Abstract

The rubber hand illusion (RHI) paradigm—in which illusory bodily ownership is induced by synchronous tactile stimulation of a participant’s (hidden) hand and a (visible) surrogate—allows one to investigate how the brain resolves conflicting multisensory evidence during perceptual inference. To identify the functional anatomy of the RHI, we used multichannel EEG, acquired under three conditions of tactile stimulation. Evoked potentials were averaged from EEG signals registered to the timing of brushstrokes to the participant’s hand. The participant’s hand was stroked either in the absence of an artificial hand (“REAL”) or synchronously with an artificial hand, which either lay in an anatomically plausible (“CONGRUENT”) or impossible (“INCONGRUENT”) position. The illusion was reliably elicited in the CONGRUENT condition. For right-hand stimulation, significant differences between conditions emerged at the sensor level around 55 msec after the brushstroke at left frontal and right parietal electrodes. Response amplitudes were smaller for illusory (CONGRUENT) compared with non-illusory (INCONGRUENT and REAL) conditions in the contralateral perirolandic region (pre- and postcentral gyri), superior and inferior parietal lobules, whereas veridical perception of the artificial hand (INCONGRUENT) amplified responses at a scalp region overlying the contralateral postcentral gyrus and inferior parietal lobule compared with the remaining two conditions. Left-hand stimulation produced similar contralateral patterns. These results are consistent with predictive coding models of multisensory integration and may reflect the attenuation of somatosensory precision that is required to resolve perceptual hypotheses about conflicting multisensory input.

INTRODUCTION

If asked about their body ownership, most people would feel confident that their perception of what constitutes a part of their body is set in stone. However, perceptual illusions like the rubber hand illusion (RHI)—which refers to the induction of illusory ownership of a plastic hand during its tactile stimulation in synchrony with the participant’s hidden hand—clearly illustrate that the feeling of bodily ownership is malleable (Botvinick & Cohen, 1998). These illusions suggest that body representation is a transitory internal construct that can be altered by external stimuli (Armel & Ramachandran, 2003). fMRI studies have linked the RHI with BOLD activations in the ventral premotor cortex (Bekrater-Bodmann, Foell, Diers, & Flor, 2012; Ehrsson, Spence, & Passingham, 2004), parietal and cerebellar areas (Ehrsson et al., 2004). In a lesion study in stroke patients, it was demonstrated that ventral premotor cortex and its connections might be crucial for mediating changes in the sense of limb ownership during multisensory stimulation (Zeller, Gross, Bartsch, Johansen-Berg, & Classen, 2011). Despite these—and a number of other studies based on the RHI and similar paradigms—the processes by which sensory information is dynamically integrated into one’s body representation are poorly understood. The ability of fMRI to resolve neuronal activity is limited by its indirect approach. Therefore, recording electrical brain activity directly might offer important complementary insights into the neural correlates of the RHI. An attractive opportunity to investigate the physiological mechanisms underlying the RHI is provided by the fact that the illusion requires repetitive tactile stimulation—thus enabling the recording of electrical cortical correlates. Surprisingly, such approaches have either limited themselves to the analysis of late responses (latencies >80 msec to ∼500 msec; Peled, Pressman, Geva, & Modai, 2003), which are believed to involve activity in and reentrant feedback from secondary somatosensory, posterior parietal, and other cortices (Allison, McCarthy, Wood, Williamson, & Spencer, 1989) or have focused on topographical representational changes in the primary somatosensory area (S1; Schaefer, Konczak, Heinze, & Rotte, 2013; Schaefer, Noennig, Heinze, & Rotte, 2006).

In this study, we examined early touch-evoked potentials elicited by the brushstrokes eliciting the RHI and two control conditions in healthy controls. Source analysis allowed...
us to ask which cortical source modulation underlies the RHI. Specifically, we appealed to predictive coding models of perceptual inference during multisensory integration. Predictive coding is a neuronally plausible scheme for (hierarchical Bayesian) inference about the causes of sensations (Friston, 2008; Friston & Stephan, 2007). The RHI rests on proprioceptive, mechanoreceptive, and visual sensations that allow inferences about the position of the arm and any tactile stimulation. Crucially, the illusion arises when a parsimonious—but incorrect with respect to the actual reality—explanation for somatosensory and visual cues assigns the experience of ownership to the artificial hand. This involves the suppression of proprioceptive evidence that the two hands are in different positions. In predictive coding, this corresponds to a reduction in the precision afforded to—or confidence placed in—sensory prediction errors (Brown, Adams, Parees, Edwards, & Friston, 2013), where precision is encoded by the postsynaptic gain of superficial pyramidal cells (Moran et al., 2013; Shipp, Adams, & Friston, 2013; Brown & Friston, 2012; Feldman & Friston, 2010). This encoding of precision or confidence has been interpreted in terms of attentional gain (Bastos et al., 2012; Feldman & Friston, 2010). This is important because superficial cortical layers are thought to be a malleable source of measured event related potentials (Petersen & Crochet, 2013; Schroeder et al., 2005). In summary, we hypothesized that the attenuation of somatosensory precision during the RHI would be manifest electrophysiologically as a relative reduction in the amplitude of evoked responses in (primary sensorimotor) sources associated with somatosensation and (parietal) sources involved in the interaction of visual and somatosensory cues at the same location in extrapersonal space.

METHODS

Participants

Experiments were performed on 13 healthy volunteers (nine men, four women) aged 21–32 years (mean = 24.7 ± 4.1 years). Ten volunteers were right-handed, three were ambidextrous according to a modified version of the Edinburgh Inventory (Oldfield, 1971). All volunteers had participated in a prior study on the prevalence of the Edinburgh Inventory (Oldfield, 1971). Only two had participated in a prior study on the prevalence of the Edinburgh Inventory (Oldfield, 1971). All volunteers were familiar with the RHI setting and the potential occurrence of the ownership illusion, they were naive to the particular purpose of this study. The study conformed to the principles of the declaration of Helsinki. It was approved by the Ethics Committee of the Medical Faculty at the University of Würzburg. All volunteers gave their written informed consent for this research study.

EEG Recording

EEG signals were recorded from the scalp with a 64-channel Quickamp system (Brain Products GmbH, Munich, Germany). The electrodes were located at extended 10–20 system locations and fixed on the participant’s head with an elastic cap (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). The electrode impedance was kept below 5 kΩ and verified before each recording. Three-dimensional electrode positions and anatomic reference points were registered using an ultrasound-based navigation system (Zebris Medical GmbH, Isny, Germany). The brain signals were average referenced in hardware, filtered between 0 and 560 Hz, and sampled at 2000 Hz.

Rubber Hand Illusion

Participants were seated comfortably in an armchair with the right or left arm resting on a table. Three conditions were sampled (two blocks of 5 min each) in a randomized, counterbalanced order: (i) REAL: The participant’s hand and forearm were resting on the table. The participant was sitting with eyes fixed on the real hand, which was repetitively touched by a brush as described below. (ii) CONGRUENT: As in the original rubber hand experimental setting (Botvinick & Cohen, 1998), the participant’s real hand was hidden from view in a shoebox with a 10 cm × 8 cm open window on both sides. A realistic, life-sized, gender- and side-matched artificial hand was placed on the top of the box in an anatomically plausible position, and the gap between the trunk of the artificial hand and the participant’s upper arm was covered with a towel. The participant sat with eyes fixed on the artificial hand, whereas the experimenter used two interconnected small paintbrushes to stroke the (visible) artificial hand and the (hidden) real hand—synchronizing the timing of the brushstrokes as closely as possible. (iii) INCONGRUENT: The artificial hand was flipped 180° around its longitudinal axis (palm upwards) with an otherwise identical setting as described for CONGRUENT (see Figure 1A for an illustration of the experimental setup). The brushstrokes were small and brisk and applied to the dorsal surface of the middle phalanx of the index; middle and ring finger at 0.5–3 Hz. Touches were registered as trigger signals by a custom-built brush handle containing an electrical switch, thereby allowing analysis of touch-evoked potentials.

Experimental Procedure

In each participant, both hands were tested sequentially in randomized order—separated by a 10-min break to avoid fatigue. For each hand, tactile stimulation was applied in
six blocks of 5 min each (two blocks per condition; see Figure 1B for a schematic overview of an exemplary experimental sequence). EEG was recorded continuously with the exception of the break. During EEG recording, a second experimenter set markers indicating the respective stroking condition. Participants were instructed to report whether they felt that the rubber hand was their own hand or not. They were asked to press a foot switch once if this feeling of ownership occurred and twice if it disappeared (in the CONGRUENT and INCONGRUENT conditions).

**Evoked Potential Analysis**

**Data Preparation**

Data from right- and left-hand stimulation were analyzed identically, though separately. The triggers were sorted based on the stimulation condition (as indicated by markers set by the second experimenter) and the presence or absence of the illusion (as indicated by foot switch markers). Individual EEG data were epoched between −200 and +300 msec relative to the touch trigger signal from the brush handle, and trials containing artifacts were rejected. Averages were computed using BESA software (BESA GmbH, Gräfelfing, Germany). Trials were considered artifact and excluded from averaging if they satisfied one of the following two conditions: (1) the amplitude difference between the largest and the smallest sample within the trial in any channel exceeded 200 μV and (2) the voltage difference between two adjacent samples in any channel exceeded 75 μV.

Participants reported (by foot switch) the presence of the illusion in 85.5% (median; range = 43–100%) of the epochs during CONGRUENT and absence of the illusion in 93.0% (median; range = 25–100%) epochs during INCONGRUENT. Therefore, averaging yielded evoked potentials under three conditions: real hand stimulation only (REAL), synchronous stimulation with an anatomically plausible position of the artificial hand and presence of the RHI (CONGRUENT), and synchronous stimulation with an anatomically impossible position of the artificial hand and absence of the RHI (INCONGRUENT). SPM12 software was used for all the subsequent steps of data analysis (Litvak et al., 2011; www.fil.ion.ucl.ac.uk/spm). The average responses were bandpass filtered between 2 and 20 Hz to establish a flat baseline and remove high-frequency noise. Because of the unavoidable jitter in the trigger times and differences between individual brush touches, sharp evoked response peaks, which are characteristic, for example, for median nerve somatosensory-evoked potentials (MN-SEP), were not expected to appear, hence the 20-Hz cutoff.

**Sensor Level Analysis**

For each participant and condition, SPM EEG sensor data were transformed to Scalp × Time images (3-D image files with the dimensions space [x, y] and time [z]). To identify significant differences between the three stimulation conditions, F-contrasts were calculated at the group level to create SPMs of significant effects in sensor space. This is the standard approach implemented in SPM software (Litvak et al., 2011; Kilner & Friston, 2010). Its advantage over more traditional peak-based analyses is that it does not assume that physiologically interesting differences are limited to response peaks. Indeed in this study, where the activity locked to brush touch consists of both somatosensory and visual components, the peaks are likely to result from the particularities of summation of several latent components and may not be particularly meaningful (Luck, 2005). Conversion of channel-based data to images increases the number of tests that should be corrected for. However, this does not lead to severe loss of statistical power because the correction for multiple comparisons using random field theory takes into account the smoothness of the data on the scalp, no matter how densely the data are sampled (Kilner & Friston, 2010).
Source Level Analysis

Post hoc analysis at the source level was based on predefined time windows showing significant differences on the sensor level. The individually measured sensor locations were coregistered with the canonical head model included in SPM. A boundary element model (Phillips, Mattout, & Friston, 2007) was used for lead field computation. Bayesian source reconstruction method (Mattout, Phillips, Penny, Rugg, & Friston, 2006) with smoothness prior (“COH” option in SPM interface) was used to reconstruct source activity for the whole epoch (−200 to 300 msec). Source activity was then averaged in the 50–55 msec window, and average power was exported in the Geometry format under the Neuroimaging Informatics Technology Initiative. This format is suitable for representing activity on the cortical mesh and can be entered directly into statistical analysis in SPM12. Following source reconstruction, t contrasts were used to test for differences between conditions to produce statistical parametric maps in source space. All the reported effects are significant at the level of $p < .05$, family-wise error (FWE)-corrected, unless stated otherwise.

RESULTS

All participants were able to follow the instructions and maintain their attention during the whole experimental session. Touch-evoked potentials (all trials of one hand side combined, irrespective of condition) displayed a positive-going wave peaking at around 50 msec, with its maximum over the posterior contralateral part of the scalp, along with a negative-going wave with its maximum over the frontocentral part at the same time (scalp topography and average scalp maps are shown in Figure 2). Subsequent analysis was performed separately for each side and condition. For the CONGRUENT condition, only trials with the illusion reported as present were included. For INCONGRUENT, only trials where the illusion was absent were considered.

Sensor Level Analysis

For right-hand stimulation, sensor level analysis of differences among the stimulation conditions revealed significant clusters near electrode F3 at 56 msec ($p = .006$) and electrode P2 at 54 msec ($p = .015$; see Figure 3A). Inspection of the F3 sensor data pointed to a decreased amplitude at the frontal negative peak around 50 msec in the CONGRUENT condition as compared with REAL and INCONGRUENT. At sensor P2, a larger parietal positive peak emerged around 50 msec in the INCONGRUENT condition as compared with CONGRUENT and REAL (see Figure 3A).

Figure 2. Scalp distribution of touch-evoked potentials. All trials of one hand were averaged, irrespective of the stimulation condition. Top: Scalp topography for right (A) and left (C) hand stimulation. A time window of −200 to +300 msec is shown. Bottom: Average scalp maps at 50 msec poststimulus for right (B) and left (D) hand stimulation. For all panels: left is left side of the head.
For left-hand stimulation, no significant clusters survived FWE correction. However, we performed an exploratory analysis, setting the significance level at $p = .001$ (uncorrected). There was a very similar contralateral pattern, appearing slightly later than with right-hand stimulation, with clusters near electrode F6 at 66 msec and next to electrode Pz at 76 msec (see Figure 3B). Again, inspection of the F6 sensor data at the frontal negative peak around 50 msec pointed to decreased amplitude in the CONGRUENT condition as compared with the others. At sensor Pz, the parietal positive peak around 50 msec appeared to be larger in the INCONGRUENT condition as compared with CONGRUENT and REAL (see Figure 3B).

**Source Analysis**

For right-hand stimulation, post hoc contrasts on the source level response estimates showed significantly smaller amplitudes for CONGRUENT as compared with INCONGRUENT and REAL at the contralateral pre- and postcentral gyri, superior and inferior parietal lobule ($p < .05$). Moreover, for the INCONGRUENT condition, source amplitudes were larger at a scalp region overlying the contralateral postcentral gyrus and inferior parietal lobule as compared with the other conditions (see Figure 4A and Table 1).

For left-hand stimulation, post hoc analysis revealed significantly lower amplitudes for CONGRUENT as compared with INCONGRUENT and REAL at a region overlying the contralateral postcentral gyrus only and higher amplitudes for INCONGRUENT as compared with the other conditions at contralateral postcentral gyrus and paracentral lobule (see Figure 4B and Table 1).

**DISCUSSION**

This study has examined how the processing of somatosensory input, as assessed by evoked potentials, is modulated by viewing of a hand to which participants correctly or incorrectly infer is their own hand. Both sensor and source space analyses revealed that, during the illusion, there was a relative attenuation of somatosensory-evoked responses in frontal electrodes that correspond to cortical...
sources in the appropriate (contralateral) perirolandic area and hierarchically higher sources in the parietal lobe. Moreover, in the absence of an illusion but in the presence of a (perceived) artificial hand, responses were larger in the parietal electrodes that correspond to parietal sources in primary somatosensory cortex and inferior parietal lobule within the limits of spatial resolution of multichannel surface EEG.

Brushstrokes evoked a broad positive wave at the contralateral parietal electrodes with a peak latency of around 50 msec, a consistent finding both at the individual and group levels. This wave, termed P50 hereafter, corresponds to a P2 wave recorded in previous studies of somatosensory responses (Nakanishi, Takita, & Toyokura, 1973; Larsson & Prevec, 1970). Consideration of the delays by mechanoelectric transduction and conduction of the impulse from the middle finger to the wrist suggests that this P50 most likely represents the equivalent to the P45 component of SEP-evoked by electrical compound median nerve stimulation (Nakanishi et al., 1973). The absence of recognizable earlier components in evoked responses agrees with the majority of studies on touch- or air-puff-evoked potentials (Longo, Pernigo, & Haggard, 2011; Sambo, Gillmeister, & Forster, 2009; Taylor-Clarke, Kennett, & Haggard, 2002; Hashimoto, Yoshikawa, & Sasaki, 1990; Halliday & Mason, 1964)—and likely is due to a lack of temporal synchrony during tactile stimulation (Hashimoto et al., 1990; Larsson & Prevec, 1970). Like early (N20, P25, and N33) components, the P45 component of MN-SEP is thought to originate from the primary sensory cortex of the hand (Lee & Seyal, 1998; Allison et al., 1989), suggesting an anatomical origin in S1 for the P50. Brushstrokes reflect the somatosensory stimulation pertinent to the RHI paradigm. Because they entail little, if any, proprioceptive stimulation, they allow the rather selective characterization of mechanoreceptive processing (Rossini et al., 1996; Halliday & Mason, 1964).

We found that the P50 was differentially modulated across stimulation conditions: Compared with REAL and INCONGRUENT, activity was reduced in CONGRUENT at electrodes overlying contralateral sensorimotor and parietal cortex. To interpret this finding, it is important to realize that the participants’ judgment of ownership was consistent with the actual reality for the REAL (“this is my hand”) and INCONGRUENT (“this is not my hand”) conditions. In contrast, during CONGRUENT stimulation, the participants erroneously (though intended by the experimental setup) perceived the artificial hand as their own. However, because of the synchronicity of touch, the participants could not easily infer that the brush they saw touching the artificial hand was actually not touching their own hand. Thus, any physiological difference that is unique to the CONGRUENT condition is likely to be related to the illusion. Source analysis located the difference between the conditions to contralateral perirolandic region (pre- and postcentral gyrus) and to the superior and inferior parietal lobule, adjacent to the intraparietal sulcus. Although previous electrophysiological studies

![Figure 4](https://via.placeholder.com/150)

**Figure 4.** Statistical parametric maps of the key statistics testing for (signed) significant differences between conditions in source space: Post hoc results on the source level for (A) right-hand stimulation and (B) left-hand stimulation. *t* Values for areas with significantly (*p* < .05, FWE-corrected) lower activation in the CONGRUENT condition (top part of figure) or higher activation in the INCONGRUENT condition (bottom part of figure) as compared with the respective other conditions are color-coded.
(Evans & Blanke, 2013; Aspell, Palluel, & Blanke, 2012; Lenggenhager, Halje, & Blanke, 2011; Dieguez, Mercier, Newby, & Blanke, 2009; Kanayama, Sato, & Ohira, 2007; Schaefer et al., 2006) have pointed to involvement of the primary somatosensory cortex in bodily illusions, the present findings provide new evidence suggesting a role of anterior parietal regions in the RHI in agreement with previous findings obtained by fMRI (Gentile, Guterstam, Brozzoli, & Ehrsson, 2013; Guterstam, Gentile, & Ehrsson, 2013; Ehrsson et al., 2004).

The question arises—what might be the principles underlying the relative attenuation of activity projecting onto the postcentral gyrus and intraparietal sulcus? Processing of somatosensory information, especially if conflicting, can be subject to top–down modulation, even in primary somatosensory cortex and even at very early timings (Longo et al., 2011; Bernier, Burle, Vidal, Hasbroucq, & Blouin, 2009; Meehan, Legon, & Staines, 2009). Simply viewing the hand as opposed to a nonhand object tended to reduce the P45 amplitude of MN-SEP (Longo et al., 2011). In CONGRUENT, attenuation of postcentral and intraparietal sulcus activity cannot be attributed to viewing an artificial hand, because the viewed hand was experienced as the participant’s own hand; hence, attenuation most likely reflects the perceptual synthesis underlying the illusory inference. Suppression of proprioceptive information to reduce interference with proper task performance has been suggested to underlie attenuation of early (e.g., P27) MN-SEP components during performance of a complex novel mirror tracking task (Bernier et al., 2009). This explanation, however, does not easily apply to this study, as mechanoreception, but not proprioception, was stimulated by brushing the skin, whereas to accomplish the illusory perceptual inference, the principal conflict to be resolved was between vision and proprioception. It thus may appear surprising that mechanoreceptive input, as indexed by the touch-evoked responses during the illusion, was attenuated. So is it possible that relative attenuation of touch-evoked potentials may reflect a general attenuation of somatosensory input? Behavioral support for this hypothesis might be provided by studies of top–down modulation of sensory input during the RHI (Zopf, Harris, & Williams, 2011; Moseley et al., 2008). Moseley and colleagues used a temporal order judgment task to examine the weighting given to tactile information from the real hand in relation to absence or presence of the RHI (Moseley et al., 2008). The “point of subjective simultaneity” shifted away from the real hand during the illusion, thus pointing to a temporary “disownership” of the real hand as known from neurological disorders like unilateral spatial neglect after stroke. Therefore, although the intersensory conflict occurred predominantly between vision and proprioception, processing of mechanoreceptive information (at least of temporal aspects) was also affected during the RHI. Zopf et al. investigated the effect of an experimentally induced feeling of body ownership on tactile perception (Zopf et al., 2011). Synchronous touch—that signaled ownership for a seen hand—led to an increased

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Zeller et al.
tactile detection threshold, whereas the discrimination performance for high-amplitude stimuli improved. These differential effects on two aspects of tactile perception might indicate a shift in gain control by top–down modulation. Against this background, relative attenuation of P50 may indeed point to a general modulation of somatosensory information processing—which includes gating of tactile inputs, but also proprioception—that is driven entirely by the perceptual processing leading to the RHI.

We also found that the P50 was enhanced in INCONGRUENT, relative to REAL and CONGRUENT. Source analysis localized the difference to postcental gyrus and inferior parietal lobule. As noted above, the RHI was absent in all trials considered for analysis in INCONGRUENT. Therefore, in contrast to CONGRUENT, the INCONGRUENT condition did not produce a percept with intermodal sensory conflict. There was no mismatch between proprioception and vision, as participants were aware that the artificial hand was not their own hand. Hence, an important difference of INCONGRUENT as compared with CONGRUENT and REAL was that vision of that stimulated hand, which was currently perceived as one’s own hand, was not provided. As mentioned above, the P45 amplitude of MN-SEP tended to be reduced by simply viewing one’s own hand (Longo et al., 2011), which could apply to REAL and CONGRUENT. In contrast, the flipped hand was viewed as not belonging to the own body during the INCONGRUENT condition. Accordingly, the P50 associated with INCONGRUENT would not be enhanced but would constitute the native condition, whereas the magnitude of the P50 source with REAL and CONGRUENT would reflect attenuation by vision of the hand. Because the embodiment of the artificial hand was largely stable when the hand was oriented in an anatomically plausible orientation, we cannot disambiguate whether reduction of P50 in REAL and CONGRUENT was because of viewing a hand or because of ownership feelings about the viewed hand.

A potential limitation of the study might be that FWE-corrected significant results were only demonstrated for right-hand stimulation. However, a similar pattern was also observed for left-hand stimulation, although expression of this pattern was somewhat weaker. Although this asymmetry may suggest a lateralization of the processing of body ownership in favor of the left hemisphere, there is a growing body of evidence from neuroimaging and neuropsychological studies favoring a right-hemispheric specificity for self-processing and for body ownership (Ocklenburg, Peterburs, Ruther, & Gunturkun, 2012; Ocklenburg, Ruther, Peterburs, Pinnow, & Gunturkun, 2011; Tsakiris, 2010; Baier & Karnath, 2008; Frassinetti, Maini, Romualdi, Galante, & Avanzi, 2008; Naito et al., 2005). The reason for this discrepancy remains largely speculative—notionally, the right-hemispheric dominance might not emerge at the early steps of sensory processing, which have been assessed in this study. Another limitation might be that there is no completely “neutral” baseline condition, so that the data need to be interpreted in terms of a relative rather than an absolute attenuation or facilitation.

Our study was motivated by predictions from Bayesian accounts of multisensory integration and illusory phenomena; specifically, the framework provided by predictive coding. Illusions are a fascinating example of Bayesian optimal inference, in which the most likely cause of sensations differs from how the sensory input was actually caused (Hohwy, 2012). The RHI represents an interesting problem because there are two competing hypotheses or inferences that could explain multisensory data (Hohwy & Paton, 2010): first, the hand that is seen is actually artificial and is receiving the same somatosensory stimulation as the real hand. Although this is a plausible explanation, it is—a priori—highly unlikely. A much simpler explanation is that the hand that is seen and felt are the same hand. However, proprioceptive information reporting the position of the hand and any potential mismatch between seen and felt touch are inconsistent with the simpler (illusory) explanation. In predictive coding, these inconsistencies correspond to increasing uncertainty or decreasing precision about proprioceptive and mechanoreceptive input. To optimally accommodate this uncertainty, predictive coding will decrease the precision of ascending proprioceptive and mechanoreceptive prediction errors—so that they have less influence on top–down predictions. In biological implementations of predictive coding, this uncertainty or precision is encoded by the gain of superficial pyramidal cells that are thought to encode prediction errors (Bastos et al., 2012; Mumford, 1992). This gain control provides a formal and physiological account of attentional bias and attentional gain as measured psychophysically and electrophysiologically (Feldman & Friston, 2010). Because event-related potentials may be modulated by projections impinging on apical dendrites (Peterson, Schroeder, & Arezzo, 1995), the hypothetical reduction in gain mediated by superficial pyramidal cells—necessary to resolve the multisensory inconsistencies or conflict under the illusory explanation—should lead to a reduction in the amplitude of evoked responses; which is essentially what we observed. From a functional perspective, this corresponds to ignoring evidence that is inconsistent with the illusion by not attending to it. Our data provide new neurophysiological evidence to suggest that higher-order cognitive processing—associated with the spatial representation of self—may selectively attenuate somatosensory processing during the RHI.

In conclusion, the occurrence of the RHI may be accompanied by a relative attenuation of proprioceptive and mechanoreceptive input. This attenuation can be localized to the primary somatosensory cortex and sources in the anterior intraparietal sulcus. Crucially, this attenuation has to be established by perceptual set (illusory beliefs) because it is expressed early in peristimulus time (before stimulus related processing at higher hierarchical levels can re-enter lower cortical levels). In other words, the presumed attenuation of sensory precision or gain in
somatosensory systems is established (and expressed electrophysiologically) before the multimodal integration of sensory afferents implicit in hierarchical inference. This integration is generally evident after 100 or so milliseconds—and is expressed in terms of late or endogenous ERP components that are mediated by backward connections (conveying modality-specific predictions; Garrido, Kilner, Kiebel, & Friston, 2007). Our results, thus, add novel neurophysiological evidence to the fMRI findings pointing to involvement of somatosensory system extending to the parietal cortex in the RHI. The results are consistent with our hypothesis that illusory perceptual inference rests on the relative attenuation of sensory precision of ascending somatosensory afferents to the contralateral motor and somatosensory cortex and subsequent updating of the inferred position of the hand in parietal cortex. They also suggest the (nonillusory) synthesis of tactile and visual signals in the rubber hand setup engages precise prediction errors in higher (parietal) hierarchical sources. This follows from enhanced response components originating in the inferior parietal lobule and is consistent with a reciprocal relationship between sensory and nonsensory precision in hierarchical predictive coding. This reciprocal relationship follows from the fact that expectations about the causes of sensations depend on, and only on, the relative precision of successive hierarchical levels (cf., Mathys, Daunizeau, Friston, & Stephan, 2011).

Acknowledgments

The study was supported by departmental research funds. V. L. was funded by the German Academic Exchange Service (DAAD). K. F. was funded by the Wellcome trust.

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