Atypical susceptibility to the rubber hand illusion linked to sensory-localised vicarious pain perception

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Atypical Susceptibility to the Rubber Hand Illusion linked to Sensory-Localised Vicarious Pain Perception

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Abstract

The Rubber Hand Illusion (RHI) paradigm has been widely used to investigate the sense of body ownership. People who report experiencing the pain of others are hypothesised to have differences in computing body ownership and, hence, we predicted that they would perform atypically on the RHI. The Vicarious Pain Questionnaire (VPQ), was used to divide participants into three groups: 1) non-responders (people who report no pain when seeing someone else experiencing physical pain), 2) sensory-localised responders (report sensory qualities and a localised feeling of pain) and 3) affective-general responders (report a generalised and emotional feeling of pain). The sensory-localised group, showed susceptibility to the RHI (increased proprioceptive drift) irrespective of whether stimulation was synchronous or asynchronous, whereas the other groups only showed the RHI in the synchronous condition. This is not a general bias to always incorporate the dummy hand as we did not find increased susceptibility in other conditions (seeing touch without feeling touch, or feeling touch without seeing touch), but there was a trend for this group to incorporate the dummy hand when it was stroked with a laser light. Although individual differences in the RHI have been noted previously, this particular pattern is rare. It suggests a greater malleability (i.e. insensitivity to asynchrony) in the conditions in which other bodies influence own-body judgments.

Introduction

The rubber hand illusion (RHI) paradigm (Botvinick & Cohen, 1998) is an established means of investigating and manipulating the sense of body-ownership including body location, image, and agency (Ehrsson, Spence & Passingham,2004; Tsakiris & Haggard, 2005; Longo, Schuur, Hammers, Tsakiris & Haggard, 2008). In this paradigm, the participant's hand is hidden from view and a dummy hand is placed in view, alongside the real hand. The hidden and dummy hands are then stroked either synchronously or asynchronously. The illusion is significantly stronger in the synchronous condition, when the participant *feels* the touch delivered to the visible dummy hand as if the hand belonged to him/her. Thus, when the illusion occurs, the rubber hand becomes temporarily incorporated in the participant's mental body representation. This is reflected in a perceived shift in the position of one's own hand towards the fake hand, a phenomenon termed proprioceptive drift. The objective measure of proprioceptive drift complements self-reported questionnaire ratings through which participants report their experience of ownership, self-location, and agency over the fake hand.

The RHI arises through the integration of multisensory information with reference to a prior mental body representation (Costantini & Haggard, 2007). According to this model, visual, proprioceptive, and somatosensory inputs are processed within higher order multimodal integration areas (Ehrsson, Spence & Passingham,2004; Tsakiris et al., 2007; Limanowski & Blankeburg, 2015). As such, the illusion is the strongest when distinct external inputs match each other (as shown by the difference between synchronous and asynchronous stroking, Botvinick and Cohen, 1998) and also when external inputs match internal representations of the body (Tsakiris, 2010). The RHI is greater when the rubber hand looks similar, has same orientation and side as the real hand (e.g. both left or both right) and when the hand is within the peripersonal space (PPS) of the person (Preston, 2013). Thus, the viewed object is tested against an abstract model of one's body for 'fit', to determine whether or not the dummy hand is incorporated within the body model in a process that involves both bottom-up and top-down mechanisms (Tsakiris, Costantini & Haggard, 2008). In some circumstances, the illusion can also occur in the absence of visuo-tactile congruency. The illusion can be induced in a 'light only' condition, when the dummy hand is 'stroked' by a laser-pointer but no light/tactile stimulation is applied to the real hand (Durgin, Evans, Dunphy, Klostermann & Simmons, 2007). Here, participants who report tactile and thermal sensations evoked by the light-beam also report stronger feeling of ownership of the dummy hand.

Atypical performance on the RHI has been linked to various psychiatric and developmental conditions, as well as sub-clinical individual differences. Differences in the RHI are observed in patients with autism (Paton, Hohwy & Enticott, 2012; Palmer, Paton, Hohwy & Enticott, 2013), schizophrenia (Thakkar et al., 2011), neurotypical variations linked to schizotypy (Germine, Benson, Cohen & Hooker, 2015; Kallai et al., 2015), in eating disorders including anorexia nervosa (Eshkevari, Rieger, Longo, Haggard & Treasure, 2012; Kaplan, Enticott, Hohwy, Castle & Rossell, 2014), and in mirror-touch synaesthesia (Aimola Davies & White, 2013). In the latter, participants report experiencing touch when seeing others touched and, during the RHI paradigm, report ownership of the rubber hand when it is stroked but no physical touch is applied to the participant's own hand. This may occur because the observed touch triggers a synchronised feeling of touch on their own body, analogous to the normal effect of synchrony in the RHI (Aimola Davies & White, 2013). However, it may also reflect more general differences in computing body ownership in this group: in effect, a tendency to misattribute other people's bodies as their own (Ward & Banissy, 2015). In the present study, we extend this to a similar are related phenomenon to mirror-touch synaesthesia (Ward, Schnakenberg & Banissy, *in press*), namely to individuals who report feeling pain when seeing pain in others.

Seeing someone else in pain activates neural circuitry involved in the physical perception of pain (Jackson, Brunet, Meltzoff & Decety, 2006; Lamm, Decety & Singer, 2011). However, for a subset of the general population this extends to reportable pain-like experiences evoked by observing others in pain (Fitzgibbon, Giumarra, Georgiou-Karistianis, Enticott, & Bradshaw, 2010; Fitzgibbon et al., 2012; Osborn & Debyshire, 2010). These individuals have been called vicarious pain responders, or mirror-pain synaesthetes. Ward and Banissy (2015), in their account of mirror-touch/pain synaesthesia, suggest that this may reflect an over-inclusive body ownership mechanism, in which all observed bodies are matched to the person's own internal body model, or as a failure in a top-down orienting mechanism for selective attention to the self that inhibits representations of the (non-self) other. Whatever the precise mechanism, the prediction is that a greater tendency to treat <u>all</u> observed bodies as self-related will result in an increased tendency to experience the RHI, as well as the tendency to report experiences on their own body as a result of observing these on other people (the defining feature of mirror touch/pain).

One study already tested the performance of vicarious pain responders on the RHI using only subjective reports (not proprioceptive drift). Derbyshire et al. (2013) showed a greater tendency to incorporate the rubber hand in the pain-responder group when compared to controls and this effect was unusually apparent for the asynchronous stroking condition (which tends not to induce the illusion in controls). We extend this to include five different manipulations of the RHI, including conditions in which the dummy hand is observed without any physical touch, and grouping participants via a new assessment tool for vicarious pain experience (Grice-Jackson, Critchley, Banissy & Ward, 2017a). The Vicarious Pain Questionnaire (VPQ) employs 16 movie clips depicting people experiencing physical pain, and probes the phenomenological characteristics of any felt pain sensations provoked in the observer (e.g. pain quality, pain intensity, pain localisation). Using a bottom-up approach of cluster analysis, three groups are identified: 1) non-responders or controls (who report no pain when watching a video with someone else experiencing physical pain), 2) sensory-localised responders (S/L) (who report a precisely localised feeling of pain at the same location as the person in the video) and 3) affective-general responders (A/G) (who report a generalised and emotional feeling of pain). The validity of these groupings is endorsed by observed difference in structural and functional brain characteristics (Grice-Jackson et al., 2017a, 2017b) and, in the present study, we demonstrate cognitive differences between the groups and provide the first assessment of test-retest reliability of the VPQ.

Using the VPQ to group and recruit participants, we tested both subjective and objective measures of the rubber hand illusion, with five different manipulation. Two of these manipulations were the standard synchronous and asynchronous conditions. Based on published findings (Derbyshire et al. 2013), we predicted that individuals within the responder groups to be less sensitive to synchrony (i.e. they will show the illusion in both conditions). We had no predictions about whether this effect would be found for one or both responder groups. Two further manipulations involved the visual presentation of touch from a paintbrush or light from a laser pointer in the absence of any physical sensation. Here, our prediction was that the sensory-localised group (who feel sensations in the same location that they observe them on others) would show the RHI illusion, as found for mirror-touch synaesthesia (Aimola Davies & White, 2013). The fifth condition involved the reverse scenario of feeling touch while observing an untouched dummy hand. We were not aware of any previous report of this manipulation inducing the RHI, hence, this serves as an important control measure across all groups to assess for a general bias in responding.

Materials and methods

Participants

Ninety-eight volunteers from the University of Sussex took part in the experiment (70 Females; 28 Males; Aged 18-34 yrs; Mean = 21.75 ± 3.11 SD). Each participant completed the Vicarious Pain Questionnaire (VPQ) and were divided into three groups based on the 2-step cluster analysis performed on the VPQ (see section 2.2 for further description). The groups were: 57 non-responders (29 F; 18 M; Aged 18-34 yrs; M = 21.88 ± 3.45 SD), 22 sensory-localised responders (S/L) (17 F; 5 M;

Aged 18-25 yrs; M = 21.6 ± 2.15 SD), and 19 affective-general responders (A/G) (14 F; 5 M; Aged 19 – 33 yrs; M = 21.53 ± 3.1 SD).

Since its development, a total sample of N=1056 individuals (Aged 18-60 yrs, M= 20.42 ± 4.16 SD, 297 Males, 759 Females) have completed the VPQ including data from N=573 reported by Grice-Jackson et al., (2017a). The larger sample also included 82 participants (Aged: 18-33 yrs, M = 20.23 ± 3.31 SD, 68 Females, 14 males) who had taken the measure twice, at least one academic year apart. We used this dataset to undertake an analysis of test-retest reliability of the VPQ and to determine how the group structure is affected by different parameters entered into the clustering model. Cluster analysis is an exploratory analysis that requires large data sets (Landwehr & Zupan, 1987) and so was run on the entire sample, and not just the experimental subsample.

Vicarious Pain Questionnaire

Description. The Vicarious Pain Questionnaire (VPQ; developed by Grice-Jackson and colleagues, 2017a) was run using Bristol Online Survey.

The questionnaire comprises 16 videos (no audio) of people experiencing physical pain (e.g. falls, sports injuries, injections), each video lasting for approximately 10 seconds.
After each video, participants were questioned about their experience. First, participants were asked if they experienced a bodily sensation of pain while viewing the video (yes/no). If the answer was "yes"', participants were asked to describe their pain by answering three more questions about their experience: 1) how intense their pain experience was (1-10 Likert scale, 1= very mild pain, 10 = highly intense pain); 2) if and where they localised the pain, answering options were either "localised to the same point as the observed pain in the video", "localised but not to the same point", and "a general/non-localisable experience of pain"; 3) to select pain adjectives from a list that best described their vicarious pain experience (10 sensory descriptors such as "tingling", "burning", "stinging", 10 affective descriptors such as "nauseating", "gruelling", "aversive" and 3 cognitive-evaluative descriptors "brief", "rhythmic", "constant"). From these answers, a Localised – Generalised score was computed from the total of "localised to the same point" and "localised to a different point" minus the total number of non-localisable (generalised) experiences. A Sensory – Affective score was computed from the total number of sensory adjectives minus the total number of affective adjectives.

Subsequently all participants (regardless of their affirmative or negative answer to the first question) were asked to rate how unpleasant their experience was (1-10 Likert scale, 1= not at all unpleasant, 10=highly unpleasant). The final section of the VPQ asked participants if they had previously experienced vicarious pain in their daily life and how regular that happened (10 point Likert Scale, -5 = hardly ever, 5 = very regularly).

Two-Step Cluster Analysis. The two-step cluster analysis comprised an initial hierarchical cluster analysis using Ward's Method (Ward, 1963) and a second k-means cluster analysis. The cluster centroids and number of clusters for the k-means analysis were provided by the hierarchical cluster analysis. We repeated an earlier clustering approach (Grice-Jackson et al., 2017a) based on three input variables (total number of pain responses, localised-generalised score, sensory-affective score). This analysis was contrasted against two similar models in which total pain responses was substituted for the conceptually related variables of mean intensity of pain responses, or the regularity of pain responses (in daily life).

Rubber Hand Illusion Questionnaire

The RHI questionnaire contained 10 items divided into three subscales: ownership, location, and agency (Longo et al., 2007), see *Table 1* for further details. The items were measured on a 7-point Likert scale (1 = strongly, 7 = strongly agree). Four extra questions were added for the light condition, in order to record any tactile or thermal sensations induced by the laser beam (see table 1 for detailed description of the items). These last four questions were added at a later stage and therefore data was gathered only from a subset of participants (N=39).

Table 1. RHI questionnaire items and subscales.

Subscale	Items
Ownership	*It seemed like…*
	1. …I was looking directly at my own hand, rather than at a rubber hand.
	2. …the rubber hand began to resemble my real hand.
	3. …the rubber hand belonged to me.
	4. …the rubber hand was my hand.
	5. …the rubber hand was part of my body.
Location	6. …my hand was in the location where the rubber hand was.
	7. …the rubber hand was in the location where my hand was.
	8. …the sensation I felt was caused by the paintbrush touching (or laser pointer playing on) the rubber hand.
Agency	9. …I could have moved the rubber hand if I had wanted.
	10. …I was in control of the rubber hand.
Light induced sensations	11. …I felt a tactile sensation in my hand.
	12. …I felt a thermal sensation in my hand.
	13. …the sensation was cold.
	14. …the sensation was warm.

Experimental procedure

In the RHI task, the participant was seated at a table, opposite to the experimenter with his/her right arm placed in a box (86cm x 60cm x 20cm). The participants were asked to rest her/his hand in the most comfortable position with the palm facing down and slightly arched. A life-size model of a right hand was placed in the box, directly in front of participant body midline. The participant could only see the dummy hand through a squared hole on top of the box, but could not see her/his own right hand which was occluded by the box cover from the top and by a piece of black fabric from the right-hand side. The distance between participant's right index finger and the index finger of the fake hand was 20cm.

Five conditions were performed in a counterbalanced order across participants: Synchronous (the timing of the brush strokes on the rubber hand and participant's own hand was synchronized); asynchronous (the timing of the brush strokes was out of phase by approximately 625ms); light (a laser beam was playing on the index finger of the rubber hand); see-touch (the brush stimulation was applied only to the rubber hand) and; feel-touch (the brush stimulation was applied only to participant's real hand). At the beginning of each condition, a cover was placed on top of the box and the participant was asked to estimate the location of her/his right index finger tip by reading the corresponding number along a one-meter ruler laid across the setting top, parallel to the frontal plane. The reading was repeated three times before each trial and the placement of the ruler varied each time to prevent the participant repeating responses in subsequent readings. These measurements were followed by 120s stimulation 'induction' at approximately 1.6Hz (75 times in 120s) for all conditions. The paintbrush stimulation was applied from the knuckle to the finger nail, while that of the laser pointer was back and forth from the knuckle to the finger nail as it was not easy to switch off/on and maintain timing. Following this, post-induction finger location judgements were obtained in the same manner as prior to the induction and the participant filled out the RHI questionnaire after each condition. The average of the three measurements taken before and after each trial was calculated. Proprioceptive drift was calculated by subtracting the pre-induction finger location judgement from the post-induction finger location judgement:

PD = mean(post-induction judgements) – mean(pre-induction judgements)

Data Analysis

The statistical software used was SPSS version 23 (SPSS Inc., USA). The significance level for all analyses was set at $p<0.05$ and the results reported are two-tailed.

Analyses were performed to test the effects of two independent variables (groups and stimulus type) on two dependent variables (proprioceptive drift and RHI questionnaire subjective ratings). 3 (group) x 2 (stimulation mode) mixed model ANOVAs were used to analyse the data of proprioceptive drift and each of the RHI questionnaire subscale for the synchronous and asynchronous conditions. For the proprioceptive drift data, outliers were excluded for each condition using SPSS based on the 3-interquartile range (IQR). Thus, one outlier was excluded from the asynchronous condition, four from the light condition and one from the see-touch condition. No outliers were found in the questionnaire data outside the 3-IQR. Subsequent post-hoc tests adjusted for multiple comparisons (Bonferroni corrections) assessed differences between and within groups. One-way ANOVAs were used for each of the other three conditions to test group effects on proprioceptive drift. For the questionnaire data, non-parametric Mann-Whitney U tests were used for each subscale.

Results

Reliability of the VPQ

For the 82 participants who completed this measure on two occasions, the test-retest scores were all significantly correlated between time 1 and time 2 as shown by Spearman's correlations for the various measures: total pain responses (rho= 0.629, $p<0.001$); mean pain intensity (rho= 0.640, $p<0.001$); reported levels of vicarious pain outside of experiment (rho= 0.349, $p=0.001$); localised-general score (rho= 0.295, $p<0.001$); and sensory-affective score (rho= 0.550, $p=0.007$). Correlation coefficients are a measure of effect size and, by convention, values >.5 are considered large, and those >.3 are considered medium. The most reliable individual difference measures in psychology, refined over decades of research, tend to have correlations around .7 or .8 (Vul, Harris, Winkielman, & Pashler, 2009). Considering the different ways of clustering the data, the inclusion of mean pain intensity led to the most consistent clustering ($\chi^2 = 48.512$, $p<0.001$; Cramer's V = 0.544, $p<0.001$), followed by reported levels of real-world vicarious pain ($\chi^2 = 47.947$, $p<0.001$; Cramer's V = 0.541, $p<0.001$), and total number of pain responses ($\chi^2 = 37.817$, $p<0.001$; Cramer's V = 0.480, $p<0.001$). Cramer's V is a measure of effect size where V>.5 is considered large. As such, we conclude that the VPQ measure is reliable over time and the reliability is enhanced by adding mean intensity rather than total number of pain responses (as used in Grice-Jackson et al., 2017a, 2017b), although it is to be noted that both methods are adequate and yield only minor differences in the clustering across the whole data set (presented in supplementary results S1).

Proprioceptive drift

Means and standard deviations of proprioceptive drift for each condition and in each group are shown in Table 1.

Table 1. Mean proprioceptive drift (mm) and standard deviations for each condition in each group

Group	Conditions				
	Synchronous	Asynchronous	Light	See-touch	Feel-touch
Controls	15.96 ± 23.38	3.04 ± 18.54	2.01 ± 11.50	1.07 ± 14.40	- 2.98 ± 14.40
S/L	21.36 ± 22.72	17.30 ± 18.46	17.42 ± 29.13	7.83 ± 24.35	-1.27 ± 17.33
A/G	23.51 ± 19.78	-5.88 ± 22.51	3.77 ± 19.15	10.96 ± 27.08	-1.12 ± 18.41

Considering first the effect of synchrony/asynchrony, the 2 x 3 ANOVA used for synchronous and asynchronous conditions showed significant main effects of stimulus type, F (1,189) = 20.808, $p<0.001$, $\eta^2 = 0.039$ and group, F (2, 189) = 3.800, $p<0.05$, $\eta^2 = 0.099$ on proprioceptive drift. There was also a statistically significant interaction between the effects of group and stimulus type, F (2,189) = 3.774, $p<0.05$, $\eta^2 = 0.038$, indicating that synchronous and asynchronous stimulations evoked different group effects. Post-hoc tests using Bonferroni corrections revealed that proprioceptive drift was significantly higher in S/L (19.332 ± 3.21) than in controls (9.503 ± 1.971), $p<0.05$. Significantly greater proprioceptive drift was found in the asynchronous condition in the S/L group when compared to controls, t(76)=-3.017, $p<0.005$, and to A/G, t(38)=3.540, p=0.001. No significant differences were found in the synchronous condition. Differences between synchronous and asynchronous conditions were assessed within the three groups. Proprioceptive drift was significantly greater in the synchronous than in the asynchronous conditions in controls, t (56) = 4.520, p <0.001, and in A/G group, t(18) = 4.723, $p<0.001$. However, there was no significant difference in proprioceptive drift in the S/L group, t(21) = 0.848, p =0.407. Figure 1 shows all these results. In short, the S/L responder group shows a disruption of body ownership insofar as they have a greater tendency to incorporate asynchronous touch to the dummy hand into their body schema.

The other three conditions were analysed using one-way ANOVAs, as the focus was on differences in between groups, rather than direct comparisons of the conditions. No significant differences were found for see-touch, F(2,94) = 2.153, p=0.122 and feel-touch, F (2,95) = 1.231, p=0.297 conditions between the groups. This is important because it suggests that there isn't a general tendency to incorporate the rubber hand (or a general response bias) but, rather, a specific tendency to do so under some conditions. There was a significant difference in the light condition, $F (2,92)= 5.601$, $p=0.005$ (results are shown in Figure 2). However, this data failed Levene's test for equality of variances and the post hoc Games-Howell test comparing S/L group with controls showed only a trend, $p=0.061$. Further exploratory analyses for the light condition can be seen in the supplementary results S2.

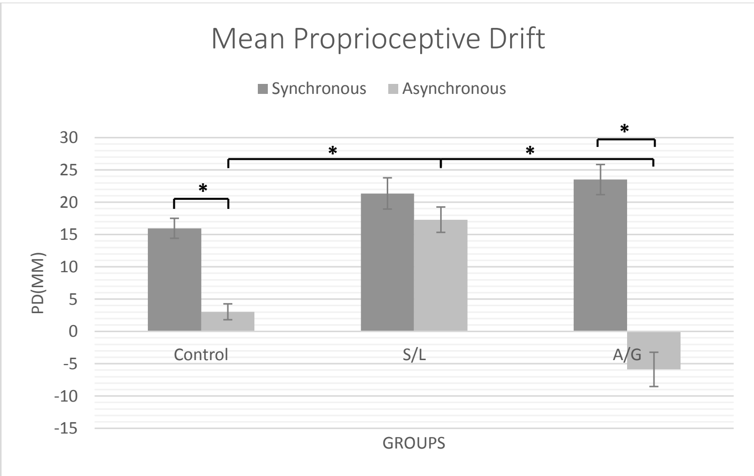


Figure 1 Mean PD (mm) of the three groups for Synchronous and Asynchronous conditions. Error bars indicate one standard error. S/L = sensory-localised; A/G = affective-general. The sensory-localised group (S/L) reported significantly higher proprioceptive drift than both controls and affective-general group (A/G) in the asynchronous condition.

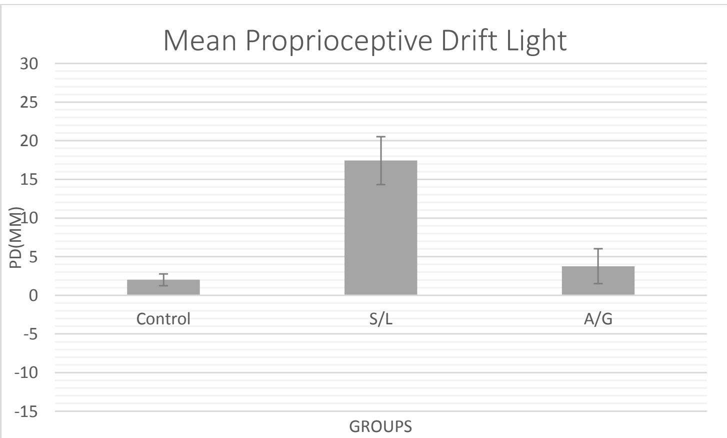


Figure 2 Mean PD (mm) of the three groups for the Light condition. Error bars indicate one standard error. S/L = sensory-localised; A/G = affective-general. The sensory-localised group (S/L) showed a trend towards higher proprioceptive drift in the light condition than both controls and affective- general group (A/G).

The results obtained for proprioceptive drift showed higher susceptibility for the illusion in the asynchronous condition in the S/L group which scored higher than the controls and a similar trend was observed in the light condition.

Subjective ratings

Since almost half of the conditions failed Shapiro-Wilk normality test, each of the three subscales of the RHI questionnaire: ownership, location, and agency were analysed using Mann-Whitney U non-parametric test. In the synchronous condition, the S/L group scored higher than controls on the ownership scale (U=423.5, p=0.026), on location (U=421.5, p=0.024) and on agency (U=449.0, p=0.05). In the asynchronous condition, they scored higher than controls on ownership (U= 103.0, p=0.03) and on agency (U=126.5, p=0.044) and A/G also on the ownership (U=103, p=0.006) and agency (U=126, p=0.027). They also scored higher than controls in the light condition on the ownership (U=423.5, p=0.026) and location (U=422.0, p=0.025) subscales. In summary, the questionnaire results show a similar pattern to the proprioceptive drift scores: the S/L responder group shows a greater tendency to incorporate the dummy hand on the asynchronous trials. In addition, there was a greater tendency for them to report the RHI on the standard, synchronous, condition.

A subset of participants (N=39) were asked about tactile/thermal sensations from the laser light stimulation. Of these participants, 60% agreed to experiencing a sensation on one or more questions, and these did not significantly differ across groups (group percentages: Controls=52%; S/L= 82%, A/G=44%; χ^2 = 3.521, p=0.172;). Participants who experienced sensations from the laser light reported higher Ownership, Location and Agency scores in the RHI in this condition (see Supplementary Results S2), thus replicating Durgin et al., 2007.

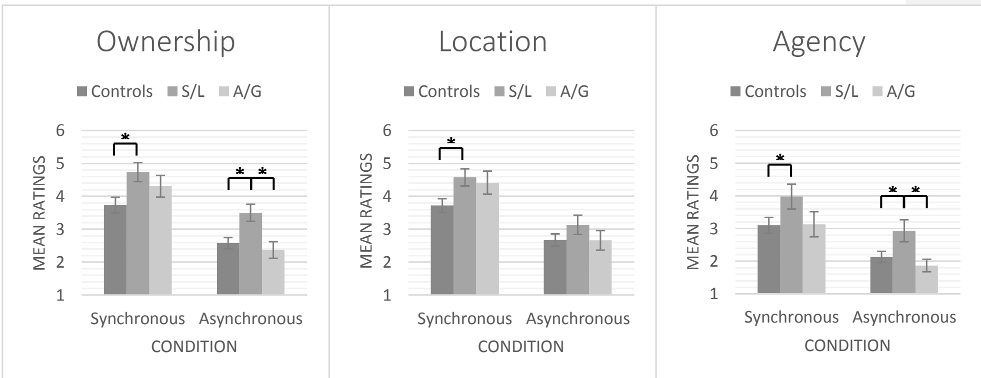
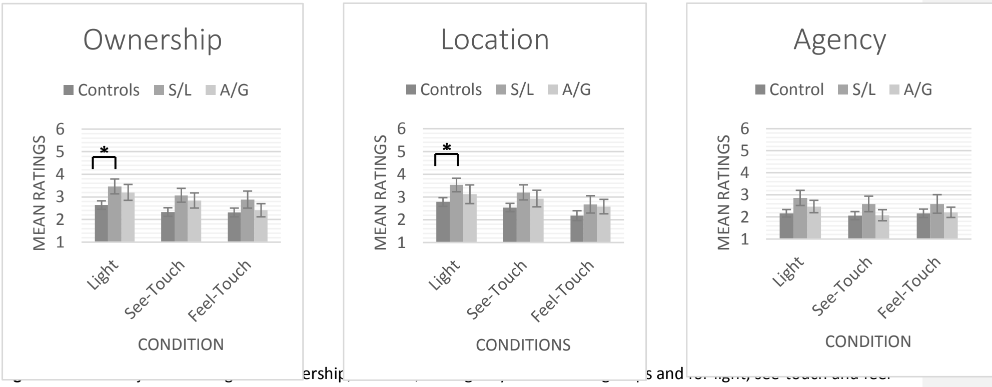


Figure 3 Mean subjective ratings for ownership, location, and agency in the three groups and for synchronous and asynchronous conditions. Error bars indicate standard errors. S/L = sensory-localised; A/G = affective-general. The sensory-

localised group (S/L) indicated higher ratings for ownership and agency than controls and affective-general group (A/G), and higher ratings for location than controls.



[illegible] ership [illegible] s and [illegible] touch conditions. Error bars indicate standard errors. S/L = sensory-localised; A/G = affective-general. The sensory-localised group reported higher ratings for ownership and location than controls in the light condition.

Discussion

Previous research has suggested an atypical propensity to experience the rubber hand illusion, a putative measure of body ownership, in people who report experiencing the pain of others (Derbyshire et al., 2013) or who report experiencing touch when seeing others touched (Aimola Davies & White, 2010). However, the mechanism behind this is not clear: is it visual capture, or an exaggeration of the normal pattern, or something else? Here we used a novel way of identifying and grouping vicarious pain responders (Grice-Jackson et al., 2017a), that divides them into two groups: a sensory/localised (S/L) group who reports localised experiences with sensory qualities on their own body when viewing pain and an affective/general (A/G) group who reports non-localised experiences with affective qualities. We show that the S/L group has a distinctive pattern on the RHI, whereas the A/G resembles controls. The S/L group show the RHI for both synchronous and asynchronous stroking (in terms of higher proprioceptive drift and subjective ratings of ownership and agency). Moreover, there was a trend towards higher proprioceptive drift in the light condition, and they also reported greater subjective ratings in the synchronous condition. None of the groups experienced the illusion when the RHI was broken down into its constituent parts (seeing the dummy touched, the ‘see-touch’ condition; or feeling one’s own hand touched, the ‘feel-touch’ condition). This demonstrates that there is not a general tendency towards incorporating the rubber hand per se, nor a general tendency for the RHI to be driven by the sight of touch (as suggested previously for mirror-touch synaesthesia). Together, these results provide evidence that the S/L group have a heightened tendency to incorporate the rubber hand within their own body representation under certain conditions. The question as to why it is found for the S/L group alone remains to be determined. Of relevance here is that the S/L group, but not the A/G group, report that their experiences are localised to the corresponding body part at least when reporting vicarious pain (and this is supported by more somatotopic activity in primary somatosensory cortex in the S/L group; Grice-Jackson et al., 2017b). Either difficulties in body ownership are limited to the S/L group or, else, difficulties in body ownership are common to both but operate on different levels (whole bodies, v. body parts) and generate different effects depending on the nature of the paradigm (e.g. rubber hand illusion v. whole body illusion; Lenggenhager, Tadi, Metzinger, & Blanke, 2007).

In the sections below we discuss the results in detail. Firstly, in relation to previously reported individual differences and group-based differences in the RHI. Secondly, we discuss our findings in relation to theoretical models of the RHI.

Previous atypical findings in the RHI

Previous literature has documented atypical RHI susceptibility patterns in clinical conditions including eating disorders, schizophrenia, and autism and our results will be discussed considering similarities or dissimilarities with these conditions.

Our results resemble findings that have been previously reported in the eating disorder literature. Patients with diagnosis of body dysmorphic disorder present no differences in proprioceptive drift between the synchronous and asynchronous conditions, scoring significantly higher in both conditions than in the recorded baseline (Kaplan, Enticott, Hohwy, Castle & Rossell, 2014). Eshkevari, et al. (2012)found that patients with anorexia nervosa score higher on both proprioceptive drift and on overall subjective ratings when compared to controls () and Zopf, Contini, Fowler, Mondraty and Williams (2016) reported higher subjective ratings in anorexia nervosa for both synchronous and asynchronous RHI conditions when compared to controls, although they didn't find it in proprioceptive drift . The pattern of results in our group is similar to these findings which may be due to abnormalities in self representations.

Eating disorders have been associated with a more unstable bodily self-representation and increased bodily plasticity (Eshkevari, wt al., 2012; Kaplan, et al., 2014) as well as interoceptive deficits (Preyde, Watson, Remers & Stuart, 2016, but also see Eshkevari, Rieger, Musiat & Treasure, 2014). Lower interoceptive awareness is associated with increased susceptibility to RHI and with a less clear perception of internal bodily processes that give rise to the bodily self (Tsakiris, Tajadura-Jimenez & Costantini, 2011) and dysfunctionalities within the insular cortex have been linked to distorted body-perceptions (Heydrich & Blanke, 2013) and to eating disorder (Strigo et al, 2013). Comparatively little is known about these mechanisms in vicarious pain responders, although the insula is also implicated. Grice-Jackson et al. (2017a) reported increased grey matter density in the insula in both S/L and A/G responders and, using fMRI functional connectivity, found greater coupling of the insula with the right tempero-parietal junction (a region implicated in selectively attending to self v. other) in the S/L group when viewing the pain of others (Grice-Jackson et al., 2017b). Insula dysfunction could therefore explain the tendency for the S/L group to have a greater RHI (found in several conditions for subjective ratings), although it does not make specific predictions about the asynchronous condition. It does, however, make the testable prediction that eating disorders and these differences in vicarious pain perception may co-occur more than chance if they share similar neurocognitive mechanisms.

The heightened tendency towards experiencing the rubber hand has also been associated with more pronounced psychotic traits, but, this manifests itself as an exaggeration of the normal (synchronous) effect (Germine, Benson, Cohen & Hooker, 2015; Kallai et al., 2015). In one study, schizophrenic patients scored higher on ownership questions of the RHI questionnaire and presented greater proprioceptive drift after the synchronous condition (Thakkar et al., 2011). Overall, psychotic traits seem to be associated with more pronounced subjective feelings of ownership, but only after the synchronous condition of the rubber hand illusion and these results are not convincingly replicated for proprioceptive drift. Compared to this group, our S/L subjects present some similarities (i.e. higher subjective ratings of ownership than controls in synchronous condition) but differ insofar as this extends to the asynchronous condition.

Conversely, lower susceptibility towards the RHI (in the standard synchronous condition) has been found in people with Autism Spectrum Conditions (ASC) or high autistic traits in non-clinical groups. This is expressed in measures of proprioceptive drift (Palmer, Paton, Hohwy & Enticott, 2013) and in reported experience of ownership, when there is no discrepancy between the felt and seen location (Paton, Hohwy & Enticott, 2012). In terms of theoretical models, it is possible that people with autism rely more on sensory input (from their own hand) and less on a top-down internal model of the body but in psychosis the reverse is true (Quattrocki & Friston, 2014). A reverse mechanism may be present in the S/L group and we will discuss possible explanations for this below.

Theoretical models explaining the RHI

Three models explaining the occurrence of the illusion have been proposed until now that would explain the illusion so we will further interpret our results within these theoretical models.

The first, classical model proposes that the RHI is enhanced by synchrony or, more generally, by matching sensory signals (tactile, visual, and proprioceptive). The Botvinik and Cohen (1998) model suggests that the visuo-tactile correlation alone is responsible for updating the spatial location of subject’s real hand and that intermodal matching is a sufficient condition for the rubber hand attribution. This model has been expanded arguing that the visuo-tactile correlation is necessary but not always sufficient. It has been proposed that not only the matching of external stimuli is important but also the matching between the external input and the pre-existing body image (e.g. body shape/size) or body-schema (e.g. body configuration) (Makin, Holmes & Ehrsson, 2008; Tsakiris, 2010). Even though the visual-tactile synchrony is the main driver of the illusion, the coherence with pre-existing visual and proprioceptive body representations is necessary for the illusion to manifest. Thus, there is a necessity of congruent posture and identity with respect to the participant’s hand (Tsakiris & Haggard, 2005; but also see Holle et al., 2011) which facilitates the integration of sensory information in favour of vision within the peripersonal space (Makin, Holmes & Ehrsson, 2008). In our study, we did observe that the illusion occurred when there was a match between visual and tactile input (synchronous condition) in all groups, however the S/L group performed similarly in the asynchronous condition too. Within this model, we would conclude that the S/L interprets asynchrony as a matching signal. This could be because they do not perceive the visuo-tactile asynchrony (a very unlikely scenario since the temporal difference was of approximately 625ms) or, more likely, that the asynchrony is perceived but does not influence the computation of body ownership in the normal way. For instance it is to be noted that both the visual and tactile signals are equally correlated in both the synchronous and asynchronous conditions. Whereas they are in-phase in the synchronous condition (occur simultaneously) they are out of phase (occur consecutively) in the asynchronous condition (i.e. correlations of +1 and -1 respectively). In our ‘see touch’ condition the dummy hand was touched and in our ‘feel touch’ condition the real hand was touched; i.e. there was never a correlation between them. It may be that the S/L group are sensitive to visuo-tactile correlations, whereas the more typical pattern is to rely also on visuo-tactile simultaneity. This generates a testable prediction that asynchronous stroking in which the strokes occurs unpredictably (i.e. with zero correlation) would not lead to the RHI in the S/L group.

A second model that has been proposed by Rhode, Luca and Ernst (2011) states that the RHI is disrupted by asynchrony rather than enhanced by synchrony or matching signals. Their study found that visual capture alone (i.e. looking at the dummy hand with no touch to either hand) produced comparable proprioceptive drift to the synchronous condition. The authors proposed that proprioceptive drift is typically found when looking at an anatomically plausible dummy hand and that the asynchronous control condition has a negative effect on the visual capture of proprioception as opposed to the synchronous condition having a positive effect on visual-proprioceptive integration. Within this model's framework, our result shows that asynchronous stroking does not weaken the visual-proprioceptive integration in the S/L group suggesting that this group is not treating the visuo-tactile signals as mismatching. The main condition that adjudicates between this model and the previous one is whether there is drift in the absence of any touch to either hand. Our study did not include this condition and it is important for future research to explore this with these groups and in terms of other individual differences.

A third theoretical model, the predictive coding or Bayesian framework, proposes that the rubber hand illusion can be construed as the interpretation that different sensory signals (tactile, visual, proprioceptive) have a common cause, i.e. that the signals are attributed to a single hand rather than two different causes namely a dummy and a real hand (see Samad, Chung and Shams, 2014). The attribution of a common cause depends on two things: the nature of the incoming sensory signals (e.g. how well they are matched) and prior expectations (e.g. how long it takes for an observed touch to be felt). With regards to the sensory signals, those that are spatially and temporally aligned are more likely to be integrated (i.e. attributed to a common cause) – as in the original Botvinick and Cohen (1998) explanation and other models in that tradition. However, there is an additional property of the sensory signal that is relevant namely it's precision. More precise sensory signals are weighted more heavily, so vision with its high spatial precision tends to dominate over proprioception and, hence, the illusion as measured by proprioceptive drift can occur just by looking at the rubber hand (Rohde, et al. 2011; Samad, et al., 2014). This may also be a source of individual differences: if an individual has poor proprioception abilities then they should show a stronger influence of vision and a greater RHI. This is a testable prediction that could account for some of the reported differences including those we observe for the S/L group (note: previous studies on the RHI measure proprioceptive drift rather than actual proprioceptive ability). The alternative, not yet considered in detail by these models, is that there are individual and group differences in priors (i.e. willingness to attribute different signals to a common cause, or to update priors on the basis of new evidence). These kinds of differences have been postulated in conditions such as autism (Van de Cruys et al., 2014) and schizophrenia (Fletcher & Frith, 2009) that also show differences in RHI susceptibility, and may also be the case in those who report experiencing the localised pain of others.

Conclusion

We have identified a new group of individuals who are highly susceptible to the rubber hand illusion. Our findings indicate particularities in body representations and self-other distinctions. The S/L group scored higher under certain conditions on both proprioceptive drift, a measure attributed to body perception and localization. Moreover, the S/L group scored higher on subjective ratings of the illusion. Even though the exact mechanisms are still unknown, there are various possible interpretations. These are not mutually exclusive and include: more unstable body image and body schema, predominant influence of visual input and lower tactile precision. Further research is needed to disentangle these aspects.

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Supplementary Results

S1. VPQ group differences comparing TPRs with intensity

Table 2. Number of subjects in each group for test and post-test generated with TPR or Intensity as cluster analysis variables.

Group	Time 1	Time 2	Entire Sample

	TPR	Intensity	TPR	Intensity	TPR	Intensity
Controls	49	49	51	55	730	773
S/L	21	21	18	17	191	158
A/G	12	12	13	10	135	125

Overall, 2 subjects changed group at time 1 when comparing TPR with Intensity representing 2.44% of the sample (N=82) and 4 subjects changed group at time 2 representing 4.88%.

At the entire sample level (N=1056), 48 subjects changed group, representing 4.5%.

S2. Baseline comparisons and Light question analysis

Further one sample t-tests were conducted for a comparison to a baseline of '0' for all groups and all conditions. Significant results were obtained in controls for synchronous condition, $t(53) = 4.632$, $p<0.001$; in S/L for synchronous, $t(20)=4.112$, $p=0.001$, asynchronous $t(20) = 4.295$, $p<0.001$ and light $t(20) = 2.528$, $p=0.02$; in A/G for synchronous $t(18) = 5.18$, $p<0.001$.

Table 3. Means and standard deviations for light subjective ratings according to the presence of light induced sensation

Light Subscale	**Sensations present**	**Sensations Absent**
Ownership	3.7 ± 1.42	2.31 ± 1.27
Location	4.00 ± 1.46	2.20 ± 1.21
Agency	3.23 ± 1.46	1.71 ± 0.94

Independent Sample t-tests showed that there was a significant difference in subjective ratings of illusion strength in the light condition between those who did report light-induced sensations and those who did not. Higher subjective ratings were found for light ownership $t(39) = 3.229$, $p<0.05$; light location $t(39)=4.162$, $p<0.001$; light agency $t(39)=3.780$, $p<0.001$. Non-parametric Mann-Whitney U test confirmed these results.

S3. Percentages of people not experiencing the illusion in each group

Table 4. Percentages of subjects ***not*** *experiencing the illusion in each group, namely participants whose mean score on subjective ratings was lower than 4.*

Group	**Synchronous**	**Asynchronous**	**Light**	**See-touch**	**Feel-touch**
Controls	28	47	46	61	60
Sensory-localised	14	18	23	41	64

Commented [jw1]: Is there a reason why we coded this as 'not'? I would find it much more intuitive to display the percetanges of people who do get the illusion

General affective	11	74	58	42	47

Table 5. Percentages of subjects not experiencing the illusion for each subscale of each condition.

Commented [jw2]: As before

	Syn			**Asyn**			**Light**			**See**			**Feel**		
Group	**Own**	**Loc**	**Age**	**Own**	**Loc**	**Age**	**Own**	**Loc**	**Age**	**Own**	**Loc**	**Age**	**Own**	**Loc**	**Age**
C	47	56	65	84	81	84	77	82	81	84	82	86	81	84	86
S/L	27	27	41	68	73	68	50	55	68	73	68	77	73	73	73
A/G	32	32	63	89	79	100	68	63	84	79	74	89	84	79	95