceptual correlations, rather it generates predictions on what could be mine or not. An explanation in terms of predictions and prediction errors for the classic RHI has been very recently provided by Apps & Tsakiris [34]. According to these authors, under synchronous multisensory stimulation between the participant’s hand and the rubber hand, touch referral and ownership would arise as the result of the brain’s attempt to minimize the prediction error of seeing and feeling touch at different locations. Conversely, in this study, the change in body ownership is not elicited by the generation of bottom-up prediction errors. Indeed, with our new induction procedure, the RHII arises as an effect of anticipation (i.e. the process of expecting stimuli or events in the spatio-temporal vicinity of the predicted state). Thus, at theoretical level, our results add to the proposal of Apps & Tsakiris [34] that anticipation of touch might be sufficient to elicit changes in sense of body ownership. In other words, the novelty of our proposal would be that violation of expectations about multisensory events is not a necessary condition for RHII to occur. This holds, however, only to the extent that the seen external object resembles the internal body-model.

This is not the whole story, though. Our experiment also revealed that embodiment of the rubber hand only occurred when the approaching stimulus (i.e. experimenter’s hand) entered participants’ peripersonal space (PPS, the space around the hand), as shown by the autonomic response. The definition of PPS [35,36] originates from electrophysiological studies based on visual–tactile neurons identified in the premotor area F4 and the ventral intraparietal area (VIP) of the monkey brain [37–39]. The receptive fields of the VIP-F4 neurons are coded in somatic coordinates and anchored to various parts of the body. In particular, the visual receptive fields of F4 neurons around the hand extend from 5 to 35 cm from the tactile receptive fields [17]. Such extension increases in depth when the speed of an approaching stimulus also increases [17]. The advantage of this dynamic mapping of space, which seems also to be a characteristic of humans [40–42], is quite obvious: it enables an efficient mapping of what is really near, thus permitting us either to take advantage of an opportunity or to avoid a threat. Thus, PPS should not be understood only as a particular region surrounding the body that acts as an interface between the body and the environment. Because of its pointing to the environment and the body, PPS cuts across any dichotomy between internal and external milieu. This would be in line with the idea of a ‘body-matrix’ [43], conceived as a dynamic neural representation of the body that extends beyond its surface to integrate visual and auditory inputs arising from the surrounding space with tactile and proprioceptive inputs.

To sum up, using a new induction procedure of the RHI, we showed that anticipation of touch is sufficient to induce, proactively rather than reactively, an SO over a dummy hand. Crucially, for tactile expectation to exert this effect, the approaching stimulus (i.e. experimenter’s hand) must fall within the participant’s PPS. We speculate that such proactive sense of self, allowed by predictive processing in the brain, plays a role in maintaining a coherent and unitary sense of bodily self.

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References


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<td>tactile expectation</td>
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<tr>
<td>just vision</td>
<td>-1.7 (± 0.3)</td>
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