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Feeling numb: Temperature, but not thermal pain, modulates feeling of body ownership

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ABSTRACT

There is an important link between pain, regulation of body temperature, and body ownership. For example, an altered feeling of body ownership – due to either chronic pain or "rubber-hand illusions" (RHI) – is associated with reduced temperature of the affected limb. However, the causal relationships within this triad are not well understood. We therefore investigated whether external manipulation of body temperature can influence body ownership. We used a thermode to make the right hand of healthy participants either painfully cold, cool, neutral, warm or painfully hot. Next, we induced the RHI and investigated its effects on the perceived position of the hand, on the subjective feeling of body ownership, and on physical changes in hand temperature. We replicate previous reports that inducing the RHI produces a decrease in limb temperature. Importantly, we demonstrate for the first time a causal effect in the opposite direction. Cooling down the participant's hand increased the strength of the RHI, while warming the hand externally decreased the strength of the RHI. Finally, we show that the painful extremes of these temperatures do not modulate the RHI. Hence, while thermosensation is an important driver of body ownership, pain seems to bypass the multisensory mechanisms of embodiment.

1. Introduction

The word "numb" is often used to describe a lack of sensation, but it is used in two very different senses. On the one hand, parts of the body may go numb due to extreme cold. The resulting lack of sensation can produce both the feeling that the body part is no longer ours but also result in physical pain. On the other hand, emotional pain, grief or exhaustion can also make us numb, which means that both our affects and sensations are reduced. Interestingly, although both senses of numbness imply a general lack of feeling, both are clearly associated with subjective feelings of pain, and with changes in homeostatic body regulation. These interactions point to an important triadic link in neuroscience that is not yet fully understood, between feeling of body ownership, body temperature and pain.

We both feel and know that we have a body (the feeling of *embodiment*), that belongs uniquely to ourselves (the feeling of *body ownership*), and that occupies a distinctive position in space, defining a first person perspective (body *localization*). Indeed, "I" am always and necessarily "here" (Longo, Kammers, Gomi, Tsakiris, & Haggard, 2009). However, although we take these feelings of localization for granted, they can be selectively disturbed. For example, out of body experiences involve the feeling that the self is located outside the physical body (Blanke, Landis, Spinelli, & Seeck, 2004). In this situation, people experience and recognize their own body from a third person perspective (Lopez, Halje, & Blanke, 2008). Conversely, in sensorimotor deficits such as somatoparaphrenia, patients experience their limb as belonging to a third person (Rode et al., 1992), rather than seeing it from the normal first-person perspective.

Such experiences of altered embodiment are caused by disintegration of the normally coherent multisensory information that flows from the body to the brain. Strikingly, multisensory disintegration produces not only an alteration in bodily self-consciousness, disembodiment, or reduced feeling of body ownership, but can also lead to a strong experience of pain. For example, loss of somatosensory afferent information can trigger both reorganization of cortical body representations, and pain in a phantom limb (Ramachandran & Hirstein, 1998). Conversely, disorders such as phantom limb pain (Hill, 1999; Ramachandran & Rogers-Ramachandran, 1996), Complex Regional Pain Syndrome (CRPS) (Moseley, 2005) and chronic back pain (Moseley, 2008) can disturb the feelings of embodiment, body ownership, and body localization. Remarkably, restoration of coherent multisensory information, for example by illusory vision of the phantom limb can reduce this pain (Flor, Nikolajsen, & Jensen, 2006; Hill, 1999;

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Ramachandran & Rogers-Ramachandran, 1996; but see Moseley, Gallace, & Spence, 2008 for a review).

Chronic pain can also disrupt representations of the body. For example, mental hand rotation is slower for the affected hand than the unaffected hand of chronic pain patients (Moseley, 2004; Schwoebel, Friedman, Duda, & Coslett, 2001). This delay is correlated with the intensity of the pain (Schwoebel, Coslett, Bradt, Friedman, & Dileo, 2002) and the duration of the symptoms (Moseley, 2004). Furthermore, chronic pain significantly increases the perceived size of the affected body part (Moseley, 2005). Manipulating the perceived size of a body part can also influence one's experience of pain. For example, manipulating the size at which Complex Regional Pain Syndrome (CRPS) patients viewed their affected hand using a combination of magnifying and reducing lenses produced directly proportional changes in pain levels (Moseley, Parsons, & Spence, 2008). Pain is thereby clearly related both to cerebral body representation and to spatial localization of the body.

Just as failure of multisensory integration in pathology produces abnormal body experiences, manipulations of multisensory input in healthy volunteers produce clear alterations in bodily awareness. For example, the Rubber Hand Illusion (RHI – Botvinick & Cohen, 1998) involves synchronous stroking of a viewed rubber hand and the participant's own unseen hand. Typically, the rubber hand is placed in a different location from the real hand. The visual-tactile correlation provided by synchronous stroking seems to be interpreted by the brain as evidence that the rubber hand and the real hand are one and the same, even though visual and proprioceptive position senses suggest they are in different locations. The brain resolves this conflict by accepting the rubber hand as part of the body and by adapting the perceived position of the real hand towards the seen location of the rubber hand (Botvinick & Cohen, 1998). That is, the representation of one's own body is spatially reorganized to integrate correlating multisensory information. The RHI can therefore be seen as acquiring a sense of ownership over the rubber hand, as well as a reciprocal disownership or disembodiment of one's own hand (Moseley, Olthof, et al., 2008). Recently, Moseley, Olthof, et al. (2008) observed a drop in temperature of the participant's own hand during the RHI, and interpreted this as a consequence of "disembodiment" associated with the illusion. Decreased limb temperature is also linked to chronic disorders of bodily awareness that involve pain, such as CRPS (Janig & Baron, 2003).

Hence, there seems to be an important triadic link relating body ownership, pain, and body temperature, though the precise relations between the three elements are not well understood. Previous studies suggested that changes in body temperature regulation are a *consequence* of the disembodiment triggered by the RHI (Moseley, Olthof, et al., 2008). However, the possibility of a causal link in the opposite direction has not been explored. In particular, it remains unclear whether changes in body temperature might themselves influence bodily awareness. This possibility seems plausible, given the strong links between pain and thermosensation (Craig, 2002), and also between pain and bodily awareness (Janig & Baron, 2003). The links between acute pain and body ownership also deserve further investigation. Chronic pain has been reported to change one's sense of body ownership (Moseley, 2004). Acute painful stimulation during the RHI however has been shown to have no additional effects on one's sense of body ownership over innocuous RHI stimulation (Capelari, Uribe, & Brasil-Neto, 2009). However, the effect of acute pain on the sense of body (dis)ownership has not been otherwise investigated.

In the present study we therefore investigated the interaction between body ownership, pain, and temperature using the RHI. During the experiment, we externally manipulated the temperature of the participant's hand, and then induced the RHI using the traditional visual-tactile stimulation (Botvinick & Cohen, 1998). We measured the RHI effect in three ways: (1) by asking participants to localize their unseen hand, (2) by a questionnaire investigating bodily awareness and feeling of body ownership, and (3) by measuring changes in the temperature of the participant's hand that are a consequence of the RHI (measured at a site remote from the external temperature manipulation). We particularly aimed to assess whether mild external body temperature changes and thermal pain would alter bodily awareness and whether they would do so in a similar way.

2. Materials and methods

2.1. Participants

Ten healthy participants took part in this experiment of which 7 were female (mean age 23.9, range: 18–30). One participant was excluded from the study due to an unusually low baseline skin temperature. All participants gave written informed consent prior to the experiment. Right-handedness was assessed by the Edinburgh Inventory (mean: 89.17, range: 83.33–100). Participants were naïve to the rationale of the experiment and received a small fee for participation. The study was approved by the local ethical committee and was conducted in accordance with the Declaration of Helsinki (1964).

2.2. Experimental setup

The participant sat in front of a framework (45 cm × 45 cm × 26 cm) containing two identical compartments. The participant placed his/her right forearm inside the right compartment with the palm facing down. In the left compartment, a right rubber hand was placed in an identical configuration. The distance between the index finger of the rubber hand and the participant's right index finger was 22 cm. A cloth covered the participant's arms. The upper surface of the framework could be lifted to reveal the left compartment holding the rubber hand, or lowered to occlude the entire framework.

The participant's right hand was placed on a thermoelectric metal plate (10 cm × 18 cm) connected to a Peltier heat pump (Electron Dynamics), so that the temperature of the plate could be adjusted electronically.

2.3. Design

During the experiment, we manipulated the temperature of the Peltier plate to expose the participant's right hand to one of five temperature categories: Painfully Cold, Cool, Neutral, Warm, and Painfully Hot. The Neutral temperature was set to the temperature of the dorsal surface of the middle phalanx of each participant's right index finger at the start of the experiment, and thus no external body temperature manipulation was used. Warm and Cool were set to 5 °C above and below neutral, respectively. The temperatures in the two painful conditions were determined separately for each participant based on individually established pain thresholds (please see Section 2.8). In addition, we manipulated the induction of the Rubber Hand Illusion (RHI). At the start of each trial, the experimenter used two identical brushes to stroke the participant's right index finger and the index finger of the rubber hand. This stroking could be done either synchronously (Illusion condition) or asynchronously (Control condition). The experiment therefore consisted of a factorial design combining 5 temperature conditions with 2 RHI stroking conditions.

2.4. Dependent measures

Three dependent measures were considered: (1) the change in the perceived position of the participant's right hand, as measured using a perceptual relocation judgment, an established proxy for the illusion (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Tsakiris & Haggard, 2005), (2) responses to a questionnaire regarding subjective experiences of the RHI, and (3) the change in temperature of the dorsum of the participant's right hand following induction of the RHI.

2.5. Perceptual relocation

Participants were instructed to make a perceptual judgment about the spatial location of their right index finger. A ruler was placed on top of the framework, and participants verbally reported the coordinate on the ruler that they felt corresponded to the perceived location of their right index finger. The difference between the indicated and veridical location of the participant's right index finger was taken as a measure of perceptual relocation. The ruler had a random offset to prevent participants from giving responses based on their memory from previous trials.

2.6. Questionnaire

In each condition, a questionnaire was administered, consisting of 5 statements regarding the subjective experience of the RHI (Table 1). The questions were based

Table 1
Questionnaire probing subjective experiences of the Rubber Hand Illusion.

1.	It seemed I was looking directly at my own hand, rather than at the rubber hand.
2.	It seemed like the rubber hand was my own hand.
3.	It seemed like I had three hands.
4.	It seemed like I couldn't really tell where my hand was.
5.	It seemed like my hand was normal.

on the original RHI study by Botvinick and Cohen (1998) (Q2), and Longo, Schüür, Kammers, Tsakiris, and Haggard (2008) (Q1, 3–5).

Participants rated their level of agreement with each statement on a 7-item Likert scale; +3 being strong agreement, −3 strong disagreement, and 0 being neither agreement nor disagreement. The order of the questions was randomized each time they were presented.

2.7. Temperature change

On each trial the temperature of the dorsal surface of the middle phalanx of the participant's right index finger was measured before and after stroking, using a range-finding infrared laser thermometer. The measure of interest was the change in temperature of the participant's right index finger over the course of the induction phase.

2.8. Procedure

Before the start of the experimental trials, both the temperature of the participant's right index finger, and the baseline temperature of the palmar surface of the participant's right hand were recorded. Subsequently, hot and cold pain thresholds were measured. To establish pain thresholds, participants placed their right hand on the thermal plate, and reported the degree of pain they experienced. Both 10 cm and 20 cm Visual Analog Scales (VAS) were used at random, to prevent participants from merely repeating their previous responses. The participant was instructed that one end of the line corresponded to "no pain at all" and the other to "the worst pain imaginable". They marked the point on the line corresponding to the level of experienced pain. The cold pain threshold was always determined first, starting at 10 °C for all participants. The temperature was reduced in 2 °C decrements until the participant rated the pain experience as exceeding 44% of the scale (Price, Patel, Robinson, & Staud, 2008). The heat pain threshold was determined in a similar way, starting at 46 °C and increasing with 1 °C increments. Mean heat pain threshold was 49.0 °C and the mean cold pain threshold was 3.0 °C. After determination of pain thresholds, the experiment began.

First, the temperature of the participant's right index finger was measured. This was followed by a 90 s induction phase in which the experimenter stroked both the participant's right index finger and the index finger of the rubber hand with two identical paintbrushes. Stroking took place at a random pace, with an average rate of ~1 Hz, and was either synchronous or asynchronous depending on the experimental condition. Directly after the induction phase the framework was covered and the temperature of the participant's finger was measured once more. The participant then judged the perceived location of his/her right index finger by reporting the appropriate position on the ruler. Each condition was tested in a separate block of three trials, and the block order was randomized between participants. After each block the questionnaire was administered. Finally, the temperature of the palmar side of the hand was taken to confirm the effectiveness of the temperature manipulations using the Peltier device.

Table 2
Relocation of perceived position of the participant's own hand towards the rubber hand, caused by visual and tactile stroking (mean ± SEM in cm).

Condition	Synchronous	Asynchronous	Difference
Painfully Cold	12.74 ± 2.64	9.04 ± 2.89	3.70 ± 0.79
Cool	13.26 ± 2.49	7.30 ± 2.40	5.96 ± 0.88
Neutral	12.44 ± 2.40	7.56 ± 2.37	4.89 ± 0.96
Warm	10.33 ± 2.16	7.70 ± 2.35	2.63 ± 0.68
Painfully Hot	13.26 ± 2.62	7.78 ± 2.61	5.48 ± 0.94

3. Results

One of five different temperatures was applied to the palm of the participant's right hand with a large thermode (Painfully Cold, Cool, Neutral, Warm, and Painfully Hot). Next, the Rubber Hand Illusion (RHI) was induced by synchronous (Illusion condition) or asynchronous (Control condition) stroking of the dorsum of the index finger of the participant's unseen right hand and the corresponding part of the rubber hand. Three measures of the RHI were obtained: (1) perceived position of the unseen right hand, (2) scores on a modified subset of a previously developed embodiment questionnaire (Longo et al., 2008) and (3) temperature change on the back of the right hand due to the RHI. Each measure was submitted to a 5 × 2 repeated measures analysis of variance.

3.1. Proprioceptive localization error due to Rubber Hand Illusion

The perceived position of the participant's hand before stroking was subtracted from that after stimulation to calculate a perceptual localization shift. These data are shown in Table 2. There was a main effect of synchronous stroking ($F(1,8) = 35.623$, $p < 0.001$), but no main effect of applied temperature ($F(4,32) = 1.42$, $p = 0.250$). Importantly, the interaction between synchronicity and applied temperature was significant: ($F(4,32) = 9.321$, $p < 0.001$). To explore this interaction further, we calculated the difference between synchronous and asynchronous conditions as a measure of RHI

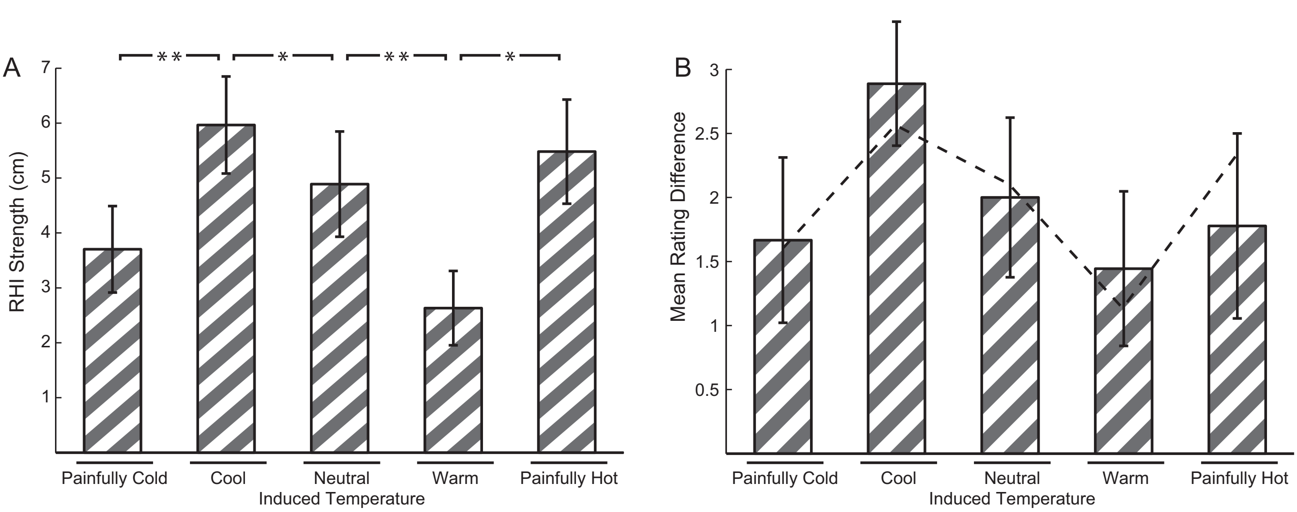

Fig. 1. (A) Strength of the RHI, measured as the difference in perceptual drift of perceived position of the hand between synchronous and asynchronous stroking. Note the effect of externally applied temperature. *$p < 0.05$; **$p < 0.01$, uncorrected – all comparisons remain significant after Holm–Bonferroni correction with a family-wise error rate of 0.05. (B) Bodily awareness questionnaire results: mean rating difference on Question 1 ("It seemed like I was looking directly at my own hand, rather than at the rubber hand") between synchronous and asynchronous stroking, as a function of temperature. The perceptual relocation errors (Panel A) are overplotted for qualitative comparison as a dashed line, using the same scale as Panel A.

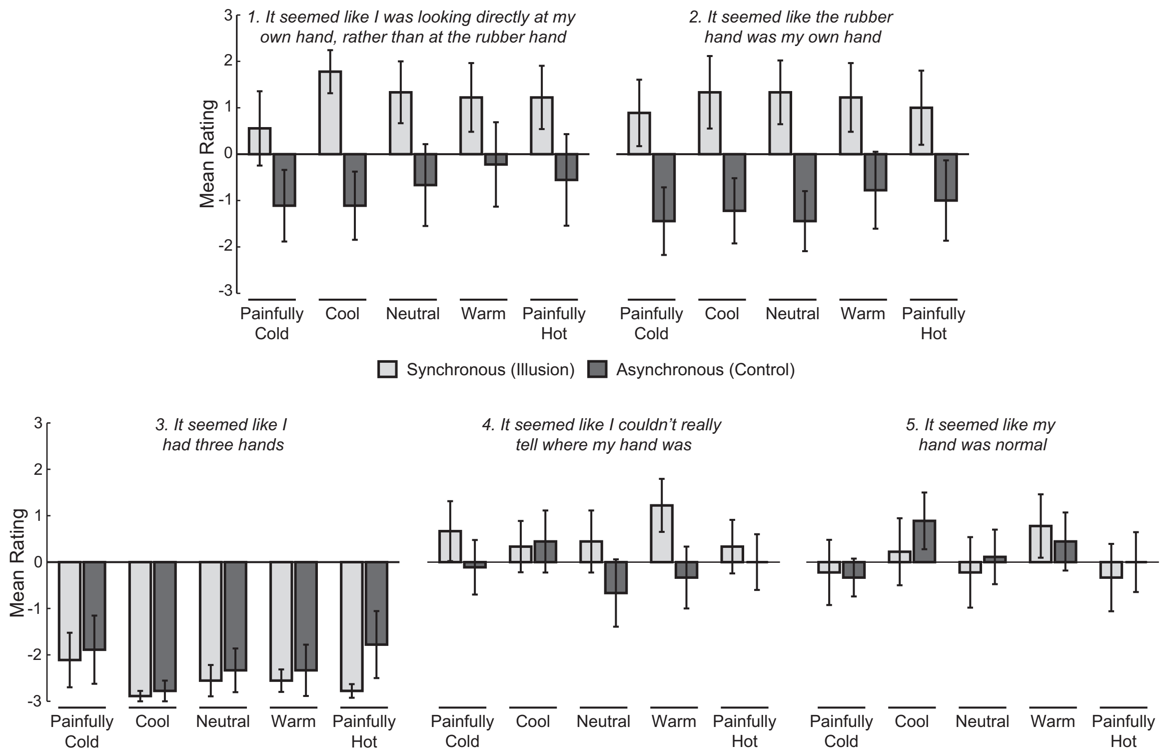

Fig. 2. Questionnaire results: ratings on all questions (mean ± SEM across participants).

Strength (Fig. 1A), and then compared this difference measure for each pair of nearest-neighbour temperature conditions (i.e., Painfully Cold vs. Cool, Cool vs. Neutral, Neutral vs. Warm, and Warm vs. Painfully Hot). We made these four comparisons because we were specifically interested in; (1) the effect of innocuous temperature deviations from neutral and (2) the difference between innocuous and noxious temperature changes. These comparisons showed that the interaction arose from an increase in strength of the RHI in the innocuous cool condition (Cool vs. Painfully Cold: $t(8) = 4.079$, $p = 0.004$; Cool vs. Neutral: $t(8) = 2.936$, $p = 0.019$), and a decrease in strength of the RHI in the innocuous warm condition (Warm vs. Painfully Hot: $t(8) = 3.277$, $p = 0.011$; Warm vs. Neutral: $t(8) = 3.815$, $p = 0.005$). All four comparisons remained significant after Holm–Bonferroni correction with a family-wise error rate of $\alpha = 0.05$. Interestingly, Painfully Hot and Painfully Cold conditions did not seem to differ from Neutral (uncorrected $p = 0.360$ and $p = 0.126$ respectively).

3.2. Rubber Hand Illusion questionnaire

Ratings on each of the RHI questionnaire questions were submitted to repeated measures analyses of variance. As expected, the two core RHI questions (1 and 2) revealed significant main effects of synchronicity ($F(1,8) = 16.407$, $p = 0.004$ and $F(1,8) = 17.376$, $p = 0.003$ respectively) (Fig. 2).

Synchronous and asynchronous conditions did not differ for questionnaire items 3–5, which are “dummy/control” questions unrelated to the RHI (all $p > 0.11$), and designed to identify any response bias. There was no main effect of temperature for ratings on Questions 1–4 (all $p > 0.15$), although unexpectedly ratings on Question 5 just reached significance ($F(4,32) = 2.807$, $p = 0.042$). The direction of this effect was that participants reported their hand to feel more ‘normal’ when it was mildly Warmed or Cooled than when it was Neutral or either Painfully Hot or Cold. This may arise because extreme temperatures are themselves an abnormal experience, however the reason why neutral temperature felt less normal than cool or warm is not clear.

The interaction between temperature and synchronicity was not significant for any of the questions (all $p > 0.18$). Although not significant ($F(4,32) = 1.643$, $p = 0.188$), it was nevertheless striking that responses on Question 1 (which captures the phenomenological core of the RHI) varied in a way that strongly resembled the variation in RHI-induced capture of perceived hand position (Fig. 1A and B).

3.3. Rubber Hand Illusion-induced temperature change

The temperature before each RHI stimulation was subtracted from that after stimulation. Temperatures were averaged across the three trials in each condition. We observed an unsurprising main effect of induced temperature ($F(4,32) = 27.93$, $p < 0.001$): temperature change on the hand dorsum varied with the temperature applied to the palm (Fig. 3).

There was also a main effect of synchronicity, with greater temperature drops in the synchronous (Illusion) condition than asynchronous (Control) condition ($F(1,8) = 5.540$, $p = 0.046$). Post hoc paired sample t-tests show that this effect is driven by the cold ($t(8) = 5.162$, $p = 0.001$) and neutral conditions ($t(8) = 3.531$, $p = 0.008$), with a trend in the warm condition ($t(8) = 1.930$, $p = 0.09$). The result in the neutral condition replicates the drop in temperature of the affected limb during the RHI, first reported by Moseley, Olthof, et al. (2008). Our results extend previous findings by showing that RHI-induced temperature changes can be measured even during application of external thermal stimulation. There was no interaction of temperature and synchronicity ($F(4,32) = 1.114$, $p = 0.367$).

4. Discussion

In the present study, we used the Rubber Hand Illusion (RHI) to investigate the interaction between thermosensation (non-painful

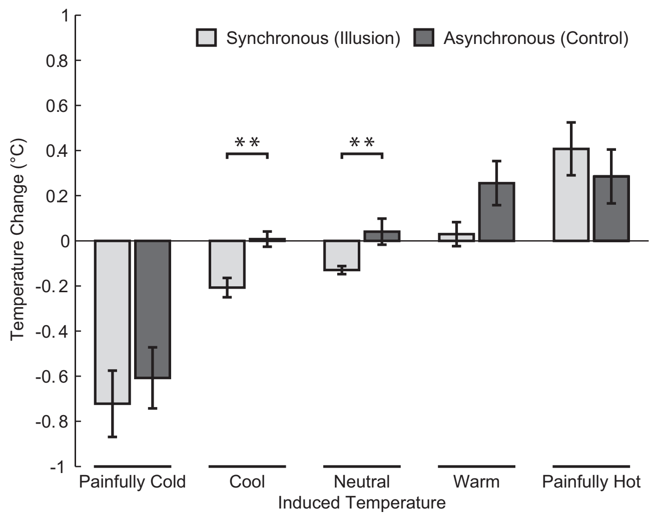

Fig. 3. Change in temperature of the hand dorsum associated with the Rubber Hand Illusion for each of five induced temperatures applied to the palm. $^{**}p < 0.01$.

and painful), thermoregulation, and the subjective experience of body ownership. We replicate previous reports that changes in bodily awareness influence thermoregulation (Moseley, Olthof, et al., 2008). More importantly, we demonstrate for the first time a causal effect in the opposite direction. We show that externally cooling a limb increases the strength of the RHI. This suggests that a cold limb is more readily disowned. Conversely, warming a limb decreases the strength of the RHI, suggesting that a warm limb is less easily disowned.

We found thermal effects on implicit measures of body ownership, i.e., adaptation of the perceived position of the hand by the viewed position of the rubber hand (Tsakiris & Haggard, 2005). Interestingly, explicit subjective judgments of body ownership as measured with a questionnaire were not significantly modulated by these thermal manipulations. This raises the question whether the effect of external manipulation of limb temperature is limited to the position sense of the hand rather than the feeling of limb ownership? The absence of significant thermal modulation of questionnaire responses should however clearly be interpreted with caution. We cannot conclude that subjective experience of embodiment is insensitive to temperature, given our restricted sample of just 9 participants. A previous large-scale psychometric study already showed that proprioceptive drift is related to, rather than dissociated from, the altered subjective experience of ownership in the RHI (Longo et al., 2008). Indeed, pooling the observations across the 5 conditions of our study confirmed a significant overall correlation between proprioceptive drift and responses to the key Questionnaire item 1 ("It seemed that I was looking directly looking at my own hand": $r = 0.344$, $p = 0.02$). However, overall correlations between proprioceptive drift and responses to questions 2–5 did not reach significance ($-0.29 < r < 0.15$, all $p > 0.05$). Further, the questionnaire items that we used focused primarily on explicit feelings of ownership over the rubber hand. In contrast, thermal effects might primarily influence the corollary feeling of disownership of one's own hand. The brain might not enforce a direct, reciprocal relation between ownership over the rubber hand and disownership of one's own hand, as the reported experience of supernumerary limbs in RHI settings demonstrates (Ehrsson, 2009). Certainly, studies investigating thermoregulation suggest that reductions in hand temperature are linked to disownership of one's own hand, rather than acquiring ownership over the rubber hand (Hohwy & Paton, 2010; Moseley, Olthof, et al., 2008).

The modulating effect of both cooling and warming on position sense might reflect the effects of moderate thermal stimulation on somatosensory processing. Cooling the body decreases conduction velocity and transmission efficiency of somatosensory afferents (Markand et al., 1990; Phillips & Matthews, 1993). Conversely, warming the body decreases somatosensory latency (Russ, Sticher, Scheld, & Hempelmann, 1987), and boosts transmission efficiency (Krnjevic & Morris, 1976). Our results are consistent with this general thermal modulation of somatosensation. The interaction we found between moderate thermal stimulation and measures of body ownership (Fig. 1A and B) suggests that the RHI is strongest during cooling, when somatosensory signals are weak. Conversely, warm conditions that boost somatosensation weaken the RHI. This pattern of results is consistent with an interpretation of the RHI as a competition between external (visual) and internal (somatosensory) signals about the body. Thus, visual information most readily captures body ownership, producing a strong proprioceptive relocation effect in the RHI, when somatosensory signals are weak, such as during cooling. However, this explanation cannot explain why more extreme cold weakens rather than increases the RHI effect.

Previously, drop in limb temperature was interpreted as an autonomic thermoregulatory response to disembodiment (Moseley, Olthof, et al., 2008). However, our results show that the causal direction of this relation might be more complicated. In particular, actively cooling the limb itself causes decreases in the sense of body ownership. The relation between temperature and body ownership may well depend on interactions in the insula, which houses thermosensory processing, and is thought to underlie bodily self-awareness (Craig, 2002, 2009; Dijkerman & de Haan, 2007).

Furthermore, altered body temperature has also been linked to disturbed feelings of ownership, pain and self-injury behavior. For example, self-mutilation is often associated with dislike and disownership of the relevant body part. Interestingly, the temperature of the affected body part is also altered (Symons, Sutton, & Bodfish, 2001). Moreover, a drop in temperature in the affected limb of chronic CRPS patients often goes together with a neglect of that limb (Moseley, 2005 – for an overview of clinical conditions characterized by body ownership and thermosensory disturbances please see Table S1 in Moseley, Olthof, et al., 2008). Our finding suggests that functional therapies that aim at restoring a sense of ownership should perhaps warm the affected limb. Similarly, when self-mutilation is focused on a specific body part, we speculate that keeping the limb slightly warm might have a preventative effect. Conversely, when it is desirable to decrease the awareness of a limb, for example during training to use a teleoperated prosthesis *instead* of one's own limb, or when attention to and use of a healthy limb is discouraged as part of constraint-induced therapy for paresis (Sirtori, Corbetta, Moja, & Gatti, 2009), cooling the limb may be useful.

A second and perhaps surprising result of our study was the failure of pain to modulate bodily awareness as measured by the RHI. The pain stimuli administered here involved more extreme versions of the warm and cool stimulation that both effectively influenced the RHI. However, both painfully cold and painfully hot stimuli activate different receptors, and recruit different peripheral and central systems from their non-painful equivalents (Craig, 2009; Craig & Dostrovsky, 2001). Therefore, the effects of painful extremes on bodily awareness need not necessarily be stronger versions of the effects found for mild thermal stimuli.

The self-intimating, private and conscious character of pain is widely recognized (Craig, 2009). Pain also reminds us of our 'real' body and thus seems to have a special status in body ownership. Here, we show that acute thermal pain during the RHI neither abolishes nor enhances the relocation of one's own hand or subjective feeling of ownership. This is in line with the results of Capelari et al. (2009) who found that the RHI could be induced as easily by painful tactile stimulation as by innocuous tactile stimulation.

Dijkerman and de Haan (2007) recently proposed a 'dual-route' model of bodily awareness. One somatosensory network, focused on primary somatosensory and parietal cortices, processes tactile and proprioceptive signals for perception. A second network, focused on the insula, processes affectively relevant stimuli. Since nociceptive input also projects preferentially to the insula, our findings are compatible with their broad framework. The RHI would be located in the S1-parietal pathway, capable of being modulated by thermal input, but largely independent of nociceptive processing.

Ehrsson and colleagues (Ehrsson, 2009; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007) investigated feelings of ownership during the RHI in terms of responses to the threat of pain (skin conductance response – SCR). They found that stabbing a rubber hand with a needle increased SCR, and also activated the insula. They concluded that "artificial limbs can evoke the same feelings as real limbs and provide objective neurophysiological evidence that the rubber hand is fully incorporated into the body" (Ehrsson et al., 2007). In our study, painful stimuli were applied continuously to the participants' own hand. The pain was not linked to the rubber hand (Ehrsson et al., 2007), and did not form part of the multisensory stimulation that induced the RHI (Capelari et al., 2009). A painful stimulus attracts more attention and receives processing priority over non-painful stimuli (Eccleston & Combrez, 2005; Van Ryckeghem et al., 2011). However, the ongoing thermal pain in our study might have been too predictable and insufficiently salient or threatening to engage pain-specific changes in multisensory processing (Moseley, 2007).

To conclude, this study investigated the links between temperature, pain and sense of body ownership. The sense of one's own body in the multisensory RHI was modulated by externally applied temperatures. Previous studies suggested that altered bodily awareness produced changes in local body temperature. Our results demonstrated a link in the opposite direction: externally induced changes in body temperature produced alterations in bodily awareness measured using the RHI. Thus, while we agree with previous work on the direction of the relation between awareness and temperature (body disownership cause a drop in temperature), we suggest that the inverse causal direction also applies (externally applied cooling causes disownership). Finally, our results confirm the strong relation between thermosensory processing and bodily awareness suggested by Craig (2009).

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