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Specificity and coherence of body representations.

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Abstract

Bodily illusions differently affect body representations underlying perception and action. We investigated whether this task-dependency is mediated by two dimensions of embodiment: the sense of agency and the sense of the body as a coherent whole. In Experiment 1 a video Rubber Hand Illusion (vRHI) was induced with either active or passive movement and proprioceptive biases were measured via active responses or perceptual judgments. The ~~R~~results showed that firstly that the vRHI is largely perceptual because it affected passive perceptual localisation judgments, but did not affect ~~the~~ active pointing responses~~ but only the passive perceptual localisation judgments~~. Secondly, within the perceptual responses there was ~~revealed~~ a congruence effect, such that perceptual biases were larger following passive induction. There was ~~only~~ a trend for ~~this~~the converse effect for the pointing responses, where~~as~~ motor biases were larger following active induction. In Experiment 2, we used the traditional RHI to investigate the coherence of body representation by synchronous stimulation of either matching or mismatching fingers on the rubber hand and the participant's own hand. Stimulation of matching fingers induced a local proprioceptive bias for only the stimulated finger, but did not affect the perceived shape of the hand as a whole. In contrast, spatial mismatch eliminated the RHI entirely. The present results show: (1) that the sense of agency has specific effects, depending on whether we represent our body for perception or to guide action, and (2) representations of specific body parts can be altered without affecting perception of the spatial configuration of the body as a whole.

Keywords: Body illusions, Rubber hand illusion, Ownership, Agency, Embodiment, Body representation

1. Introduction

There is little consensus on the precise number and type of body representations maintained by the brain (Gallagher 2005; Head and Holmes 1911; Paillard 1999; Schwoebel and Coslett 2005; Sirigu et al 1991). The most established distinction is between *body image* and *body schema* (Gallagher 2005). The body schema is thought to hold bodily information required for the on-line control of action (Buxbaum and Coslett 2001; Sirigu et al 1991). Accordingly, it is thought to contain information about the position of body parts derived principally from proprioceptive signals. In contrast, the body image is typically described as a relatively enduring representation of the physical structure of the body, which takes into account previous experiences and knowledge (Gallagher 2005; Paillard 1999).

Neuropsychology supports this broad distinction between body representations for perception and for action. For example, patients with numbsense are able to point to a stimulation site on a body part on command, but lack conscious sensory detection of the touch to which they point (Paillard 1999; Rossetti et al 1995, 2001). Autotopagnosic patients are able to detect and verbally localise stimulation on different body parts but fail to guide their actions to that location without vision, as if they cannot situate the stimulated body part relative to other parts or to the body as a whole (Buxbaum and Coslett 2001). Furthermore, a double dissociation has recently been reported between pointing to touched locations on the hand and perceptually locating these touches on a drawing of the hand in stroke patients (Anema et al~~;~~ 2008). Such deficits provide a double dissociation between body representations underlying perception and action, and also suggest a specific cognitive function of organising individual body parts into a coherent whole.

This distinction has also been found in healthy individuals: bodily illusions have different effects on perceptual and motor tasks (Kammers et al 2006; 2009a). Here, however, we focus on two other distinctive features of body representations that have received much less attention. These are the perceived control we have over our body movements, and the composition of the body from individual parts that each individually belong to and form part of a coherent, whole self. The clinical literature contains a number of dissociations relevant to these aspects. For example, loss of ability to (voluntarily) move and loss of inhibition of movements have both shown to produce abnormal relationships with the body. A clinical example of the latter is the Alien Hand Syndrome whereby the affected hand can intervene with planned actions of the unaffected hand and shows involuntary reflex like actions toward objects (Della Sala et al 1991). Regarding body composition, the condition of autotopagnosia may be selective for individual body parts (Felician et al 2003; Sirigu et al 1991). Moreover, a specific brain region – the extrastriate body area (EBA) – is selectively activated by viewing ~~different parts of the~~ body~~body parts~~ part (Downing et al 2001), but~~and~~ shows no additional response when viewing ~~whole bodies~~~~the~~ whole bod~~y~~ies. In contrast, another region – the fusiform body area (FBA) – appears to be more selective for whole bodies (Taylor et al 2007).

Here we investigate, in healthy individuals, whether the dimensions embodiment: sense of agency and body coherence are also sensitive to the perception/action distinction and to the body part/coherent whole distinction. However, this question first requires a clear definition of the two investigated dimensions of embodiment. The first dimension distinguishes the feeling of one's own body as a perceptual object or seat of sensation, from the motoric sense of agency over one's own body, i.e. the presence of *sense of agency* (Tsakiris et al 2006). This corresponds to the philosophical distinction between the body as object and the body as subject respectively (Merleau-Ponty 1962, 1963).

The second dimension, body coherence, relates to the sensations that my~~our~~ body and its parts belongs to "me". The feeling of having one body is coherent even though t~~T~~he~~is~~ *sense of body-ownership* has proven to be flexible. More specifically, ~~, in the sense that~~ the feeling of ownership~~ it~~ can be extended to external objects, leading to their incorporation into the mental body representation (Tsakiris et al 2007). An example of this is the experimental manipulation of embodiment in the Rubber Hand Illusion (RHI) (Botvinick and Cohen 1998). During this illusion participants report that a rubber hand stroked synchronously with the participant's own hand results in a feeling that the rubber hand is part of one's own body. This specific experience of embodiment is referred to as the 'sense of ownership' (Gallagher 2005; Longo et al 2008).

Although this illusion can be~~en~~ used to reveal that there are multiple body representations in the healthy brain (Kammers et al 2009a; 2009b), it is unknown whether the different manners of inducing the illusion differentially recruit these representations. To investigate these two questions we manipulated the agency component in the induction of the rubber hand illusion in Experiment 1. To do this, we used a Video version of the Rubber Hand Illusion (vRHI) paradigm (Tsakiris et al 2006), projecting a video image of the participant's hand on the table in front of them, either directly or with a short delay, instead of a rubber hand. In this way, induction could be either by active or by passive movement of the participant's right index finger. We tested what effect the resulting sense of agency given by the induction phase of the illusion might have on either a perceptual judgment (body image) or a motor response (body schema). In Experiment 2, we investigated the extent to which the localisation of the body is spatially coherent. We used a conventional RHI with an artificial hand, and investigated whether stimulation on different fingers between the rubber hand and one's own hand generalises to other body parts to produce a coherent and unified sense of the body.

2. Experiment 1

In Experiment 1, we used a Video version of the Rubber Hand Illusion (vRHI) paradigm (Tsakiris et al 2006). Previous research with this paradigm has shown that it elicits similar proprioceptive biases (Tsakiris et al 2006) and subjective reports (Longo and Haggard 2009) to the standard RHI. The multisensory conflict between the seen and felt positions of the participant's hand had a similar effect on the perceived location of the hand to the traditional RHI. In the present experiment we manipulated both the illusion induction, and the behaviour affected by the illusion. In the video paradigm, the rubber hand used in the traditional RHI is replaced by a video image of the participant's own hand.

The sense of agency was manipulated by comparing vRHI induction that included active movement of the participants' finger with vRHI induced by comparable passive finger movements (Figure 1A). Participants then indicated the perceived location of their own hand either by reporting the corresponding number from a ruler (perceptual judgments), or by actively pointing to an external object with the stimulated hand (motor response) (Figure 1B). Thus, we factorially combined a more perceptual and a more motoric vRHI induction mode with a more perceptual and a more motoric mode of response.

It has already been shown that the traditional RHI has differential effect for passive perceptual localisation tasks versus active motor localisation tasks (Kammers et al 2~~0~~009a). More specifically, passive perceptual matching localisation tasks ~~were shown to be~~ are highly susceptible to the RHI. Importantly, this was true even after active movements has been made (outside vision) with the illuded hand. In other words, even when new proprioceptive information about the veridical location of the illuded hand had been provided via active movements, there was still an effect of the RHI on a subsequent passive perceptual localisation judgement. By contrast, the active pointing movement itself showed no significant effect of the RHI. This dissociable effect was taken as evidence for two differential body representations underlying perception (body image) versus action (body schema) in healthy individuals (Kammers et al 2009a). A question that this study did not answer was whether the failure to affect the body representation underlying action was due to the lack of action or feeling of agency during the induction phase. Therefore, here we used a different type of induction that allowed us to test the effect of the RHI after passive as well as after active induction on a perceptual and a motor task. If dissociable perceptual and motoric body representations underlie the vRHI, a congruence effect between the two might be expected. Biases as measured by pointing should then be larger following induction by active than passive movement, and biases measured by perceptual judgments with the ruler should be larger following passive than active movement induction. This enabled us to investigate whether sense of agency results in a distinctive form of embodiment, compared to passive sensation.

2.1. Methods

2.1.1. Participants

Twelve healthy individuals (6 female; 6 male) at University College London participated with informed consent (mean age: 26.08 years; range: 19 – 40). Handedness was assessed by the Edinburgh Inventory (mean: 81.28, range: 5.26 – 100 – overall right-handed). Participants had normal or corrected to normal vision, and were paid for their participation. The study was performed in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee.

2.1.2. Apparatus and Materials

Participants sat in front of a table on which a framework was placed. A 15" computer monitor was positioned inside the framework aligned with the participant's body midline. The monitor was linked to a computer displaying output from a colour video camera (Sony CCD-V800E recording at 28 Hz), which viewed the participant's right hand in a first person perspective via an arrangement of mirrors. This video image was displayed on the monitor either with minimal delay (synchronous condition) or with a systematic additional delay of 500 ms (asynchronous condition). A minimal but irreducible delay of 100 ms arose from the computer acquisition and redisplay of the video image in the synchronous condition. However, this delay was well below the threshold level at which participants stop accepting action feedback as self-generated (Blakemore et al 1999; Franck et al 2001). The participant's right hand was in a pointing configuration, i.e., with only the index finger extended on a fixed point inside the framework. The left hand was irrelevant to the experiment and placed in a relaxed position inside the framework on a fixed mark. Participants' limbs were never visible directly. Instead, participants saw a projected image of their stimulated right hand presented on the monitor on their body midline, during the induction phase only.

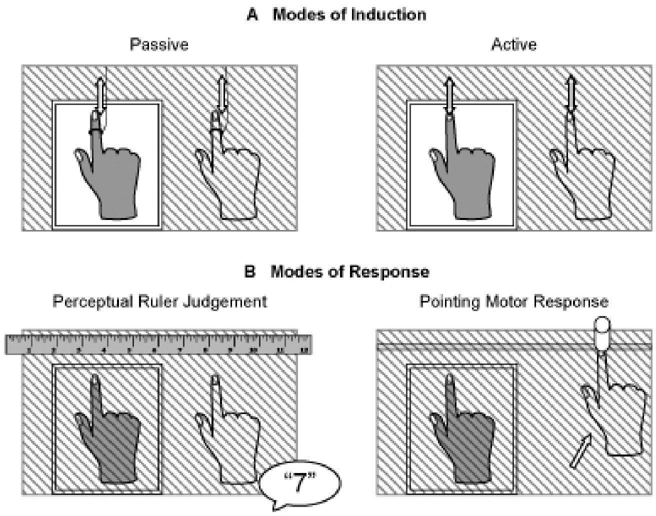

Figure 1. Experiment 1 set-up and responses. A). During the induction participants looked at a video display of their occluded right hand, and either moved their right index finger actively (right panel), or similar movements were applied passively by the experimenter (left panel). B) Participants indicated the position of their right hand either by a perceptual ruler judgement (left panel), or by pointing at a visual target (right panel).

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2.1.3. Design and Procedure

There were two tasks, i.e. modes of response: a perceptual ruler judgement, and a pointing movement. For the perceptual ruler judgement, a ruler was placed on top of the framework, and participants verbally reported the number on the ruler corresponding to the location of the tip of their right index finger (Figure 1B*,* left panel). To prevent participants from re-using remembered verbal labels from prior trials, we randomly selected from four rulers with different scale onsets, and also randomly offset the position of the ruler for each response. For pointing, participants pointed with their unseen right index finger to the location corresponding to the base of a vertical stick presented on top of the board (Figure 1B, right panel).

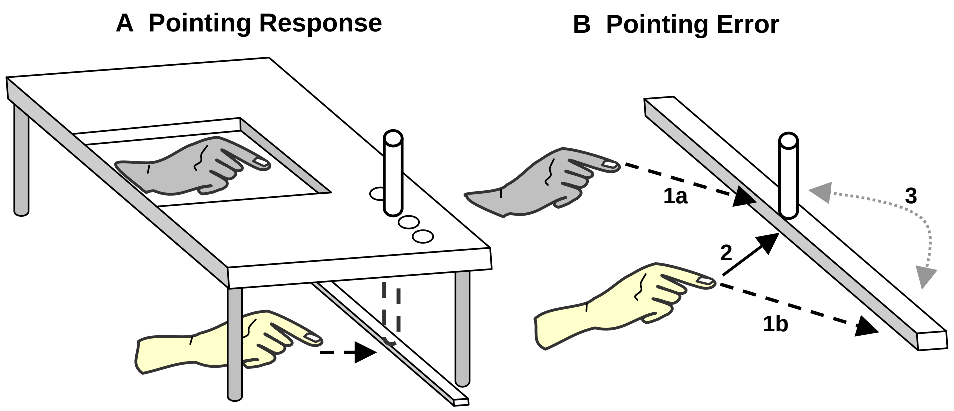

Figure **2**. Experiment 1 – Motor task. A. Pointing response. Bar presented on one of four different locations. Task is to point to its (imaginary) base inside the framework (dashed arrow). Note that the video image of the hand (grey) is not visible during the pointing movement. B. Diagram showing how a pointing error can be regarded as a measurement of the effect of the vRHI. In case the subject really feels the illuded hand is located below the video screen (grey hand), the planned movement would be executed (in this example) to the right (1a). However, since the veridical location of the subject's hand is to the right of the object, the subject will then point a corresponding amount away from the bar/video hand (1b). If there would be no relocation of the hand, the subject would point left (towards the location of the bar/video hand (2). Therefore a pointing error away from the video hand (3) can be taken as a measure of the size of the vRHI.

The instruction was to perform a single uncorrected movement initiated and completed as quickly as possible, after a verbal starting sign given by the experimenter. The movement terminated when the participant touched a ruler positioned in the frontoparallel plane beneath the stick (Figure 2A). The finger touching the ruler always provided similar tactile feedback and gave no additional information about the pointing error. The experimenter noted the position at which the participant contacted the ruler. The difference between the indicated location on the ruler and the actual location of the target was used to infer the perceived starting location of the index finger. Pointing errors *away* from the video hand were therefore taken as a shift in the perceived position of the hand *toward* the video hand (i.e. the traditional RHI effect) (Figure 2B).

On each trial ~~O~~one out of four possible different pointing targets was used for both pre- and post-test responses, the order of which was counterbalanced. After pointing, the hand was passively repositioned by the experimenter, along an unpredictable trajectory, to the original starting position.

At the beginning of each trial, the monitor was covered. Participants gave a pre-test judgement, either perceptual or by an active pointing movement according to the task indicated for that trial. Subsequently, the board was removed, and participants viewed a video image of their right hand either during passive or active movement for 60 sec. A ring, to which a thin filament was attached, was placed on the index finger of the participant. For the passive condition, the filament was pulled by the experimenter, flexing and extending the right index finger passively at an irregular, unpredictable rate averaging around 1 Hz. For the active condition participants were instructed to tap their right index finger up and down at an irregular, unpredictable rate averaging around 1 Hz. Finally, the board was replaced on top of the framework to occlude the video image, and post-judgements of right index finger position were obtained according to the task. The difference between the pre-test and the post-test was taken as a measure of the amount of relocation of the perceived location of the participant's own hand, i.e., the strength of the video hand illusion.

The factorial design thus involved eight conditions, defined by the combinations of timing (synchronous or asynchronous), induction type (active or passive), and task (perceptual ruler judgement or pointing response). Each condition was repeated four times, resulting in a total of 32 trials, which were presented in counterbalanced order.

3. Results

Results of Experiment 1 are shown in Figure 3~~2~~. Significant biases toward the video hand at post-test, compared to pre-test, were observed for both tasks - ruler (mean: 3.1 cm, SD: 1.4), $t(11) = 7.95$, $p < 0.001$, and pointing (mean: 0.7 cm, SD: 0.7), $t(11) = 3.55$, $p < 0.005$. An ANOVA on the pre-post difference scores revealed that biases were larger for ruler than pointing modes of response, $F(1,11) = 26.12$, $p < 0.001$.

In addition, there was an expected main effect of synchrony, $F(1,11) = 30.63$, $p < 0.001$, and an interaction of synchrony and task, $F(1,11) = 84.41$, $p < 0.001$. Biases toward the rubber hand as measured by ruler judgments were significantly larger when the video image was synchronous (mean:

5.3 cm, :SD: 2.0) than asynchronous (mean: 1.0 cm, SD: 1.2), *t*(11) = 8.11, *p* < 0.001; Figure 2A), consistent with previous vRHI and RHI studies (e.g., Longo et al 2008; Tsakiris and Haggard 2005; Tsakiris et al 2006; Kammers et al 2009a). In contrast, biases toward the rubber hand as measured by pointing responses were numerically larger following asynchronous video display (0.9 vs. 0.4 cm), though this difference was not significant, *t*(11) = 1.57; Figure 3~~2~~B). The interaction between synchrony and response type therefore arose because perceptual judgements displayed the classic pattern of perceived relocation, whereas pointing responses showed a small effect in the opposite direction.

Importantly, there was also a significant interaction between induction type and task, F(1,11) = 5.06, *p* < 0.050. Although this effect was independent of synchrony, it shows the expected congruence effect between type of induction and type of task (see Figure 3~~2~~). Specifically, biases on pointing responses were slightly larger following active than passive induction (0.8 vs. 0.6 cm), while biases on perceptual ruler responses were larger following passive than following active induction (3.5 vs. 2.8 cm). However, post-hoc paired samples *t*-tests comparing pair-wise differences did not reach significance for either mode of response: pointing *t*(11) = -.71, *p* = 0.246; ruler *t*(11) = 1.62, *p* = 0.067. The three-way interaction between type of induction, synchrony and response type was not significant, F(1,11) = 0.51, *p* > 0.49.

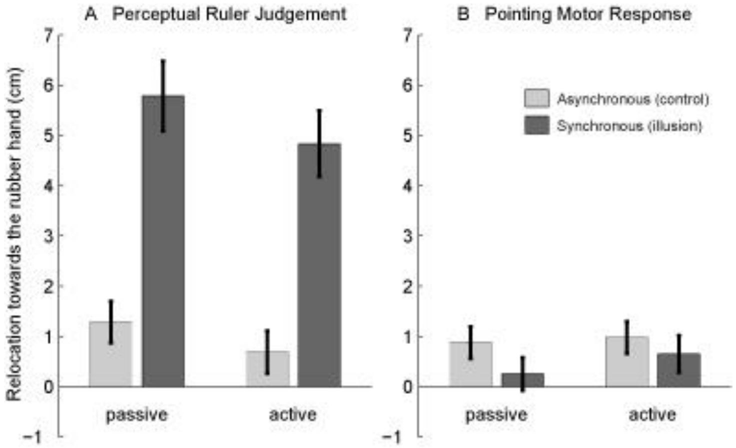

Figure 3~~2~~. Results of Experiment 1. Mean relocation of the participant's own hand toward the video hand as a function of induction mode, for asynchronous and synchronous stimulation. Error bars indicate standard errors of the mean. Relocation of the participant's hand toward the video hand was measured either using a perceptual ruler judgement (A) or by pointing movements toward a visual target (B). Pointing errors away from the video screen were taken as relocation of the perceived starting position of the participant's hand toward the video hand.

4. Discussion Experiment 1

There were two main findings of Experiment 1. Most importantly, a congruency effect was observed between the presence of agency during induction of the illusion and whether the task was perceptual or motor: pointing biases were larger following active induction and ruler judgment biases were larger following passive induction. This pattern suggests that dissociable perceptual and motoric body representations involve distinct experiences of embodiment.

Second, while significant biases toward the video hand were observed with both tasks, these biases were significantly larger for ruler judgments than for pointing responses. Moreover, only perceptual ruler judgments were influenced by the synchrony of the video display. We suggested previously (Longo et al 2008; Tsakiris and Haggard 2005) that at least two types of causes underlie the RHI: purely visual information from the perception of a hand in a plausible configuration (available in both synchronous and asynchronous conditions) and multisensory synchrony (available only in synchronous condition). The present results suggest that while the former may influence both perceptual and motor body representations, the latter influences only representations of the body as a perceptual object. The true bodily illusion in RHI is therefore an illusion of body perception, which does not affect the body representation used for action. We return to this point in the general discussion.

The present dissociation and fragmentation broadly supports the model of body representation proposed by Dijkerman and De Haan (2007). This begins with a dissociation between perceptual ('ventral') and motor ('dorsal') body representations. Experiment 1 showed that the vRHI does not 'fool' goal-directed pointing movements as it does perceptual judgements. Studies of object-oriented actions such as visually-guided grasping likewise distinguish between perceptual representations that are subject to visual illusions, and representations for action that are not (Aglioti et al 1995; Chua and Enns 2005; Haffenden and Goodale 2000). Our results suggest that the same dissociation between ventral-stream and dorsal-stream susceptibility to visual illusions may exist for representing one's own body.

5. Experiment 2

Experiment 1 supported the dissociation between perceptual and motor body representations, but also showed that the illusion is primarily perceptual. Therefore, our next investigations focussed on the body coherence dimension of embodiment only.

Tsakiris and colleagues (2006) found that perceptual induction of the RHI induced local proprioceptive bias for the stimulated finger only, while active movement induced a bias for the whole hand. They therefore showed that the *effects* of the RHI could either involve fragmenting the body into separate parts, or a more coherent global representation. However, no previous experiment has investigated the effects of stimulating one finger on the rubber hand and a different finger on the participant's hand. Is it sufficient that the rubber hand is touched synchronously with the participant's hand, or must the same specific body part (i.e., finger) be touched? If a stored coherent, structural body description is used to interpret current sensory inputs and generate sense of ownership, mismatch between viewed and touched body parts should weaken the strength of the RHI. Conversely, on Armel and Ramachandran's (2003) account that ~~if sense of~~ ownership depends ~~simply~~ entirely on bottom-up sensory regularities ~~(Armel and Ramachandran 2003)~~ , mismatch of body parts should have no effect. Therefore, the fragmentation across body parts offers a useful insight into whether RHI is primarily a top-down or a bottom-up effect (Tsakiris and Haggard 2005).

We independently manipulated which finger was stroked on the participant's hand (index or little), and on the rubber hand (index or little). Thus, the stroked fingers on the participant's and the rubber hand could either match or mismatch. We measured the RHI by measuring proprioceptive biases with a perceptual ruler judgement of both the index and little fingers, and with a questionnaire examining participant's subjective experiences of the illusion.

Furthermore, we investigated whether proprioceptive biases associated with one finger but not another, might influence the conscious model of the perceived shape of the hand. If the perceived position of the right index finger, but not the right little finger shifts toward the rubber hand at body midline, one might expect that the hand should be perceived as fatter than veridical. Conversely, if the perceived position of the right little finger, but not the right index finger shifts toward the rubber hand, one might expect that the hand should be perceived as skinnier than veridical. Thus, we used the template-matching paradigm of Gandevia and Phegan (1999) to investigate the perceived fatness of the hand, i.e., the coherence of the underlying body representation.

5.1. Methods

5.1.1. Participants

Ten healthy female participants at University College London participated (mean age: 23.2 years, range: 18–27). Handedness was assessed by the Edinburgh Inventory (mean: 89.97, range: 78.95 – 100 – all right-handed). Participants had normal or corrected-to-normal vision, and were paid for their participation. The study was in accordance with the principles of the Declaration of Helsinki, and was approved by the local ethics committee.

5.1.2. Apparatus and Materials

Participants sat at a table in front of a framework measuring 75 cm in width, 50 cm in depth, and 25 cm in height, containing a replaceable board, either occluding or revealing the rubber hand. Participants wore a cloth smock which prevented them from seeing their arms throughout the experiment. The participant's stimulated Own right Hand (OH) was placed on a fixed marker inside the framework (one for the index and one for the little finger), and the Rubber Hand (RH) was positioned in the centre of the frame, aligned with the participant's body midline. The index fingers and the little fingers of the participant's right hand and the rubber hand were 30 cm apart. The participant's left hand was irrelevant to the experiment and placed outside the framework on the table.

5.1.3. Design and Procedure

At the beginning of each trial the frame was covered. Participants made pre-test perceptual ruler judgements, as in Experiment 1. Participants made perceptual judgements of the locations of both the index and the little finger, in counterbalanced order, and with different random rulers similar to Experiment 1. Next, the cover was removed, revealing the rubber hand, but not the participant's own hand. The rubber hand and the participant's own right hand were stroked synchronously with identical paintbrushes for 60 seconds. Stroking was applied at approximately 1 Hz, but the speed and inter-stroke interval were varied randomly by the experimenter to increase the salience of the stimulation. After stroking, the rubber hand was occluded again, and post-test perceptual judgements for the index and little finger were obtained, as for pre-test. The counterbalancing of index and little finger judgments at post-test was independent of the counterbalancing in the pre-test. The difference between pre- and post-test judgements was used as a measure of the strength of the RHI.

Next, participants performed a hand template-matching test, similar to that used by Gandevia and Phegan (1999). The matching test consisted of 15 hand images presented on paper, labelled A – O (Figure 4~~3~~). One image was an original photograph of a typical human hand (template hand), without any special distinguishing characteristics. The other images were distortions of the original image stretched either in length or in width by 5 – 35% in steps of 5%. Thus, seven of the stimuli were fatter (to varying degrees) than the template hand, while seven were skinnier (to varying degrees). Sixteen sheets with different randomizations of the positions of the 15 hand images were randomly assigned to the sixteen trials for each participant. Participants verbally reported the letter corresponding with the image that most closely matched the felt shape of their right hand.

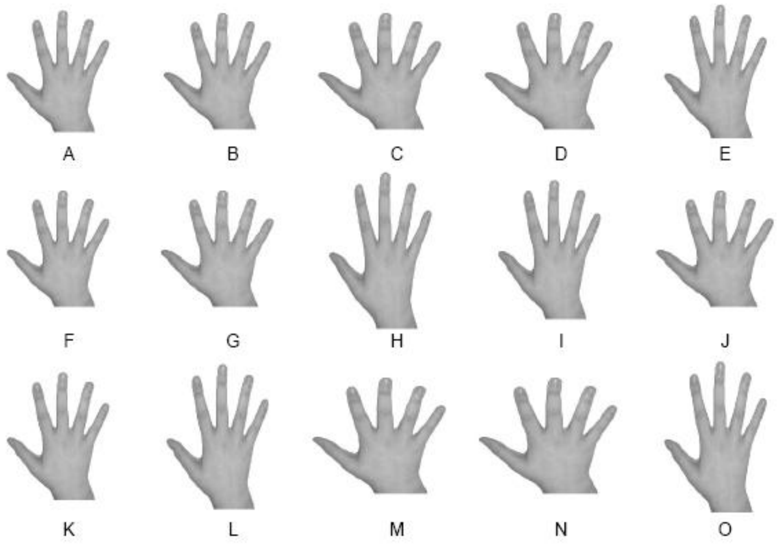

Figure 4~~3~~. Example of template matching response sheet. Participants reported the letter corresponding to the hand which most closely matched the perceived shape of their own stimulated right hand.

Participants then removed their hand from the framework whilst keeping it outside their visual field, and indicated the extent of their agreement or disagreement with 13 questionnaire statements delivered in random order. Participants responded with a 7-point Likert scale, whereby a response of +3 indicated that they "strongly agreed" with the statement, -3 that they "strongly disagreed", and 0 that they "neither agreed nor disagreed". The questionnaire items are shown in Figure 6~~5~~, and were designed to capture the key components of the sense of ownership in each experimental trial.

6. Results

6.1. Perceptual ruler judgements

A repeated-measures 2x2x2 ANOVA was conducted on the difference between post-test and pre-test judgements with factors of JUDGED FINGER (index, little), STROKED FINGER ON OH (index, little), and STROKED FINGER ON RH (index, little).

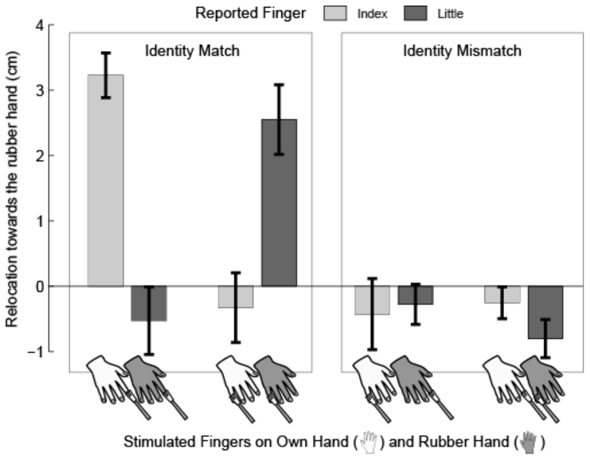

Figure 54. Results of perceptual ruler judgements in Experiment 2. Mean relocation of index and little fingers as a function of which fingers were stimulated on participants' Own Hand and the Rubber Hand. Error bars indicate standard errors of the mean.

There were significant two-way interactions between STROKED FINGER ON OH and STROKED FINGER ON RH, F(1,9) = 35.60, $p < 0.001$, and between JUDGED FINGER and STROKED FINGER ON OH, F(1,9) = 23.15, $p < 0.001$. These effects were mediated, however, by a striking three-way interaction, F(1,9) = 67.76, $p < 0.001$ (see Figure 54). Local proprioceptive biases occurred only when the same finger had been stroked on both the participant's own hand and the rubber hand. Perceived biases of the index finger occurred when both index fingers had been stroked, $t(9) = 9.42$, $p < 0.001$, but not in any other condition (all $p \geq 0.20$); conversely, biases of the little finger toward the rubber hand occurred only when both little fingers had been stroked, $t(9) = 4.79$, $p < 0.001$, (all $p \geq 0.20$). Indeed, there was a trend for a bias *away* from the rubber hand in each of the other conditions.

6.2. Hand Template Matching

The 15 hand images were assigned scores based on the relative stretching of length or width. The template hand was scored as 1; a proportionate increase of image length was added to this score; a proportionate increase of image width was subtracted from this score. Thus, the image scores ranged from 0.65 – 1.35, from relatively thin to relatively fat. Overall, there was a bias for participants to perceive their own hand as thinner than the model's hand (0.944), $t(9) = -2.93$, $p < 0.02$. Since we did not measure actual hand width, we cannot say whether this was veridical or not. Rather, our interest focussed on *modulations* of hand width associated with the different spatial match/mismatch RHI induction conditions.

A repeated-measures ANOVA was conducted with STROKED FINGER ON OH (index, little), and STROKED FINGER ON RH (index, little) as within-subjects factors. In contrast to the ruler judgement, there was no significant interaction between these two factors, $F(1,9) = 1.28$, $p > 0.20$. Local proprioceptive biases of individual fingers had no apparent effect on the explicit judgements of hand shape. This suggests that although the RHI affects the representations of *where* specific body parts are, it does not seem to affect the global conscious representation of *what* the hand is like. There was, however, an unpredicted main effect of participant's finger, $F(1,9) = 11.17$, $p < 0.010$; participants perceived their hand to be slightly thinner following brushing of their index finger (0.93), than brushing of their little finger (0.96). It is unclear what caused this effect, though it does demonstrate that template matching can be a sensitive tool to investigate perceived body shape (Gandevia and Phegan 1999).

6. 3. Subjective Reports of RHI

We used questionnaire responses to investigate whether subjective experiences of the RHI depended on the pattern of stroking. Our interest focussed on whether the experience of embodiment varied according to match/mismatch, rather than which fingers were actually stroked.

We therefore pooled the mean difference between ratings for mismatching and matching stroking for the index and little fingers (Figure 6~~5~~, upper section), except for those questions relating to a specific finger (Figure 6~~5~~, lower section).

Six questions showed a significant effect of spatial (mis)match. In a previous psychometric study (Longo et al 2008), we identified these questions with factors termed *Embodiment* (3 questions) and *Loss of own hand* (2 questions).

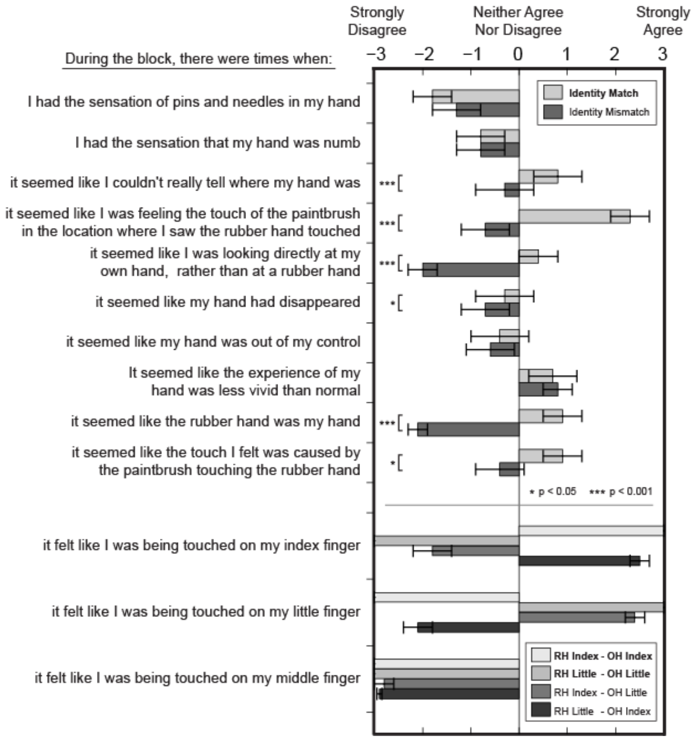

Figure 6~~5~~. Results from Subjective Reports in Experiment 2. Participants rated their subjective experience of embodiment of the rubber hand on a RHI questionnaire. Upper section shows questions unrelated to a specific finger and is pooled for matching or mismatching stimulation. Lower section shows question related to specific fingers per each stimulation condition.

7. Discussion Experiment 2

This experiment focussed on whether match or mismatch between viewed and touched body part, influences the susceptibility of perceptual body representation in the RHI. An affirmative answer would suggest that the experience of ownership, i.e. embodiment already presupposes a body representation containing a structural description in terms of distinct body *parts* (Gallagher 2005). A negative answer would suggest that embodiment of the rubber hand does not require specific body-part identity correspondence between visual and tactile stimulation, and is merely driven bottom-up by correlated stimulation.

Our results clearly show an~~d~~ influence of a mismatch between viewed and touched body parts on the RHI. A finger is felt to shift position toward the rubber hand only if the same finger experiences both seen and felt stimulation. Conversely, if the visual stimulation and tactile stimulation are applied to different fingers, no RHI is induced. Specifically, we found neither perceived relocation of the participant's own hand nor subjective experiences suggesting embodiment in the mismatch conditions. Thus, *effects* of the RHI are local and segmented. Stroking a single finger, even in the matching condition, does not influence perceptual judgements about another finger. Thus, bodily illusions associated with a single body part do not appear to transfer to other body parts. The brain appears to maintain separate representations of each distinct body part, and established ownership for each one discre~~e~~tely, on the basis of multisensory inputs.

How does the local structure of body ownership account for the fact that we experience our body as a single, coherent self? For example, a change in perceived position of one finger without parallel changes for the other fingers might imply a disunity of body representation. We showed that local changes in ownership of one finger did not appear to have general consequences, either for judgements about other fingers, or for the representation of the hand as a whole, as measured by a conscious visual judgement of body representation. This result suggests a dissociation between the brain mechanisms for body ownership, in the sense of embodying an object within the body representation or not, and the mechanisms for bodily coherence, in the sense of integrating information about the body and relating it to continuous and stable identity over time. The computation of local multisensory correlations between structured body parts appears to operate below this second level of conscious body representation.

8. General discussion

We have investigated whether two key dimensions of embodiment, sense of agency and body coherence, influence body representations for perception and for action in the same way. During the induction of a bodily illusion we manipulated the sense of active body control ~~one has over one's body~~ (agency), and the sense ~~one has~~ that one's body is a coherent and integrated physical object. More specifically, in Experiment 1 we focussed on the specific effect sense of agency might have on a perceptual representation of the body (body image), and a representation used for action (body schema). We explored this distinction both in the processes *inducing* the illusion, by evoking the vRHI through similar passive or active movements, and also in the *effects* of the vRHI, by measuring both perceived hand position and pointing movements with the hand subject to the illusion. Our results showed that embodiment can be induced either with of without sense of agency (active versus passive movement). However, we also showed that induction by active movements has less effect on perceived hand position than passive movement. That is, we showed a congruency effect between the conditions that induce the bodily illusion (active, passive), and the experiences produced by the illusion. Additionally, we showed that motor responses remain largely robust to the illusion, even when agency was involved in the induction.

In Experiment 2, we investigated the relation between representing individual body parts and representing the body as a whole. Previous studies had shown that visual-tactile induction of the rubber hand illusion on one finger influences the perceptual representation of that finger only, but not of other fingers (Tsakiris and Haggard 2005). We explored whether this local and fragmented body representation might extend also to the processes of *inducing* the illusion. We used a novel variant of the RHI in which stroking is applied to one finger of the participant's hand, but viewed on either the same or a different finger of the rubber hand. When different fingers are stimulated, there is a multisensory conflict concerning the body parts involved. We replicated the previous finding (Tsakiris and Haggard 2005), that an illusion induced by simultaneous stroking of one finger does not transfer to other fingers. More importantly, we found that simultaneous stroking of *different* fingers abolishes the illusion. This contradicts the view that body representations are simply driven by multisensory correlation (Schaefer et al 2006, Armel and Ramachandran 2003). Rather, a body representation which includes at least the identities of individual fingers seems to modulate (Tsakiris and Haggard 2005) or gate (Tsakiris et al 2008) the effects of multisensory input on embodiment. Sensory evidence regarding the body is interpreted with respect to existing structural models of the body.

Taken together, the present results show first of all that there is not a single mental representation of the body, but a number of distinct body representations. Our results suggest that these differ along at least two dimensions of embodiment. The first dimension concerns the body as a perceptual object, and corresponds to the classical perceptual body representation of body image. The second dimension concerns the body as an acting subject, and corresponds to classical motoric body representations such as body schema. Moreover, the present results show first specific effect of agency on especially the perceptual body representation, whereby sense of agency reduced the susceptibility of the perceptual body representation to the vRHI. Second, the results show a local feeling of embodiment of a single finger on the rubber hand that still can result in a coherent sense of the shape of the body as measured with the template matching. In other words, we show that although feeling of body coherence (template matching task) is resistant to the rubber hand illusion, feeling of embodiment can be locally de-localized without re-structuring the coherence of the body.

In a recent study, we demonstrated that the subjective *experience* of ownership of the rubber hand consists of several dissociable phenomenal components (Longo et al 2008). Here, we show that both motor and perceptual factors of embodiment may shape the occurrence of the illusion, and that motor and perceptual *representations* are differentially susceptible to the illusion and the type of induction. Thus, the selective manipulations of cognitive body representations in the present study reach the same conclusion as previous psychometric studies (Longo et al 2008): there are multiple facets to the feeling of embodiment. At the very least, we can distinguish between a perceptual and a motor experience of the body. Experiment 2 also revealed a specific feature of the perceptual representation of the body. We found that the illusion effects induced by tactile simulation are local, not global, in the sense that they require an exact match between the viewed and stimulated body part. Temporally correlated visual and tactile stimulation induces a strong sense of embodiment when delivered to the same body part, but not when delivered to different body parts. That is, a stored representation of body structure which contains information about finger identity appears to 'gate' the illusion. If visual and tactile stimulation refer to the same structural part of the body, their correlation is used to interpret current sensation, which in turn modulates the sense of ownership. However, we show for the first time that this relation is not reciprocal. Correlated stimulation is not sufficient to cause integration or perceptual integration between two structurally different body parts. Indeed, correlated stimulation of different body parts does not alter the representation of the body, according to our dependent measures. This suggests that current sensory input is referred to an existing representation of the body, which already contains structural information that individuates distinct body parts, or at least individual fingers. The perceptual representation of the body therefore reflects the division of the body into structural parts. In contrast, the body representations associated with motor action are thought to be more unified, and not to reflect these divisions to the same extent (de Vignemont et al 2008). In other words, ~~Whereaswhereas~~while the perceptual body is composed of parts which are each perceived individually, the body representation considered as the output channel of voluntary motor action might not reflect the fragmentation of the body into parts, and- therefore may be less susceptible to bodily illusions in general.

Our results therefore make an interesting contrast with the hypothesis that mere correlation between visual and tactile stimuli suffices to induce the rubber hand illusion (Armel and Ramachandran 2003; Ramachandran and Hirstein 1998). Those authors proposed that correlated stimulation was sufficient to produce a sense of self and embodiment of the visual stimulated object. In contrast, our results suggest that susceptibility to effects of correlated stimulation already presupposes a sense of one's own body, including, at the very least, segmentation into specific body parts.

Finally, the fragmented view of the perceptual body in the rubber hand illusion contrasts with a different bodily illusion: the vibrotactile kinaesthetic illusion. This illusion has been shown to affect the location of body parts through vibration of a tendon, which can be transferred easily to other body parts that are held with the illuded limb (de Vignemont et al 2005; Kammers et al 2006; Lackner 1988). Kammers and colleagues (2006) used this illusion to dissociate body representations in healthy individuals, and showed that the effect of this illusion is task dependent. Furthermore, de Vignemont and colleagues (2005) evoked a subjective elongation of the left index finger by vibrating the right biceps tendon while participants held the left index finger with the right hand. This produced a rapid bias toward overestimation of tactile distances applied to the left index finger. Thus, the vibrotactile illusion has not only shown a rapid, plastic interaction between proprioception and touch and task dependency, but also a propagation of perceptual illusions across body parts. Finally, Lackner (1988) showed that this transfer can even induce anatomically impossible bodily sensations, i.e. elongation of the nose held by the vibrated limb. This result suggests a relatively coherent perceptual representation of the body as a whole, in contrast to our results from Experiment 2.

There are, however, several differences between the bodily illusions which might account for the coherence of the bodily self in the vibrotactile illusion, and the fragmented representation in our data. Firstly, the RHI involves multisensory integration instead of a unimodal conflict and taps on higher order bodily experiences like feeling of ownership instead of "just" localisation of body parts. Secondly, visual attention is absent during the vibrotactile illusion. Visual attention in situations like the RHI might be directed to specific body parts, which may lead to a fragmented representation of the body. A third difference is the occurrence of self touch during transfer of the vibrotactile illusion. Self-touch provides a strong cue to coherence of the bodily self (Merleau-Ponty 1963), which has no counterpart in our experiment. At this point, we can only speculate whether the local, non-coherent sense of bodily self apparent in our data reflects either a feature of local vision of body parts (Urgesi et al 2007), or an anomaly that arises in situations like the rubber hand-type illusion where the normal somatic sensations arising from interaction with the world and with other body parts are artificially absent (Merleau-Ponty 1962).

In sum, we show that bottom-up perceptual mechanisms or actions alone are not sufficient to explain how all our somatosensation seems to belong to a single, coherent 'self'. Rather, in our data, synchrony between vision and touch established local correlations, but not a coherent sense of one's entire body. We encounter our bodies only as separate loci of sensation, but when we act these loci become integrated to form a complete self (Tsakiris et al 2007). More generally, the sense of one's own body seems to depend both on the pattern of sensory inputs (induction), and on the measures used to study the body representation itself.

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