

Laterality in the rubber hand illusion

Sebastian Ocklenburg, Naima R ther, Jutta Peterburs,
Marlies Pinnow, and Onur G nt rk n

Ruhr-Universit t Bochum, Bochum, Germany

In patient studies, impairments of sense of body ownership have repeatedly been linked to right-hemispheric brain damage. To test whether a right-hemispheric dominance for sense of body ownership could also be observed in healthy adults, the rubber hand illusion was elicited on both hands of 21 left-handers and 22 right-handers. In this illusion, a participant's real hand is stroked while hidden from view behind an occluder, and a nearby visible hand prosthesis is repeatedly stroked in synchrony. Most participants experience the illusionary perception of touch sensations arising from the prosthesis. The vividness of the illusion was measured by subjective self-reports as well as by skin conductance responses to watching the rubber hand being harmed. Handedness did not affect the vividness of the illusion, but a stronger skin conductance response was observed, when the illusion was elicited on the left hand. These findings suggest a right-hemispheric dominance for sense of body ownership in healthy adults.

Keywords: Cerebral asymmetry; Handedness; Body ownership.

One of the fundamental questions of modern neuroscience is ‘‘Where in the brain is the self?’’ (Feinberg & Keenan, 2005). Answers to this question have for example been given by studies on self-awareness, which typically reveal a right-hemispheric dominance (for an extensive review of this topic see Keenan, Rubio, Racioppi, Johnson, & Barnacz, 2005). Further evidence for this assumption is provided by studies with brain-damaged patients with an impaired sense of body ownership, and thus a reduced ability to experience a limb as part of the self. Typically, such impairments are associated with right-hemispheric damage (Feinberg & Keenan, 2005). For example, studies on somatoparaphrenia, a rare neurological disorder characterised by a delusion of disownership of body parts contralateral to the lesioned

Address correspondence to: Sebastian Ocklenburg, Abteilung Biopsychologie, Institut f r Kognitive Neurowissenschaft, Fakult t f r Psychologie, Ruhr-Universit t Bochum, Universit tsstra e 150, D-44780 Bochum, Germany. E-mail: sebastian.ocklenburg@rub.de

We would like to thank Jessica Upadeck and Kathrin Korzyck for their help.

hemisphere, are suggesting a right-hemispheric generator for sense of body ownership. More than 90% of the reported cases had delusions of disownership of left-sided body parts associated with rather extensive lesions in the right hemisphere (Vallar & Ronchi, 2009).

To test whether this lateralisation could also be observed in healthy individuals, one needs an experimental paradigm that allows for lateralised testing of sense of body ownership. The rubber hand illusion (Botvinick & Cohen, 1998) offers this possibility. In this illusion, the participant's hand is hidden behind an occluder, and a rubber hand (or hand prosthesis) is placed in a position similar to the real hand. The visible rubber hand and the hidden real hand are then stroked in synchrony with two paintbrushes. After about 3 minutes of synchronous stroking, most participants experience the felt touch as being produced by the visible stroking on the rubber hand. If rubber and real hand are not stroked in synchrony, participants do not experience this illusion.

Besides a high temporal synchronicity between stroking of the real and fake hand, spatial alignment of fake and real hand as well as spatial synchronicity of stroking have been reported as factors influencing the illusion's vividness (Costantini & Haggard, 2007).

There are three main methodological approaches to assess the experience and vividness of the rubber hand illusion. Botvinick and Cohen (1998), who first reported the illusion, used a questionnaire with nine statements (e.g., "I felt as if the rubber hand were my hand") to obtain subjective self-reports about the illusion's vividness. Participants had to indicate their agreement with these statements on a seven-step scale. Because these subjective self-reports could easily be faked by participants who wanted to respond to task demands even if they did not experience the illusion, two more objective approaches of measurement have been developed. Armel and Ramachandran (2003) recorded the participants' SCRs (skin conductance responses) to watching the rubber hand being harmed, to measure autonomic nervous system arousal in anticipation of pain. Since autonomic nervous system responses cannot be faked by the participant, and one would only anticipate pain if the rubber hand is actually incorporated into the body image, this is considered a more objective measurement than self-reports. Another possibility for assessing the illusion's vividness is the proprioceptive drift measure. The illusion leads to a shift of the perceived location of the real hand towards the rubber hand, which correlates with the strength of the illusion. The magnitude of the proprioceptive drift can be recorded by asking participants to verbally indicate the position of their unseen real hand, by naming a number on a ruler that is mounted on a special mirror desk while both rubber and real hand are underneath the desk top and only the rubber hand is visible (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005).

To test whether healthy individuals experience an asymmetry in illusion vividness between the left and the right hand, one would have to elicit the illusion on both hands of the same participant and compare the results. However, in most of the studies conducted so far the rubber hand illusion was elicited only at the right hand (e.g., Costantini & Haggard, 2007; Ehrson, Holmes, & Passingham, 2005; Lloyd, 2007), whereas in other studies the illusion was elicited only at the left hand (e.g., Botvinick & Cohen, 1998; Haans, Ijsselstein, & de Kort, 2008; Kanayama, Sato, & Ohira, 2007). In a few studies the illusion was elicited at both hands, but the authors did not calculate statistical comparisons between the two hands (e.g., Pavani, Spence, & Driver, 2000; Walton & Spence, 2004). To date there is only one study, in which the illusion was elicited at both hands and handedness effects were analysed. Mussap and Salton (2006) measured the vividness of the illusion by subjective self-reports and did not find a difference between left and right hand. Taking into account the already mentioned shortcomings of self-reports it would be interesting to assess this effect using either the proprioceptive drift measure or SCRs to get more objective results.

A factor that is of crucial importance when investigating functional asymmetries is handedness, since it is strongly related to other lateralised brain functions. Typically, left-handers exhibit a reduced or reversed lateralisation pattern more often than right-handers.

For example, the right hemisphere is dominant for visuospatial abilities in right-handers, whereas in left-handers no functional lateralisation was observed in a meta-analysis (Vogel, Bowers, & Vogel, 2003). The often-reported left-hemispheric dominance for language has been observed in both right-handers and left-handers, but there is a greater incidence of an atypical right-hemispheric dominance in left-handers (Corballis, 2003). Therefore, handedness should be taken into account when assessing laterality effects in the rubber hand illusion. However, a study systematically assessing differences in the experience of the illusion between left- and right-handers has yet to be performed. In most studies, only right-handers were tested (e.g., Kammers, de Vignemont, Verhagen, & Dijkermann, 2009; Kanayama et al., 2009; Tsakiris, Prabhu, & Haggard, 2006). To this date there has been no study in which the rubber hand illusion was investigated in a sample consisting of only left-handers. However, there are a few studies that tested mainly right-handed participants but also included a small number of left-handed or ambidextrous participants (e.g., Schütz-Bosbach, Avenanti, Aglioti & Haggard, 2009a; Schütz-Bosbach, Mancini, Aglioti & Haggard, 2006; Schütz-Bosbach, Tausche & Weiss, 2009b). Typically, effects of handedness on the vividness of the illusion were not analysed in these studies due to the low number of left-handers, with one notable exception: Haans et al. (2008) elicited the illusion on the left hand of 18 right-handed and 5 left-handed participants, and measured its vividness with both

self-reports and the proprioceptive drift measure. They did not observe a handedness effect with either measure, a result that should be interpreted very carefully, because of the small number of left-handers in the sample. Taken together, there has been no study in which side and handedness effects on the vividness of the rubber hand illusion were systematically tested in a sufficiently large sample. Therefore the aim of the present study was to assess such effects. To this end, we tested left- and right-handers and elicited the illusion at both the left and the right hand. Participants were asked to give subjective self-reports about the illusion's vividness using the classic questionnaire from Botvinick and Cohen (1998). Moreover, in order to get a more objective measure of illusion strength we also assessed the arousal of the autonomic nervous system by recording the participants' SCRs to watching the rubber hand being harmed (Armel & Ramachandran, 2003; Ehrsson, Wiech, Weiskopf, Dolan & Passingham, 2007).

Based on the findings that delusions of body ownership are almost always reported in patients with right-hemispheric lesions, we assume a right-hemispheric dominance for sense of body ownership. Therefore we would expect participants to experience a more vivid illusion on the left compared to the right side. This asymmetry may, however, interact with the participants' handedness. As left-handers exhibit a reduced or reversed lateralisation pattern more often than right-handers, we assume a reduced difference in illusion vividness between the two hands in left-handers.

METHOD

Participants

A total of 43 neurologically healthy volunteers participated in this study, which was conducted in accordance with the local ethic guidelines. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), and a laterality quotient (LQ) with a range between -100 and $+100$ (with positive values indicating right-handedness and negative values left-handedness) was calculated. Each participant was then assigned to one of two experimental groups—left-handers (LHs) or right-handers (RHs)—based on the LQ. Participants were considered right-handed if the LQ was larger than zero and left-handed if it was smaller than zero. However, there were no participants with LQs between -25 and 25 in the present sample. The LH group consisted of 21 participants (13 males) with a mean age of 25.42 years ($SD = 5.35$) and a mean handedness LQ of -69.12 ($SD = 26.67$, range -100 to -27). The RH group consisted of 22 participants (10 males) with a mean age of 27.18 years ($SD = 6.30$) and a mean handedness LQ of 86.72 ($SD = 14.72$, range 50 to 100). There were no

significant differences in sex, $\chi^2(1) = 1.17$; $p = .28$, or age, $t(41) = 0.98$; $p = .33$, between the two groups.

Procedure

Each participant experienced four different rubber hand illusion trials: an illusion and a control trial, both with the left and the right hand. The four trials were conducted in randomised order, with the exception that the two trials with each hand were always conducted successively in order to minimise possible artefacts in the SCR data due to a transfer of the electrode from one hand to the other. Participants sat upright at a table, with two identical 40 cm \times 60 cm white occluders mounted 27.5 cm to the left or to the right of the midline of the table.

Prior to the beginning of a left-hand trial, a prosthesis of the left hand and forearm was placed 11 cm to the right of the left occluder. Prior to the beginning of a right-hand trial, a prosthesis of the right hand and forearm was placed 11 cm to the left of the right occluder.

The prostheses were life-sized rubber models that were highly realistic in terms of skin colour, texture, and shape. The outlines of a hand were drawn 6 cm to the left of the left occluder and the right of the right occluder, respectively, and participants were asked to place their real hands onto these outlines during the experiment. This set-up occluded the participant's real hand and arm from view, while the rubber hand was visible. Taking into account the 0.5-cm width of the occluders, the distance between real hand and rubber hand was 17.5 cm, which is, according to Lloyd (2007), the most effective distance to elicit the illusion. To minimise contributions of the non-stroked hand to the illusion, participants were asked to also place it behind the appropriate occluder. After the participants sat down and placed their own hands onto the outlines, a black hairdressing cape was placed over their shoulders. The forearm of the prosthesis and the real arm were covered by the cape. This was done in order to prevent the participants from seeing that the prosthesis was not connected to their body, which might have reduced the vividness of the rubber hand illusion.

During trials, the fingers of the rubber hand and the hidden real hand were stroked with a paintbrush for 3 minutes by a trained experimenter. In the experimental condition strokes were synchronously applied to rubber hand and real hand according to a specified protocol. Conversely, in the control condition strokes applied to rubber and real hand were random and asynchronous. After 3 minutes of stroking, the experimenter used a syringe equipped with a needle, which had been hidden from the participant's view until then, to make rapid stabbing movements towards the rubber hand while the participant was watching. The needle of the syringe was moved

very close (about 1 cm) to the rubber hand but without actually touching it (Ehrsson et al., 2007).

After each trial, participants filled out a questionnaire that was adapted from Botvinick and Cohen (1998), to determine the degree to which participants subjectively identified with the rubber hand. The nine questions/statements were slightly modified so that all of them were valid for both hands, as the original questionnaire was intended only to assess an illusion being elicited at the left hand. The questions were:

1. It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched.
2. It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.
3. I felt as if the rubber hand were my hand.
4. It felt as if my (real) hand were drifting towards the rubber hand.
5. It seemed as if I might have more than one left/right hand or arm.
6. It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.
7. It felt as if my (real) hand were turning rubbery.
8. It appeared (visually) as if the rubber hand were drifting towards my hand.
9. The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.

Participants had to indicate their agreement with these questions on a 7-step scale from “disagree strongly” (−3) to “agree strongly” (+3). Scores higher than zero indicate a subjective perception of the rubber hand illusion.

To get a more objective measure of participants' identification with the rubber hand, their SCRs to watching the fake hand being “harmed” with the syringe were recorded during all four trials. The protocol used to collect and analyse these SCR data was adopted from Armel and Ramachandran (2003). SCRs were recorded with Ag-AgCl electrodes from the thenar and hypothenar eminence of the hand that was not stroked in the ongoing trial. Data were recorded through a Varioport Portable Recorder system (Becker Meditec, Karlsruhe, Germany) and were analysed with the accompanying Variograph software. Conductivity was measured in micro-Siemens (1/Ohm). The amplitude of the largest SCR greater than 0.03 micro-Siemens recorded 1–5 seconds after the syringe had approached the rubber hand was counted as peak amplitude. In addition to that, a SCR baseline for each of the four trials was determined by calculating the mean of the SCR data for 120 s starting 10 s after the onset of stroking. To deal with possible differences in SCR baselines between recordings from the left and the right hand, we used baseline-corrected amplitudes as the dependent variable.

RESULTS

To investigate the participants' subjective identification with the rubber hand, a $2 \times 2 \times 2 \times 9$ repeated-measures ANOVA with Handedness (LH, RH) as between-participants factor and Condition (experimental condition, control condition), Hand (left, right), and Question (number 1 to 9) as within-participants factors was calculated for the questionnaire data (see Figure 1 for mean questionnaire scores).

Overall, participants had a stronger subjective identification with the rubber hand in the experimental (synchronous) condition than in the control (asynchronous) condition, as indicated by a main effect Condition, $F(1, 41) = 133.87$; $p < .001$. Only questions 1, 2, and 3 yielded scores over zero in the experimental condition, thus indicating a subjective perception of the illusion. Therefore the differences between experimental and control conditions were much more marked in these questions than in the others (see Figure 1), as reflected by a Condition \times Question interaction, $F(8, 328) = 57.89$; $p < .001$. Also, a significant main effect of Question, $F(8, 328) = 46.28$; $p < .001$, indicated that some questions did overall yield higher scores than others. Moreover, a significant Side \times Question interaction, $F(8, 328) = 2.61$; $p < .05$, revealed that a difference between the left and the right side was observed in some questions, whereas in others it was not. Bonferroni-corrected post-hoc tests revealed that participants reported a stronger subjective identification with the rubber hand on the left side than

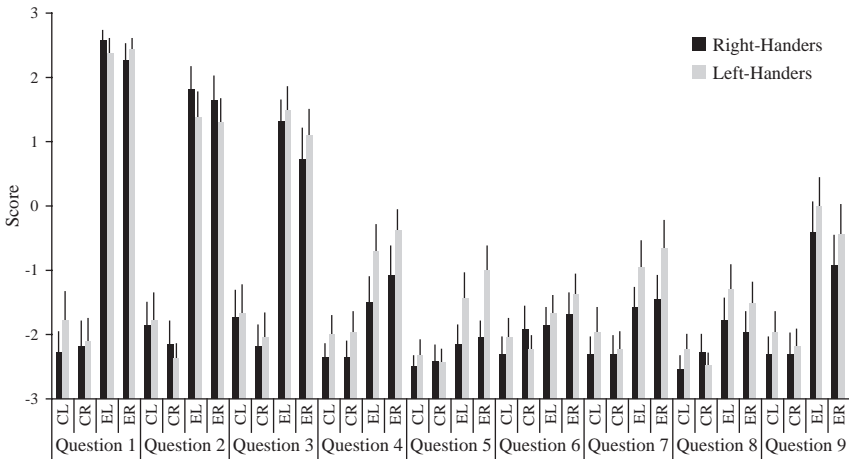


Figure 1. Mean questionnaire scores for RHs and LHs for the control (CL: left hand; CR: right hand) and the experimental condition (EL: left hand; ER: right hand) for all nine questions ranging from “disagree strongly” (-3) to “agree strongly” ($+3$). Scores higher than zero indicate a subjective perception of the rubber hand illusion. Error bars show standard error.

on the right side in question 3 (“I felt as if the rubber hand were my hand”) ($p < .05$). For all other questions, the post-hoc tests did not reach significance (all $p > .10$). Handedness did not influence the subjective ownership of the rubber hand, $F(1, 41) = 1.06$; $p = .31$, and all other main effects and interactions also failed to reach significance, all $F(1, 41) < 1.62$; all $p < .21$.

The average baseline SCRs for the control (left hand: 3.26 microsiemens; right hand: 3.53 microsiemens) and the experimental trials (left hand: 3.28 microsiemens; right hand: 3.36 microsiemens) did not differ significantly from each other, $F(3, 126) = 0.62$; $p = .57$. To test whether there was decline of SCR magnitude as a function of trial averaged over all four conditions, a repeated-measures ANOVA with trial number (one to four) as within-participants factor was calculated for the SCR data. Overall, there was a significant trial effect, $F(3, 126) = 3.97$; $p < .05$, indicating that participants showed a stronger SCR on the first (0.74 microsiemens) than on the second (0.40 microsiemens), third (0.46 microsiemens), and fourth trial (0.34 microsiemens). Bonferroni-corrected post-hoc tests revealed that only the decline from the first to the second trial was significant ($p < .05$), whereas all other comparisons were not (all $p > .08$).

To investigate the participants’ autonomic nervous system arousal to watching the rubber hand being “harmed”, a $2 \times 2 \times 2$ repeated-measures ANOVA with Handedness (LH, RH) as between-participants factor and Condition (Experimental, Control) and Hand (left, right) as within-participants factors was calculated for the SCR data (see Figure 2 for mean SCR responses).

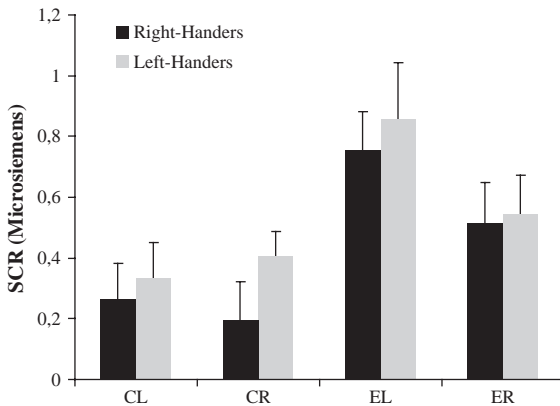


Figure 2. Mean baseline-corrected SCRs for RHs (black bars) and LHs (grey bars) for the control (CL: left hand; CR: right hand) and the experimental condition (EL: left hand; ER: right hand). Error bars show standard error.

TABLE 1
Bivariate Pearson correlation coefficients

	<i>Question 1</i>	<i>Question 2</i>	<i>Question 3</i>
CL	-0.07	-0.05	0.17
CR	0.20	0.19	0.18
EL	0.17	0.25	0.32
ER	0.20	0.14	0.20

Bivariate Pearson correlation coefficients between mean SCR amplitude and mean score for questions one to three for the control (CL: left hand; CR: right hand) and the experimental condition (EL: left hand; ER: right hand).

There was a much stronger SCR in the experimental condition compared to the control condition as revealed by a main effect Condition, $F(1, 41) = 19.72$; $p < .001$. In the experimental condition the SCR was stronger when the illusion was elicited at the left compared to the right hand, an asymmetry that was not present in the control condition as shown by a Condition \times Side interaction, $F(1, 41) = 4.68$; $p < .05$. This side difference was also found when only the experimental condition was analysed: one-sided t test, $t(42) = 1.88$; $p < .05$; effect size Cohen's $d = 0.58$. Handedness did not influence the strength of the SCR, $F(1, 41) = 0.56$; $p = .49$, and all other main effects and interactions also failed to reach significance, all $F(1, 41) < 1.77$; all $p < .19$.

To investigate the relation of self-rating and SCR, bivariate Pearson correlation coefficients between mean SCR amplitude and mean score for questions 1 to 3 were calculated (see Table 1). To control for multiple comparisons, the p -values were Bonferroni corrected. All correlation coefficients failed to reach significance (all $p > .48$).

DISCUSSION

The aim of the present study was to find out whether handedness and the side on which the illusion was elicited had an impact on the vividness of the rubber hand illusion. Both subjective self-reports and objective SCRs revealed that participants experienced the rubber hand illusion in the experimental condition, but not in the control condition. In accordance with the findings of Botvinick and Cohen (1998) and other studies (e.g., Ijsselstein, de Kort, & Haans, 2006) the first three questions yielded the largest differences between the control and the experimental condition. Furthermore, only these three questions yielded scores over 0 in the experimental condition, indicating a subjective perception of the illusion. Hence they seem to have a higher sensitivity to detecting the rubber hand illusion than the other six questions, and one may consider omitting these non-sensitive questions from the questionnaire for future use. Watching the

rubber hand being “harmed” by a syringe after the rubber and real hand had been stroked in synchrony in the experimental condition was associated with greater SCR amplitude than in the control condition in which the rubber and real hand had not been stroked in synchrony. Since participants would only anticipate pain and therefore exhibit larger SCR amplitudes if they actually felt that the rubber hand was their own hand, we could replicate the findings of previous studies (Armel & Ramachandran, 2003; Ehrsson et al., 2007), showing that measurement of SCRs is a valid and objective method to assess the vividness of the illusion.

Contrary to our first hypothesis, only question 3 revealed a more vivid illusion on the left, while the other questions evinced no asymmetry. This is in accordance with the findings of Mussap and Salton (2006) who also measured the vividness of the illusion by subjective self-reports and did not find a difference in illusion strength between the two hands. Remarkably, only question 3 (“I felt as if the rubber hand were my hand”) directly asks for sense of body ownership for the rubber hand, whereas the other questions ask for the location at which the touch of the paintbrush is felt (questions 1 and 6), the cause of this feeling (question 2), perceived movements of the real or the rubber hand (questions 4 and 8), feelings of having more than one hand or arm (question 5), or resemblance of rubber and real hand (questions 7 and 9). Therefore one would expect question 3 to be the most sensitive to detecting subtle differences in subjective feeling of body ownership between the two sides of the body. This may explain why the results of the other questions failed to show similar laterality effects. Thus, in accordance with our hypothesis, the data for question 3 suggests a right-hemispheric dominance for sense of body ownership. The difference between this result and the findings of Mussap and Salton (2006) may be explained by the fact that these authors used a composite score for the complete questionnaire and did not analyse the questions separately, so that possible asymmetry effects in their results of question 3 may have been masked by the results of the other questions. The assumption that question 3 is the most reliable item to detect body ownership feeling is at least partly supported by the correlations between SCRs and the questionnaire data. The largest correlation coefficient was observed in the left experimental condition. In this condition a higher autonomic nervous system arousal to watching the rubber hand being harmed was related to higher scores on question 3. However, since this and all other correlations failed to reach significance, the overall relation between questionnaire and SCR data seems to be rather weak. Thus, subjective self-reports do not reflect the more objective physiological measures of illusion strength to a large extent, an assumption that is also supported by the rather weak correlations between questionnaire data and proprioceptive drift measurements (Holmes, Snijders, & Spence, 2006). This may be explained by the fact that subjective self-reports could

easily be faked by participants who wanted to respond to task demands even if they did not experience the illusion. Thus the present findings further highlight the importance of using one of the two more objective measurement techniques when assessing the rubber hand illusion.

An effect of the side on which the illusion was elicited was also observed in the SCR data. In accordance with our hypothesis, a stronger SCR response was observed in the experimental condition, when the illusion was elicited at the left compared to the right hand. Since this asymmetry was not observed in the control condition, it can be assumed that this effect is a genuine result of the illusion and not due to a general arousal of watching the rubber hand being “attacked” with the syringe independent of whether it was incorporated into the body image or not. Thus the present results suggest a right-hemispheric dominance for sense of body ownership in healthy adults. This assumption is in alignment with the neuropsychological literature on somatoparaphrenia, since more than 90% of the reported cases experienced delusions of disownership of left-sided body parts after lesions in the right hemisphere (Vallar & Ronchi, 2009). Also, further evidence for a right-hemispheric dominance for sense of body ownership comes from studies investigating the neural basis of the rubber hand illusion. In general, it has been suggested that the rubber hand illusion critically depends on multisensory integration in perihand space (Makin, Holmes, & Ehrsson, 2008), a process in which the anterior intraparietal sulcus is critically involved (Makin, Holmes, & Zohary, 2007). This view is in line with findings that the strength of the illusory experience is reflected by activity in the intraparietal cortices (Ehrsson et al., 2005). Moreover, the illusion has also been related to activity in the premotor cortex and the right lateral cerebellum (Ehrsson, Spence, & Passingham, 2004). Interestingly, two recent studies found evidence for a right-hemispheric generator for the rubber hand illusion. Tsakiris, Hesse, Boy, Haggard, and Fink (2007), who elicited the illusion at the right hand, found that the incorporation of the rubber hand into the representation of the participant’s own body is reflected by activity in the right frontal operculum and the right posterior insula. Tsakiris, Constantini, and Haggard (2008), who elicited the illusion at the left hand, found that disruption of the right temporo-parietal junction using transcranial magnetic stimulation reduced the vividness of the illusion when it was elicited with a rubber hand, but increased it when a neutral object not resembling a hand was used. Thus, the right temporo-parietal junction seems to play a critical role in maintaining a coherent sense of one’s body and distinguishing it from external objects.

When interpreting the results of the present study, it has to be noted that an enhanced pain sensitivity on the left hand compared to the right hand has been reported (Klemenz, Regard, Brugger, & Emch, 2009; Sarlani, Farooq, & Greenspan, 2003). However, since the rubber hand was not touched by the

syringe in the present study and thus no real pain was inflicted upon it, it is unlikely that laterality in pain perception had an impact on the present data. To completely rule out the possibility that laterality in pain expectation interacts with laterality in the rubber hand illusion, it would be a meaningful approach to assess laterality in the rubber hand illusion with the proprioceptive drift measure, which is independent of pain perception.

Since a high temporal synchronicity between stroking of the real and fake hand is critical for the experience of the illusion (Botvinick & Cohen, 1998), another factor possibly interacting with laterality effects in the rubber hand illusion could be the finding that there is a left hemisphere/right hand superiority for perception of synchrony (Efron, 1963; Geffen, Rosa, & Luciano, 2000). However, as there are also results that speak in favour of the opposite view—namely that the capacities of both hemispheres for perception of synchrony are equivalent (Mason & Geffen, 1996)—it is unclear to what extent this might affect the present results, and more research on this topic is needed before any conclusions can be drawn.

Contrary to our second hypothesis, handedness did not modulate the vividness of the illusion. Thus, left-handers do not exhibit a reduced or reversed lateralisation for sense of body ownership more often than right-handers as was observed for lateralisation of spatial abilities (Vogel et al., 2003) or language (Corballis, 2003). This corroborates the findings of Haans et al. (2008) who also did not observe any handedness effects on the illusion's vividness measured with both self-reports and proprioceptive drift measure in a sample with only five left-handers. However, although the handedness effect clearly did not reach significance, the means suggest that left-handers had slightly stronger SCRs than right-handers in all four conditions. Since the inter-individual SCR differences in the presents study were rather large, statistical power might have been too low to successfully detect a subtle handedness effect. Although this possibility is rather unlikely, given that the handedness effect did not even approach significance, it may nevertheless be reasonable to re-examine the influence of handedness on illusion strength in a larger sample with the proprioceptive drift measure, which possibly yields less inter-individual variability.

In conclusion, the present study extends the knowledge about the lateralisation of sense of body ownership by providing the first systematic assessment of side and handedness effects in the rubber hand illusion, showing that a more vivid illusion was elicited at the left compared to the right hand. These findings suggest a right-hemispheric dominance for sense of body ownership in healthy adults.

Manuscript received 23 September 2009

Revised manuscript received 11 November 2009

First published online 1 March 2010

REFERENCES

- Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings of the Royal Society of London Biological Sciences*, *270*, 1499–1506.
- Austen, E. L., Soto-Faraco, S., Enns, J. T., & Kingstone, A. (2004). Mislocations of touch to a fake hand. *Cognitive, Affective and Behavioural Neuroscience*, *4*, 170–181.
- Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, *391*, 756.
- Corballis, M. C. (2003). From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral Brain Sciences*, *26*, 199–208.
- Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, *16*, 229–240.
- Efron, R. (1963). The effect of handedness on the perception of simultaneity and temporal order. *Brain*, *86*, 261–284.
- Ehrsson, H. H., Holmes, N. P., & Passingham, R. E. (2005). Touching a rubber hand: Feeling of body ownership is associated with activity in multisensory brain areas. *The Journal of Neuroscience*, *25*, 10564–10573.
- Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in promoter cortex reflects feeling of ownership of a limb. *Science*, *305*, 875–877.
- Ehrsson, H. H., Wiech, K., Weiskopf, N., Dolan, R. J., & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 9828–9833.
- Feinberg, T. E., & Keenan, J. P. (2005). Where in the brain is the self? *Consciousness and Cognition*, *14*, 661–678.
- Geffen, G., Rosa, V., & Luciano, M. (2000). Effect of preferred hand and sex on the perception of tactile simultaneity. *Journal of Clinical and Experimental Neuropsychology*, *22*, 219–231.
- Haans, A., Ijsselstein, W. A., & de Kort, Y. A. (2008). The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image*, *5*, 389–394.
- Holmes, N. P., Snijders, D., & Spence, C. (2006). Reaching with alien limbs: Visual exposure to prosthetic hands biases proprioception without accompanying illusions of ownership. *Perception and Psychophysics*, *68*, 685–701.
- Ijsselstein, W. A., de Kort, Y. A., & Haans, A. (2006). Is this my hand I see before me? The rubber hand illusion in reality, virtual reality and mixed reality. *Presence*, *15*, 455–464.
- Kammers, M. P., de Vignemont, F., Verhagen, L., & Dijkerman, H.C. (2009). The rubber hand illusion in action. *Neuropsychologia*, *47*, 204–211.
- Kanayama, N., Sato, A., & Ohira, H. (2009). The role of gamma band oscillations and synchrony on rubber hand illusion and crossmodal integration. *Brain and Cognition*, *69*, 19–29.
- Keenan, J. P., Rubio, J., Racioppi, C., Johnson, A., & Barnacz, A. (2005). The right hemisphere and the dark side of consciousness. *Cortex*, *41*, 695–704.
- Klemenz, C., Regard, M., Brugger, P., & Emch, O. (2009). Laterality of pain: Modulation by placebo and participants' paranormal belief. *Cognitive and Behavioral Neurology*, *22*, 186–189.
- Lloyd, D. M. (2007). Spatial limits of referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain and Cognition*, *64*, 104–109.
- Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research*, *191*, 1–10.
- Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *Journal of Neuroscience*, *24*, 731–740.
- Mason, C., & Geffen, G. (1996). Temporal integration of events within and between the cerebral hemispheres. *Cortex*, *32*, 97–108.
- Mussap, A. J., & Salton, N. (2006). A 'rubber hand' illusion reveals a relationship between perceptual body image and unhealthy body change. *Journal of Health Psychology*, *11*, 627–639.

- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97–113.
- Pavani, F., Spence, C., & Driver, J. (2000). Visual capture of touch: Out-of-the-body experiences with rubber gloves. *Psychological Science*, *11*, 353–359.
- Sarlani, E., Farooq, N., & Greenspan, J. D. (2003). Gender and laterality differences in thermosensation throughout the perceptible range. *Pain*, *106*, 9–18.
- Schütz-Bosbach, S., Avenanti, A., Aglioti, S. M., & Haggard, P. (2009a). Don't do it! Inhibition and self-attribution during action observation. *Journal of Cognitive Neuroscience*, *21*, 1215–1227.
- Schütz-Bosbach, S., Mancini, B., Aglioti, S. M., & Haggard, P. (2006). Self and other in the human motor system. *Current Biology*, *16*, 1830–1834.
- Schütz-Bosbach, S., Tausche, P., & Weiss, C. (2009b). Roughness perception during the rubber hand illusion. *Brain and Cognition*, *70*, 136–144.
- Tsakiris, M., Constantini, M., & Haggard, P. (2008). The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. *Neuropsychologia*, *46*, 3014–3018.
- Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 80–91.
- Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural signatures of body ownership: A sensory network for bodily self-consciousness. *Cerebral Cortex*, *17*, 2235–2244.
- Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, *15*, 423–432.
- Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia: A body delusion. A review of the neuropsychological literature. *Experimental Brain Research*, *192*, 533–551.
- Vogel, J. J., Bowers, C. A., & Vogel, D. S. (2003). Cerebral lateralisation of spatial abilities: A meta-analysis. *Brain and Cognition*, *52*, 197–204.
- Walton, M., & Spence, C. (2004). Cross-modal congruency and visual capture in a visual elevation-discrimination task. *Experimental Brain Research*, *154*, 113–120.