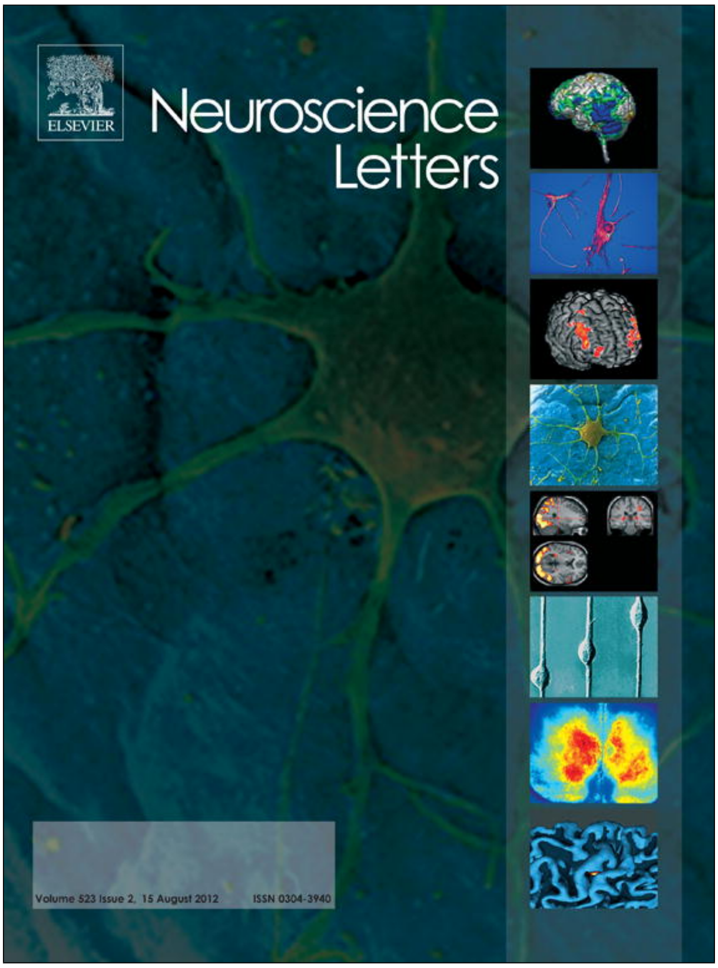
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The rubber hand illusion modulates pseudoneglect

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HIGHLIGHTS

- ► We examine how the rubber hand illusion (RHI) influences pseudoneglect.
- ► Pseudoneglect is reduced after RHI application.
- ► Elimination of pseudoneglect after left sided RHI application in high RHI responders.
- ► Integration of rubber hand into body schema shifts the perceived body midline.

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ABSTRACT

The rubber hand illusion (RHI) refers to the illusory perception of ownership of a rubber hand that may occur when covert tactile stimulation of a participant's hand co-occurs with overt corresponding stimulation of a rubber hand. It is proposed that integrating the rubber hand into one's body image may shift the subjective body midline away from the rubber hand. The present study investigated the influence of the RHI on pseudoneglect on the line bisection task, i.e. the leftward bias when marking the centre of horizontal lines, in 79 neurologically healthy adults. Overall, pseudoneglect was reduced after RHI application. Importantly, this effect was specific for individuals who reported having vividly experienced the illusion (high responders) as opposed to individuals who did not (low responders). Moreover, pseudoneglect was eliminated only after RHI application to the left hand. This pattern of results is consistent with functional hemispheric asymmetry for spatial processing and suggests that integrating the left sided rubber hand into one's body image shifts the subjective body midline to the right, thus counteracting pseudoneglect.

1. Introduction

The rubber hand illusion (RHI) [3] refers to the illusory perception of ownership of a rubber hand that may occur when tactile stimulation of a participant's hand (which is hidden from view) co-occurs with visually observed corresponding stimulation of a rubber hand placed in full view. After several minutes of synchronous stroking, the participant may report the perceived touch on the real hand as being produced by the visible stimulation of the rubber hand. Previous studies have applied the RHI to systematically investigate and manipulate the experience of embodiment, i.e. the subjective integration of an external object into one's body image [e.g. 14,4,15]. For instance, the RHI is perceived as stronger when elicited on the left compared to the right hand, suggesting right-hemispheric dominance for body ownership [17]. This finding is well consistent with studies on somatoparaphrenia, a rare neurological disorder characterized by a delusion of body part disownership, which report rather extensive righthemispheric lesions to be associated with delusions of disownership of left limbs [24]. Accordingly, several functional imaging studies have yielded evidence for prominent involvement of right sided premotor, posterior parietal and insular regions for the incorporation of a rubber hand into the body image, and for distinguishing one's own body from external objects [5,6,21,23]. Interestingly, the RHI has been shown to be accompanied by a phenomenon referred to as *proprioceptive drift*. The perceived position of a participant's index finger is shifted towards the rubber hand [22]. Integration of the rubber hand into the body image may therefore alter the body image by shifting the subjective body midline, e.g. if the rubber hand is placed closer to the body midline than the real hand, the subjective body midline may be perceived as further away from the rubber hand. The line bisection task [e.g. 1] constitutes a simple tool to investigate the potential shift of the subjective body midline. When healthy adults are asked to mark the centre of a horizontal line on this task, they exhibit a leftward bias, i.e. the perceived

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centre of the line is shifted to the left of the veridical centre [2]. This leftward bisection bias – referred to as *pseudoneglect* – is attributed to righthemispheric dominance for spatial processing which leads to a systematic overrepresentation of the left compared to the right visual half field. In contrast, patients suffering from hemispatial neglect, i.e. a deficit in attention to and awareness of one side of space following (mostly righthemispheric) lesions to the posterior parietal and/or superior temporal cortex, have been shown to exhibit a strong rightward bisection bias (ipsilateral to the side of the lesion) which is consistent with neglect of the left hemispace [e.g. 20, 11, for a review see 12].

Interestingly, unilateral neglect in many patients may also involve the patient's own body, strongly suggesting an accompanying distortion of the body image [for a review see 12]. It is thus conceivable that an alteration of the body image in healthy individuals, e.g. a shift of the subjective body midline as elicited by the RHI, influences pseudoneglect. Along these lines, a shift of the subjective body midline to the right after application of RHI to the left hand, for instance, would be expected to counteract pseudoneglect, thus decreasing the leftward bisection bias. The present study therefore was aimed to investigate the influence of the RHI on line bisection. It was expected that the RHI effect on pseudoneglect would be most pronounced in individuals in whom the illusion was vividly perceived compared to individuals who did not experience a vivid illusion.

2. Materials and methods

Overall, 79 participants (44 females and 35 males) with no history of neurological or psychiatric diseases and a mean age of 27.78 years (SEM = 1.00) were tested in the present study. All participants gave written informed consent and were free to withdraw from participation at any time. The study was carried out in accordance with the code of ethics of the world medical association for experiments involving humans (declaration of Helsinki).

The setup consisted of two identical 40 cm by 60 cm white wooden occluders mounted 27.5 cm to the left or to the right of the midline of a table. About 6 cm to the left of the left occluder and the right of the right occluder the outline of a hand was drawn on the tabletop. Prior to the beginning of the experiment, participants were asked to place their real hands onto these outlines. A black cape was subsequently placed over their shoulders. The rubber hand illusion was then elicited at both the left and the right hand, in randomized order. For left-hand trials, a life-sized rubber model of the left hand and forearm was placed to the right of the left occluder, while for right-hand trials, a life-sized rubber model of the right hand and forearm was placed to the left of the right occluder. During trials, participants were instructed to concentrate on the rubber hand, and a trained experimenter stroked both rubber hand and real hand with identical paintbrushes for 3 min. Overall there were nine different types of stroke movements (e.g. from the knuckle of the index finger to below the finger nail, or corresponding movements for middle or ring finger). Each stroke lasted 1 s, and each of the nine movement types was applied twenty times during the 3 min stimulation period. During experimental trials, rubber and real hand were stroked synchronously with the same types of stroke movements. In addition to the two experimental trials, there was a left and right control trial in which the strokes were applied asynchronously in a random fashion (e.g. while the index finger was stroked at the visible rubber hand, the thumb was stroked at the real hand).

Immediately after each trial, a visual line bisection task [9] was conducted. Participants were asked to bisect 17 horizontal lines into two equal parts [see 8 for further methodological details]. The line bisection task was conducted once with the right and once with the left hand, in randomized order, in order to prevent confounding effects of hand use. The line bisection task was also conducted once with the left and the right hand before the start of the rubber hand illusion trials, in order to get a baseline. After the line bisection task, participants filled out a German adaption of the Botvinick and Cohen [3] questionnaire in order to determine subjective perception of the rubber hand illusion [see 17 for questions and further details]. The questionnaire contained nine questions about the illusion that had to be answered on a seven step-scale from "disagree strongly" (1) to "agree strongly" (7). Thus, higher scores reflect a stronger subjective perception of the illusion. Additionally, handedness was assessed using the Edinburgh Handedness Inventory (EHI) [18], since handedness has been shown to possibly be a confounding factor when analyzing the line bisection test [9].

3. Results

Since the score distributions for the nine questionnaire items (see Fig. 1) were not normally distributed (two-tailed Kolmogorov–Smirnoff tests, all p's < 0.02), perception of the rubber hand illusion was analyzed using non-parametric statistics (separate two-tailed Wilcoxon signed ranks tests for the left and right hand). When using the total score for all nine questionnaire items as a dependent variable, participants reported a significantly stronger perception of the rubber hand in the experimental condition than in the control condition at both the left hand (experimental condition: mean = 34.35, SEM = 1.08; control condition: mean = 17.24, SEM = 1.00; $Z = -7.68$; $p < 0.001$) and the right hand (experimental condition: mean = 33.51, SEM = 1.08; control condition: mean = 16.81, SEM = 1.00; $Z = -7.38$; $p < 0.001$).

Similar results were obtained when the composite score for questionnaire items one to three was used as dependent variable. In parallel to the results for the total score, participants reported a significantly stronger perception of the rubber hand in the experimental condition than in the control condition at both the left hand

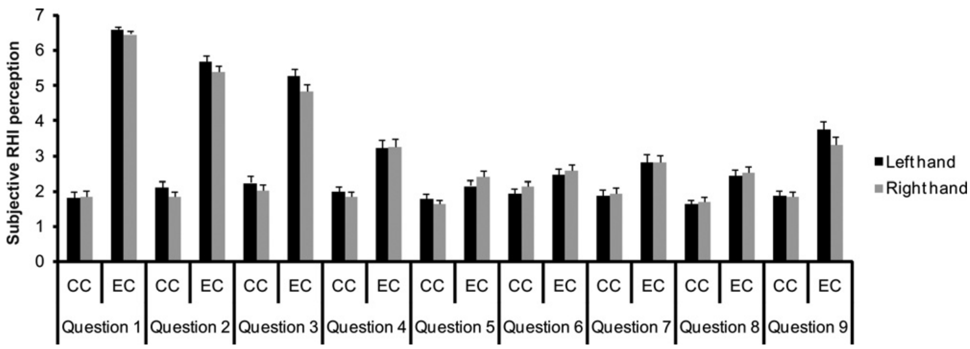

Fig. 1. Mean scores of subjective RHI perception according to the questionnaire for the left and right hand in experimental and control condition. Error bars show standard error.

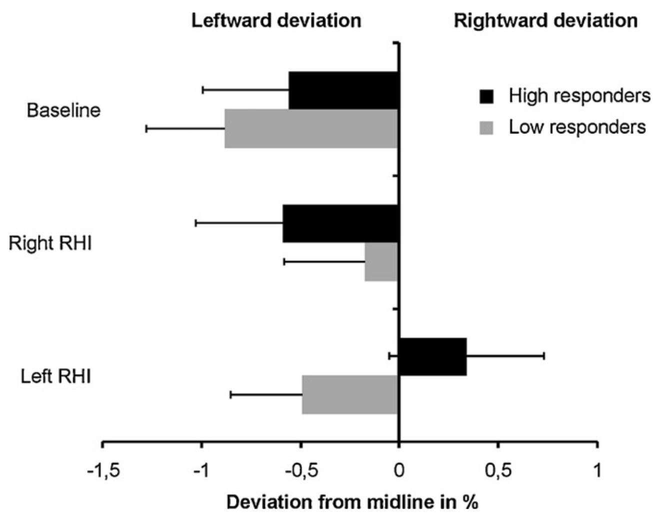

Fig. 2. Percentage and direction of the deviation from the veridical centre on the line bisection task according to condition (baseline, RHI elicited at right hand, RHI elicited at left hand) for high and low responders.

(experimental condition: mean = 17.53, SEM = 0.39; control condition: mean = 6.15, SEM = 0.48; $Z = -7.63$; $p < 0.001$) and the right hand (experimental condition: mean = 16.66, SEM = 0.38; control condition: mean = 5.69, SEM = 0.45; $Z = -7.60$; $p < 0.001$).

In order to investigate the impact of the strength of subjective RHI perception on pseudoneglect, participants were then grouped into high and low responders, based on a median-split of the total questionnaire score for both experimental conditions. Low responders ($n = 42$) had a score of less than 69 (mean = 54.98, SEM = 1.79) and high responders a score of more than 69 (mean = 82.49, SEM = 1.99).

The line bisection data (see Fig. 2) were normally distributed (two-tailed Kolmogorov–Smirnoff tests; all p's > 0.84) and thus were analyzed parametrically using a 3×2 repeated-measures ANCOVA with condition (baseline, after left sided RHI, after right sided RHI) as within-subjects factor, group (high responders, low responders) as between-subjects factor and lateralization quotient, a continuous measure of handedness [see 18 for details] as a covariate.

Overall, participants showed a stronger leftward deviation in the baseline condition (−0.72%, SEM = 0.30) than after the perception of a RHI on their right side (−0.38%, SEM = 0.30) or after the perception of a RHI on their left side (−0.08%, SEM = 0.26) as revealed by a main effect condition ($F_{(2, 148)} = 3.79$; $p < 0.05$; partial $\eta^2 = 0.05$). Moreover, a significant interaction condition × group emerged ($F_{(2, 148)} = 3.98$; $p < 0.05$; partial $\eta^2 = 0.05$). Two-sided Bonferroni-corrected post hoc tests revealed that high responders showed a significant rightward shift ($p < 0.05$) after perception of the RHI on their left side (0.30%, SEM = 0.39), compared to the perception of the RHI on their right side (−0.59%, SEM = 0.44). A similar, but non-significant trend emerged ($p = 0.08$) when perception of the RHI on their left side was compared to the baseline condition (−0.56%, SEM = 0.43). For low responders, none of the Bonferroni-corrected post hoc tests reached significance (all $p > 0.11$). The main effect of group failed to reach significance ($F_{(1, 74)} = 0.23$; $p = 0.63$).

To further investigate the relation of illusion strength and pseudoneglect we calculated a measure of illusion strength for each participant by subtracting the overall questionnaire score for the control condition from the overall questionnaire score for the experimental condition for each hand. This measure was then correlated with a relative measure of pseudoneglect-reversal, calculated by subtracting the deviation in the line bisection task after elicitation of the illusion at the right/left hand from the baseline. While none of the correlations reached significance for the overall group (left hand: $p = 0.20$; right hand: $p = 0.19$) or the low responders (left hand: $p = 0.40$; right hand: $p = 0.34$), there was a significant correlation for the left hand in high responders ($r = 0.36$, $p < 0.05$), indicating that a stronger subjective perception of the illusion was related to stronger pseudoneglect modulation in this group. Moreover, there was a trend towards a significant correlation for the right hand ($r = 0.33$, $p = 0.056$).

4. Discussion

The aim of the present study was to investigate the influence of the RHI on pseudoneglect on the line bisection task. In line with the hypothesis, pseudoneglect was reduced after RHI application. More specifically, in high responders, i.e. individuals who experienced the illusion as very vivid, pseudoneglect was eliminated after RHI on the left hand. Such an effect was absent in low responders, i.e. individuals who did not report having perceived the illusion as strong. This pattern of results is well consistent with a previous study reporting a temporary reduction of unilateral visual neglect on a midline pointing and a cancellation task after RHI induction [13], and appears to indicate that a shift of the subjective body midline occurred in response to the integration of the rubber hand into one's body image. In high responders, left sided RHI shifted the subjective body midline to the right, thus counteracting pseudoneglect in subsequent line bisection. In low responders, the absence of any effects suggests that the rubber hand may not have been integrated into the body image.

Notably, line bisection performance was unaffected after RHI application to the right hand. This is consistent with functional hemispheric asymmetries, since left sided RHI predominantly affects the right hemisphere which is dominant for spatial processing [25]. Moreover, it is also consistent with the findings of a recent study, which reported a dominance of right fronto-parietal networks for perception of own limb movements [16]. Two recent functional imaging studies provided evidence for a pivotal role of the ventral premotor and the parietal cortex for the RHI, and neural activity in the ventral premotor cortex has been interpreted to reflect the feeling of ownership of the rubber hand [5,6]. Interestingly, while in both of these studies the RHI was elicited at the right hand, activation in these areas was found bilaterally and not restricted to the left hemisphere, further supporting the idea of a right-hemispheric dominance for the feeling of body ownership. Repetitive transcranial magnetic stimulation (rTMS) over the inferior posterior parietal lobule (IPL) was shown to attenuate the RHI for immediate perceptual body judgments [10]. More recently, these findings have been corroborated by a lesion study reporting RHI failure in about 26% of stroke patients [26]. Voxel-based lesion-symptom mapping located RHI failure-associated voxels subcortically adjacent to the insula, basal ganglia, and within the periventricular white matter. Probabilistic diffusion tractography revealed that these voxels were connected to premotor, prefrontal, and parietal cortex [26]. Parietal regions have also been implicated with regard to spatial processing and pseudoneglect. Perceptual line centre judgements have been shown to be associated with increased neural activity in the IPL [7]. Righthemispheric rTMS over the IPL was shown to induce a rightward error in line bisection judgements, hence eliminating pseudoneglect [19]. Therefore, both pseudoneglect and the RHI appear to share some of the underlying neural circuits.

Nevertheless it has to be noted that the present data may not exclusively be interpreted in terms of an altered body image, i.e. a shift of the subjective body midline, in response to RHI induction. It is also conceivable that the RHI may have modulated the participants' arousal or attentional state. It has been argued that during the illusion, attention may be shifted from the ipsi- to the contralesional side (i.e. away from the own hand towards the rubber hand) [13]. However, this explanation appears rather unlikely, as a shift of attention to the left after right sided RHI would be expected to enhance pseudoneglect. Crucially, such an effect could not be observed in the present data. Mere arousal effects have already been refuted as an explanation for reduced unilateral visual neglect following RHI induction.

5. Conclusion

Taken together, the present results suggest that vivid experience of the RHI shifts the subjective body midline, supporting the notion that during the illusion, the rubber hand is integrated into one's body image. Future studies will have to determine if this effect – similar to RHI-induced amelioration of unilateral visual neglect [13] – can also be measured for up to 45 min after experiencing the illusion.

Author contributions

Authors S.O., J.P., N.R. and O.G. designed and planned the study. Authors S.O. and N.R. conducted literature searches and analyses. Authors S.O. and N.R. collected the data. Author S.O. conducted the statistical analyses. Authors S.O., J.P. and O.G. wrote the manuscript. All authors contributed to and have approved the final manuscript.

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