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Psychosis-proneness and the rubber hand illusion of body ownership

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ABSTRACT

Psychosis and psychosis-proneness are associated with abnormalities in subjective experience of the self, including distortions in bodily experience that are difficult to study experimentally due to lack of structured methods. In 55 healthy adults, we assessed the relationship between self-reported psychosis-like characteristics and susceptibility to the rubber hand illusion of body ownership. In this illusion, a participant sees a rubber hand being stroked by a brush at the same time that they feel a brush stroking their own hand. In some individuals, this creates the bodily sense that the rubber hand is their own hand. Individual differences in positive (but not negative) psychosis-like characteristics predicted differences in susceptibility to experiencing the rubber hand illusion. This relationship was specific to the subjective experience of rubber hand ownership, and not other unusual experiences or sensations, and absent when a small delay was introduced between seeing and feeling the brush stroke. This indicates that individual differences in susceptibility are related to visual–tactile integration and cannot be explained by differences in the tendency to endorse unusual experiences. Our findings suggest that susceptibility to body representation distortion by sensory information may be related or contribute to the development of psychosis and positive psychosis-like characteristics.

1. Introduction

Before the rise of symptom-based classifications of mental illness, schizophrenia was described as an abnormality in self representation by both Kraepelin (1913) (the "orchestra without a conductor") and Bleuler (1916) (the loss of the "individual self") (Parnas, 2011). Viewing schizophrenia from a phenomenological perspective, Sass and Parnas suggested that a key factor in the pathogenesis of psychosis is a deficit in "ipseity" or the basic sense of inhabiting the self (Sass and Parnas, 2003). This is consistent with findings in the cognitive neuroscience literature where schizophrenia is linked to basic deficits in self processing, such as source monitoring (Frith, 1992; Ditman and Kuperberg, 2005) and self-referential processing (Vinogradov et al., 2008). Deficits in self processing may underlie the deficits in social cognitive processing characteristic of schizophrenia (Fisher et al., 2008) and deficits in emotion perception in psychosis-prone individuals (Germine and Hooker, 2011).

Individuals with psychosis or high risk for developing psychosis report disruptions to the bodily self (Chapman et al., 1978; Lenzenweger, 2006, 2010), including abnormalities in the experience of inhabiting the body (Sass and Parnas, 2003; Nelson et al., 2008) or the perception that the body has undergone some morphological change (Chapman et al., 1978; Nelson et al., 2008). These body image aberrations are thought to be part of a broader set of perceptual deficits in psychosis (Chapman et al., 1978; Lenzenweger, 2010).

The perception of one's body is a basic dimension of subjective experience, and is unique in its stability and consistency relative to external percepts (James, 1890; Merleau-Ponty, 1962). Understanding how body representation stability differs in individuals with varying levels of psychosis-proneness (i.e. with varying levels of vulnerability to developing psychosis) may offer key insights into the disturbances of self processing that may contribute to psychosis development (Nelson et al., 2008).

Despite the stability of the body in our perceptual experience, illusions of body ownership are readily inducible in healthy individuals (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). The rubber hand illusion, in particular, has been used to investigate the structure of body representations (Tsakiris, 2010) and the phenomenology of the bodily self (Longo et al., 2008). In this illusion, the participant feels the touch of a brush on their own hand, hidden from view, at the same time that they see a brush touching a rubber hand. After a brief period of simultaneous stimulation of the participant's own hand and the rubber hand, approximately 40% of healthy participants will experience the bodily sense that the rubber hand is their own hand (Botvinick and Cohen, 1998). This distortion in bodily experience has been linked with biased judgments of the body's location in space (proprioceptive drift; Botvinick and Cohen, 1998), illusory sensations on the rubber hand

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(Durgin et al., 2007), and cooling of the participant's own hand (Moseley et al., 2008).

Susceptibility to the rubber hand illusion varies across individuals and experimental conditions (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). The tendency to experience the illusion can be reduced or eliminated by disrupting perceptual cues that drive visual–tactile integration through asynchronous stimulation (i.e. by stroking the rubber hand and the participant's hand asynchronously, such that the brush is seen to touch the rubber hand at a different time than the touch is felt on the participant's own hand; Tsakiris and Haggard, 2005) or by violating constraints related to knowledge about the body (e.g. substituting a wooden block for the rubber hand; Tsakiris, 2010; Tsakiris et al., 2010).

The rubber hand illusion provides an experimentally tractable way of tapping into the subjective experience of the body and investigating how individual differences in psychiatric vulnerability relate to the bodily self. Psychosis and psychosis-proneness are associated with deficits in somatosensory processing (Chapman et al., 1978; Lenzenweger et al., 2003; Chang and Lenzenweger, 2005; Lenzenweger, 2010) and abnormalities in the experience of the body are evident in the prodromal stages of psychosis, representing a basic aspect of disturbed phenomenology (Sass and Parnas, 2003; Lenzenweger, 2006, 2010; Nelson et al., 2008). Given these previous findings, susceptibility to distortions of body representations may be related to individual differences in psychosis-like characteristics (psychosis-proneness) even in the absence of psychotic symptoms. If this is the case, body representation abnormalities may be part of the fundamental vulnerability to developing psychosis or psychosis-like experiences.

Two previous studies have attempted to link psychosis with susceptibility to the rubber hand illusion. Peled et al. (2000) and Thakkar et al. (2011) showed that participants with schizophrenia are more prone to experiencing the rubber hand illusion than healthy control participants, and that these relationships were related to positive symptoms. The results of Peled et al. (2000) are hard to interpret though, as they lacked a comparison condition and thus could not control for the general tendency to endorse unusual experiences or bodily sensations among schizophrenia patients. In contrast, the findings from a comprehensive study by Thakkar et al. (2011) are more interpretable, as the experimental design included a control condition to look at rubber hand illusion experiences and proprioceptive bias after asynchronous stimulation. Thakkar et al. (2011) found that schizophrenia was associated with greater proprioceptive drift after synchronous as compared with asynchronous stimulation, indicating greater proprioceptive sensitivity to synchronous visual–tactile information among individuals with schizophrenia. Furthermore, schizophrenia patients also had greater self-reported experiences of the rubber hand illusion when compared with healthy controls. The difference in self-reported experiences after synchronous and asynchronous stimulation was similar for both patients and controls, however (that is, the group × condition interaction was not significant for self-report), leaving the possibility that differences in self-reported experiences among schizophrenia patients may be related to an overall elevated tendency to experience a feeling of ownership over a rubber hand regardless of the experimental manipulation. Thakkar et al.'s finding of a schizophrenia-related dissociation in proprioception between synchronous and asynchronous stimulation conditions argues against this possibility, but conclusions about the relationship between psychosis and the rubber hand illusion would be strengthened by a similar dissociation in self-reported experience of the illusion.

In the current manuscript, we approach the relationship between illusions of body ownership and psychosis from the perspective of psychosis vulnerability or variations in psychosis-like characteristics among healthy individuals. This approach allows us to look at whether flexibility in body representations is a pre-existing or even predisposing characteristic in psychosis-prone individuals, as has been suggested by previous work (Chapman et al., 1978; Lenzenweger, 2010; Thakkar et al., 2011). The goal of the current study was to identify whether there is a specific relationship between experimentally-induced illusions of body ownership and psychosis-proneness. We hypothesized that greater psychosis-proneness, as measured by self-reported psychosis-like characteristics, would be related to a greater tendency to experience the rubber hand illusion after synchronous stimulation (stroking the rubber hand and the participant's own hand at the same time). We predicted that this relationship would be reduced or absent after asynchronous stimulation (stroking the rubber hand and the participant's own hand with a small temporal offset), as temporal synchrony is needed for multisensory integration (Tsakiris and Haggard, 2005). In other words, we predicted that the relationship between psychosis-proneness and the rubber hand illusion would be driven by differences in the tendency to alter the body representation in response to visual–tactile cues that lead to illusion formation in healthy adults. We further predicted that the experience of the rubber hand illusion would be more closely associated with positive psychosis-like characteristics (e.g. cognitive and perceptual distortions) than negative psychosis-like characteristics (e.g. anhedonia), as positive symptoms often include abnormalities in bodily experience. Finally, we predicted that psychosis-proneness would be specifically related to subjective feelings of body ownership/agency and not a general tendency to have or endorse unusual experiences. For example, the experimental procedure can induce feelings of diminished or abnormal sensory perception in the participant's own hand (which we refer to as "reduced afference", e.g. feelings of tingling or numbness; Longo et al., 2008). We expected that variations in psychosis-proneness would not predict variations in feelings of reduced afference. Confirmation of a link between individual differences in psychosis-like characteristics and susceptibility to illusions of body ownership would provide an avenue for further exploration into how the phenomenology of self, body, and psychosis are related.

2. Methods

2.1. Participants

Participants were 55 healthy volunteers (20/55 males) with a mean age of 28 (S.D.=11) recruited through the community-wide Harvard University study pool. All participants spoke English as a native language, were neurologically healthy, and had no DSM-IV Axis I psychiatric disorders based on administration of the MINI clinical interview (Sheehan et al., 1998). All participants gave informed consent before participating and the protocol was approved by the Committee for the Use of Human Subjects at Harvard University.

2.2. Psychosis-proneness measures

We assessed psychosis-proneness with several widely used self-report questionnaires that measure positive and negative psychosis-like characteristics. Our measure of positive psychosis-like characteristics (positive psychosis-proneness) included 132 items taken from the cognitive-perceptual subscale of the Schizotypal Personality Questionnaire (33 items; Raine, 1991), the Chapman Magical Ideation Scale (30 items; Eckblad and Chapman, 1983), the Chapman Perceptual Aberration Scale (35 items; Chapman et al., 1978), and the Referential Thinking Scale (34 items; Lenzenweger et al., 1997). Our measure of negative psychosis-like characteristics (negative psychosis-proneness) included 73 items taken from the interpersonal subscale of the Schizotypal Personality Questionnaire (33 items; Raine, 1991) and the Chapman Revised Social Anhedonia Scale (40 items; Eckblad et al., 1982; Mishlove and Chapman, 1985). We omit disorganized psychosis-like characteristics from our analysis due to a relative dearth of evidence that disorganized characteristics are predictive of psychosis development and the relatively few items included in the above scales (16 in total from the Schizotypal Personality Questionnaire) for measuring disorganized features.

These scales all have established associations with vulnerability to schizophrenia spectrum disorders (Chapman et al., 1994; Gooding et al., 2005; Kwapil, 1998; Lenzenweger et al., 1997; Raine, 1991; Raine et al., 1994; Startup et al., 2010).

Mean scores for psychosis-proneness were lower in our sample than in reported norms for positive psychosis-like characteristics (Eckblad and Chapman, 1983; Chapman et al., 1978; Lenzenweger et al., 1997; Raine, 1991), but comparable for negative psychosis-like characteristics (Eckblad et al., 1982; Raine, 1991; Chapman et al., 1994). The expected impact of the lower positive psychosis-proneness scores in our sample would be floor effects and a reduced likelihood of detecting associations between positive psychosis-proneness and other variables. Scores for positive psychosis-proneness were comparable to scores from other healthy control samples, however, and 10–20% of the sample exhibited levels of positive psychosis-like characteristics within one standard deviation of the scores of samples of schizophrenia patients (Rossi and Daneluzzo, 2002; Camisa et al., 2005; Startup et al., 2010).

2.3. Rubber hand illusion procedure

After completing the questionnaires, participants sat at a table and placed their nondominant hand inside of a large box. An opening at the top of the box allowed the participant to see a lifelike rubber hand at their midline (Tsakiris and Haggard, 2005), with 20 cm between the middle finger of the rubber hand and of the participant's hand (Lloyd, 2007). Participants wore a smock that hid both their arms. Two paintbrush heads were attached to a rod that passed through the box lengthwise. The paintbrush heads were 20 cm apart, so that rotating the rod caused the paintbrushes to brush the participant's hand and the rubber hand in the same location. Fig. 1 provides an illustration of the experimental set-up.

There were two stimulation phases (Botvinick and Cohen, 1998). During the synchronous phase, the paintbrush heads were aligned so that the participant saw the rubber hand being touched by the paintbrush at the same time as the paintbrush was touching their own hand. During the asynchronous phase, the paintbrush heads were misaligned by 90° along the rod, so that the brush touched the rubber hand a quarter of a second before or after touching the participant's hand (~250 ms based on a one rotation/second frequency of brushing). Each stimulation phase lasted 10 min.

Before and after each stimulation phase, the participant indicated the perceived location of the middle finger of their hand by reading off a meter stick held just above the box and randomly translated left or right. Proprioceptive drift was estimated as the difference between pre and post-stimulation hand location judgments (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). The participant was then asked a series of questions to assess their experience of the illusion (see Table 1; taken from Longo et al. (2008) and Botvinick and Cohen (1998)) and any nonspecific feelings of reduced afference (Longo et al., 2008).

Subjective experience of rubber hand ownership was measured using five items rated from −3 (strongly disagree) to 3 (strongly agree) (see Table 1; Botvinick and Cohen, 1998; Longo et al., 2008). These questions distinguish between experiences after synchronous versus asynchronous stimulation and are specifically related to the rubber hand illusion (Longo et al., 2008). Feelings of agency over the rubber hand were measured with two questions (Longo et al., 2008). We measured agency and ownership separately based on dissociations in the literature (Gallagher, 2000), particularly in schizophrenia (Frith, 2005) and in the rubber hand illusion (Longo et al., 2008). Finally, three questions assessed feelings of reduced afference in the participant's own hand (e.g. numbness or tingling) (Longo et al., 2008). Feelings of reduced afference are not directly related to the rubber hand illusion, but rather are more prominent during asynchronous stimulation (Longo et al., 2008). Our prediction was that psychosis-proneness would be associated with feelings of rubber hand agency and ownership, but not reduced afference.

Psychosis is related to differences in suggestibility and sensitivity to experimenter demand (Young et al., 1987; Haddock et al., 1995; Waters et al., 2012). If participants know what types of experiences the experimenter is expecting, differences in suggestibility could confound any observed relationships between rubber hand illusion susceptibility and psychosis-proneness.

To avoid potential false positives arising from individual differences in suggestibility, the experiment was arranged so that the asynchronous stimulation condition always followed the synchronous stimulation condition. Participants were naïve about the expected effect during synchronous stimulation, but generally knew what to expect (either because of their experiences or post-stimulation assessment) during the asynchronous stimulation condition. Although this likely reduced our ability to detect dissociations between synchronous and asynchronous conditions, it enabled us to confidently interpret any dissociations that we were able to detect.

3. Results

Summary information on psychosis-proneness scores, question ratings, and proprioceptive drift is shown in Table 2.

As distributions of scores in our measures of psychosis-proneness and subjective ratings of the rubber hand illusion were all positively skewed and non-normal (Kolmogorov–Smirnov test for normality; all $P<0.05$), we report our main findings in terms of both parametric and nonparametric statistics.

To verify our experimental procedure, we compared measures of the rubber hand illusion after each stimulation phase. Based on previous findings, the illusion should be significantly stronger after synchronous stimulation than asynchronous stimulation (Tsakiris and Haggard, 2005; Longo et al., 2008). Compared with asynchronous stimulation, synchronous stimulation produced higher rubber hand ownership ratings (Wilcoxon Signed-Rank Test, one-tailed, $z=-5.0$, $P<0.001$; paired samples t-test, one-tailed, $t(54)=6.0$, $P<0.001$), higher agency ratings ($z=-2.4$, $P<0.05$; $t(54)=2.6$, $P<0.01$) and greater proprioceptive drift ($z=-1.7$, $P=0.07$; $t(54)=1.9$, $P<0.05$). Proprioceptive drift measures may have been biased by differences in baseline hand location judgments, as baseline hand position was

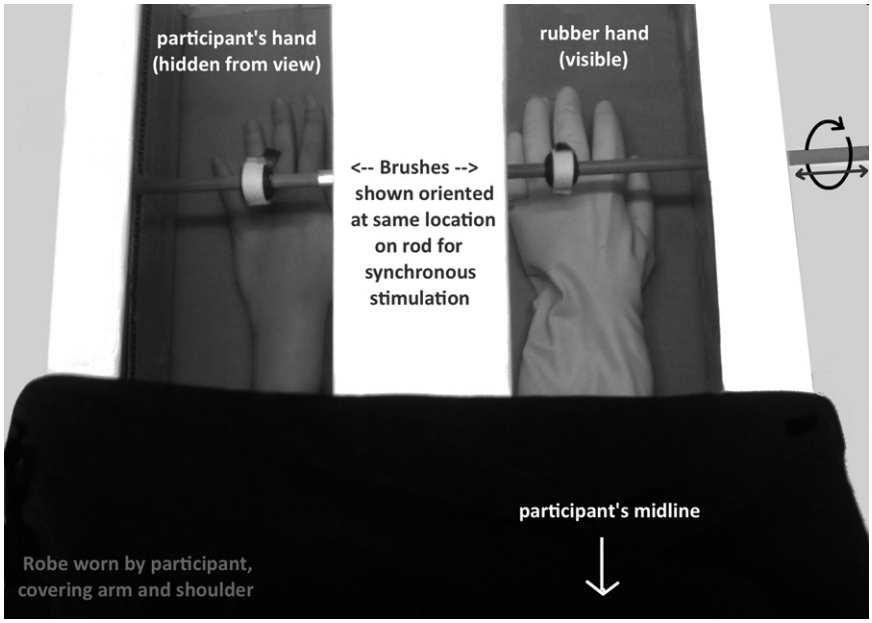

Fig. 1. Experimental set-up for inducing the rubber hand illusion: during synchronous stimulation (shown), brushes were oriented on the rod so that when the rod was moved by the experimenter, a brush was observed touching the rubber hand at the same time and in the same location as the participant felt the brush touching their own hand. During asynchronous stimulation, brushes were misaligned by 90° around the rod, so that the brush touched the participant's hand at a different time than the brush was observed touching the rubber hand.

Table 1
Self report items used to measure subjective experiences after synchronous and asynchronous brushing of the participant's hand and the rubber hand.

Question	Category	Source
1. It seemed as if I was feeling the touch of the paintbrush in the location where I saw the rubber hand touched	Ownership	Botvinick and Cohen (1998)
2. It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand	Ownership	Botvinick and Cohen (1998)
3. I felt as if the rubber hand was my hand	Ownership	Botvinick and Cohen (1998)
4. It seemed like I was looking directly at my own hand, rather than at a rubber hand	Ownership	Longo et al. (2008)
5. It seemed like my hand was in the location where the rubber hand was	Ownership	Longo et al. (2008)
6. It seemed like I could have moved the rubber hand if I wanted	Agency	Longo et al. (2008)
7. It seemed like I was in control of the rubber hand	Agency	Longo et al. (2008)
8. I had the sensation of pins and needles in my hand	Reduced afference	Longo et al. (2008)
9. I had the sensation that my hand was numb	Reduced afference	Longo et al. (2008)
10. It seemed like the experience of my hands was less vivid than normal	Reduced afference	Longo et al. (2008)

Table 2
Summary of independent and dependent measures.

	Mean	S.D.	Range
Positive psychosis-proneness scales			
Referential thinking	2.6	4.2	0 to 17
Magical ideation	3.3	2.8	0 to 12
Perceptual aberration	1.4	2.1	0 to 10
SPQ: Cognitive-perceptual factor	4.7	5.7	0 to 23
Total positive score	*12*	*13*	*0 to 60*
Negative psychosis-proneness scales			
Social anhedonia	9.5	8.4	0 to 34
SPQ: Interpersonal factor	6.9	7.6	0 to 30
Total negative score	*16*	*15*	*0 to 54*
Synchronous stimulation			
*Baseline position (cm)^*	−0.2	3.4	−9 to 10
*Proprioceptive drift (cm)^*	1.3	3.4	−9 to 10
Ownership ratings (average of Q1–5)	−0.23	1.9	−3 to 3
Agency ratings (average of Q6,7)	−1.5	2	−3 to 3
Deafference ratings (average of Q8–10)	−1.3	1.7	−3 to 3
Asynchronous stimulation			
*Baseline position (cm)^*	1.1	3.6	−8 to 19
*Proprioceptive drift (cm)^*	0.24	2.7	−6 to 6
Ownership ratings (average of Q1–5)	−1.6	1.7	−3 to 2.4
Agency ratings (average of Q6,7)	−2	1.6	−3 to 3
Deafference ratings (average of Q8–10)	−1.3	1.8	−3 to 2.7
^Positive numbers represent distances from the participant's hand towards the rubber hand			

Shown are mean, standard deviation (S.D.), and range of psychosis-proneness scores across the sample of 55 individuals. Also shown are mean, S.D., and range of dependent measures of the rubber hand illusion after synchronous and asynchronous brushing of the participant's hand and a rubber hand.

judged somewhat closer to the rubber hand before asynchronous stimulation as compared with synchronous stimulation (see Table 2; $z=-2.7$, $P<0.01$; $t(54)=-2.8$, $P<0.01$), potentially resulting in smaller overall differences in proprioceptive drift between the two conditions.

Although feelings of reduced afference were present in both conditions ($z=-4.4$ for both, $P<0.001$; $t(55)=-5.6$, $P<0.001$), there was no difference between conditions ($z=-0.21$, $P=0.83$; $t(54)=0.16$, $P=0.43$).

Based on these data, we confirm that our manipulation induced experiences associated with the rubber hand illusion in the synchronous condition compared with the asynchronous (control) condition.

We predicted that positive psychosis-proneness would be associated with greater susceptibility to the rubber hand illusion, as measured by feelings of rubber hand ownership and agency after synchronous stimulation. We examined ownership and agency separately because of ownership/agency dissociations in the schizophrenia literature (Frith, 2005) and rubber hand literature (Longo et al., 2008).

3.1. Rubber hand ownership and psychosis-proneness

Ownership is the degree to which the participant experiences the bodily sense that the rubber hand is his or her own hand. Consistent with our hypothesis, positive psychosis-proneness was significantly associated with subjective experiences of rubber hand ownership after synchronous stimulation (Spearman rank correlation, $\rho=0.32$, $P<0.05$; Pearson correlation, $r=0.42$, $P<0.01$), even when controlling for rubber hand ownership after asynchronous stimulation (Spearman rank partial correlation, $\rho=0.28$, $P<0.05$; Pearson partial correlation, $r=0.35$, $P<0.05$). After asynchronous stimulation, the association between rubber hand ownership and positive psychosis-proneness was weak or absent ($\rho=0.17$, $P=0.2$; $r=0.26$, $P=0.06$). As the relationship between positive psychosis-proneness and rubber hand ownership after synchronous stimulation remained significant even after differences related to asynchronous stimulation were removed, the correlation between positive psychosis-proneness and rubber hand ownership experiences cannot be explained

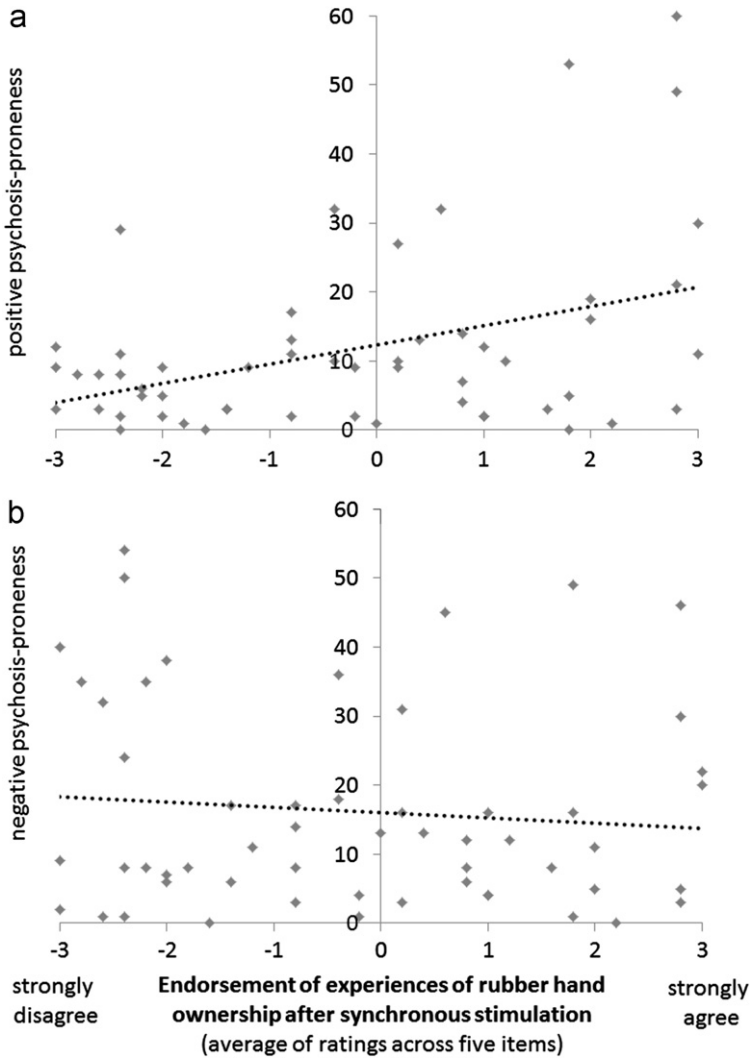

Fig. 2. Psychosis-proneness and the subjective experience of the rubber hand illusion after synchronous stimulation: the *y*-axis shows the number of psychosis-like characteristics a participant endorsed based on questionnaire measures. The *x*-axis shows how much the participant tended to agree or disagree with statements regarding feelings of body ownership over the rubber hand, after a period of synchronous brush strokes on the rubber hand and the participant's own hand. (a) Endorsement of positive psychosis-like characteristics (e.g. cognitive-perceptual distortions, referential thinking) was associated with a greater tendency to experience feelings of rubber hand ownership. (b) Endorsement of negative psychosis-like characteristics (e.g. social anhedonia) was not associated with feelings of rubber hand ownership.

by a general tendency to endorse unusual experiences among psychosis-prone participants.

Negative psychosis-proneness was not associated with the subjective experience of rubber hand ownership ($\rho = -0.08$, $P = 0.58$; $r = -0.1$, $P = 0.48$).

Fig. 2 shows the relationship between ratings of rubber hand ownership after synchronous stimulation, as related to positive and negative psychosis-proneness. Correlations between scores on each individual psychosis-proneness measure and experiences of rubber hand ownership are given in Tables S1–S3 in Supplementary Materials.

3.2. Agency and psychosis-proneness

Another component of the rubber hand illusion is the subjective experience of agency. Positive psychosis-proneness was significantly associated with the subjective experience of agency after synchronous stimulation ($\rho = 0.28$, $P < 0.05$; $r = 0.3$, $P < 0.05$), but also after asynchronous stimulation ($\rho = 0.24$, $P = 0.08$; $r = 0.33$, $P < 0.05$). Controlling for agency after asynchronous stimulation abolished this relationship ($\rho = 0.14$, $P = 0.3$; $r = 0.09$, $P = 0.52$). It is possible that order effects (asynchronous stimulation always followed synchronous stimulation) created a residual sense of agency that impacted experiences during asynchronous stimulation among psychosis-prone individuals. Alternatively, differences in the experience of agency that vary with psychosis-proneness may be less closely related to visual–tactile integration.

Negative psychosis-proneness was not associated with agency after either synchronous ($\rho = -0.05$, $P = 0.7$; $r = -0.04$, $P = 0.8$) or asynchronous stimulation ($\rho = -0.05$, $P = 0.7$; $r = 0.02$, $P = 0.9$).

3.3. Reduced afference and psychosis-proneness

To understand the specificity of the relationship between subjective experiences and psychosis-proneness, we assessed whether positive psychosis-proneness was associated with bodily experiences unrelated to the rubber hand illusion by measuring experiences of reduced afference after illusion induction (Longo et al., 2008).

Positive psychosis-proneness was not associated with feelings of reduced afference after synchronous ($\rho = 0.06$, $P = 0.67$; $r = 0.08$, $P = 0.58$) or asynchronous stimulation ($\rho = 0.11$, $P = 0.41$; $r = 0.13$, $P = 0.35$). Differences in negative psychosis-proneness, similarly, showed no association with feelings of reduced afference

(synchronous: $\rho=0.09$, $P=0.51$; $r=0.13$, $P=0.35$; asynchronous: $\rho=-0.04$, $P=0.8$; $r=-0.1$, $P=0.46$).

3.4. Proprioceptive drift and psychosis-proneness

The rubber hand illusion is often associated with biases in proprioception, where the participant judges their own hand as being closer to the rubber hand after synchronous stimulation (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005; Longo et al., 2008). We predicted that psychosis-proneness would be associated with greater proprioceptive drift towards the rubber hand after synchronous stimulation.

Contrary to our hypothesis, proprioceptive drift after synchronous stimulation was not associated with positive psychosis-proneness ($\rho=0.03$, $P=0.85$; $r=0.07$, $P=0.62$) or negative psychosis-proneness ($\rho=0.01$, $P=0.96$; $r=0.06$, $P=0.64$). Dissociations between drift and subjective experience of the rubber hand illusion have been documented in previous studies (Holmes et al., 2006; Kammers et al., 2009, 2011; Rohde et al., 2011), and these two measures may map onto dissociable aspects of the illusion.

4. Discussion

We have shown that positive psychosis-like characteristics in otherwise healthy individuals are associated with a greater susceptibility to illusions of body ownership like the rubber hand illusion. These positive psychosis-like characteristics include a tendency towards referential thinking (Lenzenweger et al., 1997), magical ideation (Eckblad and Chapman, 1983), cognitive-perceptual distortions (Raine, 1991), and perceptual aberrations (Chapman et al., 1978). Our data suggest that susceptibility to distortions in body representations may be a vulnerability factor for developing psychosis, consistent with abnormalities in bodily experience among individuals at high risk of developing psychosis (Sass and Parnas, 2003; Nelson et al., 2008; Lenzenweger, 2010). A tendency to experience distortions in body representations may be linked to the development of positive psychosis-like experiences and to broader deficits in self processing related to psychosis risk.

The relationship between positive psychosis-proneness and the experience of ownership in the rubber hand illusion was specific to the synchronous stimulation condition, where the participant saw a brush stroking a rubber hand at the same time as feeling a brush stroking their own hand. When a small delay was introduced between these two events (asynchronous stimulation), the relationship between positive psychosis-proneness and illusion strength was weak or nonexistent. Our results show that the relationship between positive psychosis-proneness and rubber hand illusion strength was not being driven by a tendency to endorse unusual experiences. Along similar lines, psychosis-proneness was specifically related to feelings of rubber hand ownership, and not to feelings of reduced afference that were also induced by the experimental procedure (Longo et al., 2008). The specificity of the relationship between positive psychosis-proneness and the experience of rubber hand ownership after synchronous stimulation rules out alternative explanations that previous experiments looking at body ownership and psychosis/psychosis vulnerability have failed to exclude.

The rubber hand illusion is thought to be a consequence of multisensory (visual–tactile) information overriding pre-existing representations of the body (Tsakiris, 2010). Thus, greater illusion susceptibility could arise from either enhanced multisensory integration or weaker pre-existing body representations among individuals with positive psychosis-like characteristics. Previous studies suggest that psychosis and psychosis-proneness are related to reduced rather than enhanced multisensory integration (de Gelder et al., 2005; Ross et al., 2007; Asai and Tanno, 2008; Ujiee et al., 2011), so enhanced visual–tactile integration is an unlikely explanation for our findings. Instead, greater illusion susceptibility could arise from weaker body or somatosensory representations (Chapman et al., 1978; Chang and Lenzenweger, 2005; Lenzenweger, 2010). One previous study, for example, found abnormalities in somatosensory evoked potentials during the rubber hand illusion in a sample of schizophrenia patients (Peled et al., 2003).

Along similar lines, previous research has suggested that schizophrenia-related cognitive and perceptual abnormalities result from a failure to adequately couple sensory information with context and existing representations (Fleminger, 1992; Fletcher and Frith, 2009; Gilbert and Sigman, 2007; Hemsley, 1987, 2005; Schneider et al., 2002). Increased rubber hand illusion susceptibility among individuals high in positive psychosis-proneness may result from a reliance on multisensory information over pre-existing, but potentially less robust representations of the body. Having body representations that are susceptible to distortion may further contribute to positive psychosis-like characteristics by disrupting the stability of self experience (Sass and Parnas, 2003; Nelson et al., 2008; James, 1890).

Two previous studies have looked at the relationship between psychosis-related personality variables and the rubber hand illusion (Asai et al., 2011; Thakkar et al., 2011). Asai et al. (2011) found that positive psychosis-proneness was related to differences in proprioceptive drift and unusual perceptual experiences after synchronous stimulation, but these unusual experiences were not experiences that are related to the rubber hand illusion in the literature (e.g. the sensation that the participant's own hand is moving; see Asai et al., 2011, Supplementary materials). Asai et al. (2011) found no significant relationship between psychosis-proneness and self-report items that validly measure rubber hand illusion experiences. The lack of significant findings between psychosis-proneness and the experience of the rubber hand illusion may have been due to the relatively low number of positive psychosis-like characteristics assessed (eight items from the brief version of the Schizotypal Personality Questionnaire, compared to 132 items in the current study; Asai et al., 2011).

In contrast, Thakkar et al. (2011) were able to detect a significant relationship between psychosis-proneness and rubber hand illusion experiences in their control sample, using the 74-item Schizotypal Personality Questionnaire (SPQ; Raine, 1991). Thakkar et al. did not report differences in the relationship between psychosis-proneness and the rubber hand illusion after synchronous as compared with asynchronous stimulation, however, making it more difficult to conclude that psychosis-proneness related differences in the rubber hand illusion were not related to an increased tendency to endorse unusual experiences. The current study builds on this investigation by assessing a broader range of psychosis-like characteristics (five self-report scales across six domains) in a much larger sample, finding that positive psychosis-proneness specifically predicts rubber hand ownership experiences after synchronous visual–tactile stimulation. Altogether, our findings demonstrate that the relationship between psychosis-proneness and the rubber hand illusion is not an artifact of a generic tendency to experience body distortions or a tendency to endorse unusual experiences (regardless of the experimental manipulation).

One limitation of our study is the absence of any relationship between psychosis-proneness and proprioceptive drift after synchronous stimulation. Although self-reported experiences of the rubber hand illusion and proprioceptive drift are generally highly associated (Longo et al., 2008), dissociations between these two measures have now been noted in several studies (Holmes et al., 2006;

Kammers et al., 2009, 2011; Thakkar et al., 2011; Rohde et al., 2011). These dissociations suggest that proprioceptive drift and self-reported experiences may tap into different aspects of the rubber hand illusion. At least one previous study found that positive psychosis-proneness predicts proprioceptive drift after synchronous stimulation (Asai et al., 2011), so it may be that our experimental set-up was not well suited for detecting individual differences in proprioceptive drift related to psychosis-proneness. Alternatively, positive psychosis-proneness may be related specifically to distortions in the subjective experience of the body and not to differences in proprioceptive localization of the body in space.

An unexpected finding in our study was a relationship between psychosis-proneness and the experience of rubber hand agency (but not ownership) after both synchronous and asynchronous stimulation conditions. Previous evidence indicates that body ownership and agency are dissociable aspects of subjective experience (Frith, 2005; Gallagher, 2000; Longo et al., 2008). For example, a patient with schizophrenia-related delusions of control may recognize that their hand is moving, but believe that some other agent is controlling that movement (Frith, 2005). Positive psychosis-proneness may be related to a tendency to feel a sense of agency over a rubber hand based on visual similarity alone. Alternatively, the sense of agency induced by synchronous stimulation (always occurring first) may have carried over to the asynchronous stimulation condition, suggesting that the experience of agency might be more durable and/or less dependent on visual–tactile integration than the experience of ownership in psychosis-prone individuals.

Previous research has found that greater illusion susceptibility is related to other individual differences measures aside from psychosis-proneness, including low interoceptive sensitivity (Tsakiris et al., 2011), malleable body image characteristics of eating disorders (Mussap and Salton, 2006; Eshkevari et al., 2012), and greater empathic concern (Asai et al., 2011). We did not screen for sensory deficits or variations in body mass index (BMI) that might impact rubber hand illusion susceptibility, so do not know how much variations in BMI, interoceptive sensitivity, or exteroceptive sensitivity may have driven our results.

Understanding individual differences in psychosis-proneness can shed light on the mechanisms that underlie psychosis development without the side effects, treatment confounds, and generalized impairments that are associated with psychotic disorders (Lenzenweger, 2006, 2010). This individual differences perspective fits well with the increasing emphasis in psychiatry on dimensional aspects of mental disorders (Cuthbert and Insel, 2010; Insel et al., 2010). Evidence suggests that biological mechanisms do not respect diagnostic categories or boundaries (Hyman, 2010) and genetic studies indicate that mental disorders like schizophrenia are associated (in large part) with variations in commonly occurring alleles (e.g. International Schizophrenia Consortium, 2009).

Our findings indicate that differences in psychosis vulnerability in otherwise healthy samples are associated with a tendency to experience distortions in body representations. Further, these distortions are measurable and sensitive to experimental manipulations. Our findings are consistent with findings in schizophrenia samples showing that body representation distortions are linked with positive symptoms (Peled et al., 2000; Thakkar et al., 2011) and not negative symptoms (Chapman et al., 1978). Flexibility in body representations in psychosis-prone individuals may increase the tendency to experience distortions in body image (Chapman et al., 1978; Lenzenweger, 2010) as well as lead to abnormalities in the sense of inhabiting one's body (Sass and Parnas, 2003; Nelson et al., 2008). An increased understanding of the way body ownership illusions are related to other forms of self representation and psychosis-proneness can shed light on the distortions in bodily experience that accompany positive symptoms and psychosis-like characteristics, and ultimately those factors that lead to psychosis development.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.psychres.2012.11.022.

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