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Original Research

Perceptual instability in schizophrenia: Probing predictive coding accounts of delusions with ambiguous stimuli

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ABSTRACT

Background: Delusions, a core symptom of schizophrenia, are thought to arise from an alteration in predictive coding mechanisms that underlie perceptual inference. Here, we aimed to empirically test the hypothesized link between delusions and perceptual inference.
Method: 28 patients with schizophrenia and 32 healthy controls matched for age and gender took part in a behavioral experiment that assessed the influence of stabilizing predictions on perception of an ambiguous visual stimulus.
Results: Participants with schizophrenia exhibited a weaker tendency towards percept stabilization during intermittent viewing of the ambiguous stimulus compared to healthy controls. The tendency towards percept stabilization in participants with schizophrenia correlated negatively with delusional ideation as measured with a validated questionnaire.
Conclusion: Our results indicate an association between a weakened effect of sensory predictions in perceptual inference and delusions in schizophrenia. We suggest that attenuated predictive signaling during perceptual inference in schizophrenia may yield the experience of aberrant salience, thereby providing the starting point for the formation of delusions.

1. Introduction

Our perception not only is determined by the sensory input we receive, but is strongly shaped by previous experience. In line with this, perception can be described in the framework of predictive coding as an inferential process by which incoming information is combined with endogenous predictions (Friston, 2005; Kersten et al., 2004; Mumford, 1992). Such predictions are generated from an internal model that represents beliefs about the world built up by past experience, and these predictions enable stable and unequivocal percepts despite the noisiness and ambiguity of sensory signals. An important characteristic of such predictive coding is that it is adaptive: whenever a prediction is violated by incoming sensory information, a prediction error signal initiates learning by an update of the internal model resulting in adjusted beliefs about the world. An alteration in the brain's predictive machinery has been suggested to lie at the core of delusion formation in schizophrenia. In this context, delusions are explained by an altered integration of predictions with sensory signals, whereby the concomitant aberrant prediction error signal is assumed to drive erroneous updates of the internal world model resulting in maladaptive predictions and unfounded beliefs, i.e. delusions (Corlett et al., 2010; Fletcher and Frith, 2009; Adams et al., 2013). At the experiential level, the weakened influence of predictions in perceptual inference is thought to have the effect that expected events are perceived as if they were unpredicted and surprising (Hemsley, 2005), and the search for a cognitive explanation for this perceived aberrant salience is then assumed to result in the formation of delusions (Heinz, 2002; Kapur, 2003).

A powerful tool for probing the brain's predictive mechanisms and their alterations in delusions is ambiguous stimuli, which are compatible with two different, mutually exclusive perceptual interpretations. Prolonged viewing of such stimuli results in bistable perception fluctuating spontaneously between the two possible interpretations (Leopold and Logothetis, 1999; Sterzer et al., 2009). Such bistable perception has been conceptualized as an ongoing competition between two predictions that can never fully account for all the visual information in the ambiguous stimulus, with the effect that increasing prediction error signals trigger switches between the two interpretations (Clark, 2013; Hohwy et al., 2008). The ambiguity inherent in ambiguous stimuli maximizes the need for perceptual inference, and, hence, the potential influence of endogenous predictions. A simple and efficient way to experimentally induce such predictions is the intermittent presentation of an ambiguous stimulus: when an ambiguous stimulus is temporarily removed from view, the percept after re-onset of the stimulus strongly

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Table 1
Demographic and clinical characteristics of schizophrenia patients and healthy controls.

	patients	controls	two-sided
	(n = 29)	(n = 32)	p-value
age	34.0 ± 7.1[a]	31.9 ± 6.9[a]	0.25[b]
gender	7 F–22 M	8 F–24 M	0.94[c]
PDI			
yes/no	17.6 ± 9.1[a]	6.1 ± 5.9[a]	<0.001[b]
conviction	53.8 ± 36.3[a]	15.6 ± 15.8[a]	<0.001[b]
distress	52.7 ± 32.7[a]	11.4 ± 12.8[a]	<0.001[b]
preoccupation	49.7 ± 30.7[a]	12.0 ± 13.1[a]	<0.001[b]
sum	156.2 ± 95.9[a]	39.1 ± 40.7[a]	<0.001[b]
PANNS			
positive	13.4 ± 4.6[a]	–	–
negative	12.7 ± 5.2[a]	–	–
general	25.3 ± 8.9[a]	–	–

[a] Mean ± SD.
[b] Two-sample t-test.
[c] Chi-squared test.

tends to be the same as the last percept before stimulus removal, resulting in a substantial reduction of perceptual fluctuations (Leopold et al., 2002; Orbach et al., 1963). This stabilization of perception during the intermittent presentation of an ambiguous stimulus can be conceptualized as a special case of perceptual priming, which is thought to be mediated by the incorporation of predictions based on previous perceptual outcomes (Friston, 2005). Such stabilizing predictions are thought to be implemented at low levels of the cortical hierarchy, within sensory cortices (Pearson and Brascamp, 2008; Sterzer and Rees, 2008). Accordingly, attenuated sensory predictions, as suggested to underlie the formation of delusions, would translate into a decreased tendency to percept stabilization. In line with this, we previously found a negative correlation between the propensity towards delusional ideation and the tendency towards percept stabilization in a cohort of healthy individuals (Schmack et al., 2013). Here we asked whether the observed alteration of perceptual inference might also account for delusions of clinical relevance. To this end we empirically tested whether a weakened influence of sensory predictions in perceptual inference is related to delusions in schizophrenia. Patients with schizophrenia and healthy controls participated in a visual perception experiment with intermittent presentation of an ambiguous stimulus. In addition, they underwent a specific quantitative assessment of delusional ideation. We hypothesized that the tendency towards percept stabilization (1) is lower in patients with schizophrenia compared to healthy controls, and, (2) is negatively correlated with the degree of delusional ideation.

2. Methods

2.1. Participants

29 patients diagnosed with schizophrenia and 32 healthy controls matched for age and gender completed the study (see Table 1 for demographic and clinical characteristics). All patients fulfilled the ICD-10 criteria for paranoid schizophrenia and had no other psychiatric axis I disorder (SCID I). In addition to the specific assessment of delusional ideation (see 2.3 below), psychopathological symptoms were quantitatively assessed using the Positive and Negative Symptoms Scale (PANNS) (Kay et al., 1987). Patients were clinically stable and recruited as outpatients. Except for two unmedicated patients, all had been on stable doses of second generation antipsychotic medication for at least four weeks. Healthy volunteers had no axis I psychiatric disorder (SCID I) and no family history of psychiatric disorders. Exclusion criteria in both groups were neurological disorders and drug abuse up to seven days before testing. All participants had normal or corrected-to-normal vision and gave written informed consent before participation. The study was approved by the local ethics commitee of the Charité - Universitätsmedizin Berlin.

2.2. Experimental task

All participants took part in a visual perception experiment that was aimed at measuring the influence of sensory predictions in perceptual inference by the intermittent presentation of an ambiguous stimulus. Stimuli were presented on a on a CRT monitor (1024 × 768 pixels resolution, 60 Hz frame rate) using Matlab (MathWorks Inc.) and the Cogent2000 toolbox (http://www.vislab.ucl.ac.uk/cogent.php).

We used an ambiguous stimulus that consisted of 450 yellow square dots moving coherently on a black background with central white fixation cross and framed by a white square (Fig. 1). Due to the structure-from-motion phenomenon this stimulus is perceived as a sphere rotating in depth around a vertical axis (diameter 4.1° of visual angle, rotation speed 1/6 revolutions/s). The rotation direction of the sphere is ambiguous so that during prolonged viewing perception keeps fluctuating every few seconds between the percept of a sphere rotating towards the left and a sphere rotating towards the right. To familiarize participants with the two possible percepts evoked by the sphere, the experiment started with an initial training session during which the sphere was continuously presented for four minutes in which participants' perception fluctuated between the two percepts.

In the main experimental session, we then assessed sensory predictions by presenting the ambiguous sphere stimulus intermittently. Such a repeated exposure to an ambiguous stimulus results in the generation of sensory predictions that facilitate perceptual inference at each recurrence of the stimulus such that the appearance of the stimulus is stabilized. In other words, when removing an ambiguous stimulus temporarily from view, perception after re-onset of the stimulus strongly tends to be the same as the last percept before stimulus removal. During 20 min, participants viewed the sphere stimulus repeatedly for short intervals of 0.6 s interleaved by blank screens of 0.8 s duration (Fig. 1A). At each stimulus reappearance, participants indicated whether they perceived the sphere rotating to the left or to the right by key presses on the computer keyboard.

To quantify the influence of sensory predictions, we calculated the survival probability of percepts across temporary stimulus removals in each participant. A lower survival probability indicates a weaker tendency towards percept stabilization and thus a weaker influence of sensory predictions in perceptual inference. Due to the relatively fast but long sequence of stimulus presentations, in some trials participants missed the required response, and we found the number of missed trials to be higher in schizophrenia patients than in healthy controls (4.2% vs 1.1% of trials [medians], $z = 2.7$, $p < 0.01$, Wilcoxon rank-sum test). This raises the possibility that between-group differences in the number of missed responses would systematically bias the results in favor of our hypothesis of lower survival probabilities in schizophrenia patients compared to healthy controls. To preclude such a type-I-error, we considered trials in which participants did not make a response as trials in which the percept had survived the preceding stimulus removal. This procedure not only seems reasonable given that in the vast majority of trials the stimulus was indeed perceived in the same configuration as in the preceding trial (see Results), but also implies that in participants with high numbers of missed responses (i.e. schizophrenia patients) survival probabilities would be rather over- than underestimated, thereby rather decreasing than inflating the hypothesized group difference between schizophrenia patients and healthy controls.

2.3. Measurement of delusional ideation

As we hypothesized that the influence of sensory predictions on perception would relate particularly to delusions, we obtained a specific measure of delusional ideation in all participants using the Peters et al. Delusions Inventory (PDI, Peters et al., 1999). This self-rating questionnaire was originally designed to measure delusional ideation in the general population, but is also an established tool for the quantitative