



No evidence for abnormal priors in early vision in schizophrenia

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ABSTRACT

The predictive coding account of psychosis postulates the abnormal formation of prior beliefs in schizophrenia, resulting in psychotic symptoms. One domain in which priors play a crucial role is visual perception. For instance, our perception of brightness, line length, and motion direction are not merely based on a veridical extraction of sensory input but are also determined by expectation (or prior) of the stimulus. Formation of such priors is thought to be governed by the statistical regularities within natural scenes. Recently, the use of such priors has been attributed to a specific set of well-documented visual illusions, supporting the idea that perception is biased toward what is statistically more probable within the environment.

The Predictive Coding account of psychosis proposes that patients form abnormal representations of statistical regularities in natural scenes, leading to altered perceptual experiences. Here we use classical vision experiments involving a specific set of visual illusions to directly test this hypothesis. We find that perceptual judgments for both patients and control participants are biased in accordance with reported probability distributions of natural scenes. Thus, despite there being a suggested link between visual abnormalities and psychotic symptoms in schizophrenia, our results provide no support for the notion that altered formation of priors is a general feature of the disorder. These data call for a refinement in the predictions of quantitative models of psychosis.

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1. Introduction

For an accurate perception of the world it is insufficient to base our inferences solely on the information provided to us by our senses. For example, the 2D projection of light on the retina is necessarily ambiguous and conveys only limited information about the motion, position, size and orientation of a real-world 3D object. The observer solves this inverse optics problem by attributing the sensory stimulus to its most likely cause – an effortless process shaped by evolution and post-natal development (Attneave, 1954; Barlow, 1961; Geisler and Diehl, 2002; Simoncelli, 2003; Simoncelli and Olshausen, 2001). The final percept therefore reflects a combination of sensory information and probabilistic predictions (or priors, as they are termed within a Bayesian framework) about the source of that sensory stimulus, weighted in accordance with its likelihood (K. Friston, 2005; Hohwy, 2012; Knill and Kersten, 1990; Knill and Richards, 1996; Lee and Mumford, 2003; Stocker and Simoncelli, 2006; Weiss et al., 2002). According to

predictive coding models, perception involves making predictions about sensory inputs and minimizing prediction error. Thus, the strategy of vision that can best ensure appropriate visually guided behaviours in response to retinal stimuli of uncertain provenance is to generate percepts according to the probability distributions of their possible sources.

Predictive coding has recently provided a promising mechanistic framework to explain psychosis based on Bayesian inference. The predictive-coding account of psychosis postulates the abnormal encoding of priors and an increased weighting of sensory data, which leads to maladaptive “false” perceptual inferences away from the prior (Adams et al., 2013; Corlett et al., 2009; Fletcher and Frith, 2009). In particular, a decreased precision in the encoding of priors at lower stages of the brain's hierarchy is hypothesised to engender alterations in predictive signalling at higher levels, leading to drastic effects on the patient's worldview which characterises psychotic states (i.e., the experience of delusions and hallucinations) (Adams et al., 2013; Corlett et al., 2009; Fletcher and Frith, 2009; Sterzer et al., 2018).

Research on predictive coding in psychosis has primarily focused on abnormal belief (prior) formation and altered perceptual inference at hierarchical levels of processing where top-down computations on

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sensory input may play a role (e.g., Schmack et al., 2013; Schmack et al., 2015). For example, in healthy participants, Schmack et al., 2013 used ambiguous visual stimulation to probe the relationship between delusion-proneness and the effect of learned predictions on perception. They found that delusional ideation was associated with a stronger belief-induced bias on perception in addition to an enhanced functional connectivity between frontal areas that encode beliefs and sensory areas that encode perception. Moreover, sensory isolation can induce the same effect as a perceptual bias toward prior expectations that engenders hallucinations (Corlett et al., 2009; Daniel et al., 2014; Harris, 1959). Importantly, current models of hierarchical predictive coding assume that prior beliefs are fundamentally embodied even at the lowest levels of sensory processing (Adams et al., 2013; K. Friston, 2005), where they can take effect automatically and often without conscious introspection (Clark, 2013; Lee and Mumford, 2003; Notredame et al., 2014). For instance, research on the perception of natural scenes shows a strong agreement between psychophysical measurements of perceptual distortions (i.e., visual illusions) and statistical regularities within the natural visual environment (Howe and Purves, 2002; Lotto and Purves, 1999; Sung et al., 2008; Wojtach et al., 2008). This research suggests that the human visual system is efficiently optimised for processing the statistical information in natural scenes and that perception is biased toward what is statistically more probable (Atick and Redlich, 1992; Geisler and Diehl, 2002; Laughlin, 1981; Purves and Lotto, 2003; Ruderman, 1994; Simoncelli and Olshausen, 2001; Tadmor and Tolhurst, 2000; van Hateren, 1992). Failure to encode statistical regularities in natural scenes would result in weak priors for early vision as has been proposed in schizophrenia.

Consistent with this account of weak priors in early vision, patients with schizophrenia appear resistant to the Hollow Mask illusion, where a concave face is typically perceived as convex by healthy controls (Gregory, 1970, 1997). This illusion is assumed to stem from the automatic and unconscious use of a prior (or prediction) that convex faces are statistically more probable in natural scenes. Patients with schizophrenia show a decreased precision in the encoding of this prior, reporting the illusory convex percept less often than controls (Dima et al., 2010; Dima et al., 2009; Keane et al., 2013; Keane et al., 2016). Other studies using visual illusions also provide some support for the abnormal representation of priors in early vision in schizophrenia (Dakin et al., 2005; Tibber et al., 2013; Yang et al., 2013), however no study has assessed whether this might be explained by a failure to encode statistical regularities in natural scenes.

In the present set of experiments, we build on work conducted in the field of natural scene statistics to ask whether patients with schizophrenia form priors about the visual world in the same way as healthy controls. We test three well-documented illusions that have previously been explained in terms of using encoded representations (i.e., priors) about the probability distributions of characteristics in natural scenes (Howe and Purves, 2002; Lotto and Purves, 1999; Sung et al., 2008; Wojtach et al., 2008). Susceptibility to these illusions is thus a marker for the intact formation or encoding of priors in early vision. We predict that if schizophrenia is associated with a failure to encode statistical regularities in natural scenes and thus a failure to encode priors for visual perception, patients will generally report percepts that are less in accordance with what is statistically more probable in the natural world.

2. Materials and methods

2.1. Participants

Nineteen individuals who met the DSM-IV criteria for schizophrenia participated in the study. All patients were stable at the time of testing and were recruited as outpatients. The clinical interview was conducted by an experienced psychiatrist and included the Positive and Negative Symptoms Scale (Kay et al., 1987). The mean positive symptom score was 11.9 (SD = 4.6), the negative score was 13.9 (SD = 5.2), with a

general score of 24.8 (SD = 7.9). Patients were receiving antipsychotic medication at the time of testing (Chlorpromazine equivalent: 282 mg/day (SD = 256.7) and had a mean illness duration of 9 years (SD = 6.9)). 21 healthy controls were recruited from the general population and matched on age (patients 33.3 yo (SD = 5.6), controls 33.7 yo (SD = 6.4)), gender (half of the participants in both groups were female) and years of education (patients 15.8 y (SD = 4.2), controls 15.4 (SD = 3.7)). All participants had normal or corrected-to-normal visual acuity. Participants gave written informed consent to participate in the study and the study was approved by the Charité Universitätsmedizin Berlin Medical Ethics Review Committee.

2.2. Apparatus

All stimuli were presented on a CRT monitor (1024 × 768 resolution at 100 Hz) using Matlab and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) or Cogent2000 version 1.27 (J. Romaya, Wellcome Dept. of Imaging Neuroscience, London; http://www.vislab.ucl.ac.uk/cogent_graphics.php). Participants viewed stimuli from a distance of 57 cm.

2.3. Visual task battery

A battery of three well-documented visual illusions was administered. For more detailed descriptions of the methods, please refer to the cited original papers on which the experiments are based as well as the supplementary material. The relationship between the illusions tested here in this battery and the probability distributions of natural scene statistics are also well-documented in the referenced articles of this section.

1. Brightness contrast illusion

The simultaneous brightness contrast illusion arises when a grey square embedded in a darker surround appears brighter than the same grey square embedded in a lighter surround (Fig. 1). Lotto and Purves, 1999 argue that the perception of brightness is not a faithful representation of the physical characteristics of the stimulus but governed by contextual information that helps compute the most probable source of the stimulus. Thus, prior knowledge about how stimuli ought to look in light or shade, and the direction of illumination in natural environments contribute to our perception of brightness.

To examine whether patients with schizophrenia fail to develop appropriate priors about brightness compared to healthy controls, we replicated a set of Brightness Experiments described in Lotto and Purves, 1999. In all three experiments (i.e., 1a–c), participants were presented with two coloured arrays. Embedded within each of these arrays, was a grey square of identical luminance. Participants were asked to adjust the luminance of the grey square that appeared darkest (i.e., *test*) to match the grey square that appeared lightest (i.e., *reference*). The point of subjective equality (PSE; where the reference and test square appeared equal in brightness) was determined as the amount of adjustment required to match the squares in perceived brightness.

1a Testing priors for light and shadow

Here we tested the integrity of priors about light and shadow and their effect on perceived brightness. We used five pairs of stimuli as shown in Fig. 1A & B. The sets of coloured tiles on the left were ten times less luminant than those on the right, consistent with a “shadow” percept. Typically, participants perceive the grey test squares on the right to be darker than the grey reference squares on the left (consistent with a shadow interpretation) and increase their luminance accordingly. If patients with schizophrenia form weaker priors as a result of a failure to learn environmental contingencies, then it is expected that their perception of brightness would be less affected by such manipulations. In replicating Lotto and Purves (1999), we used four unicoloured

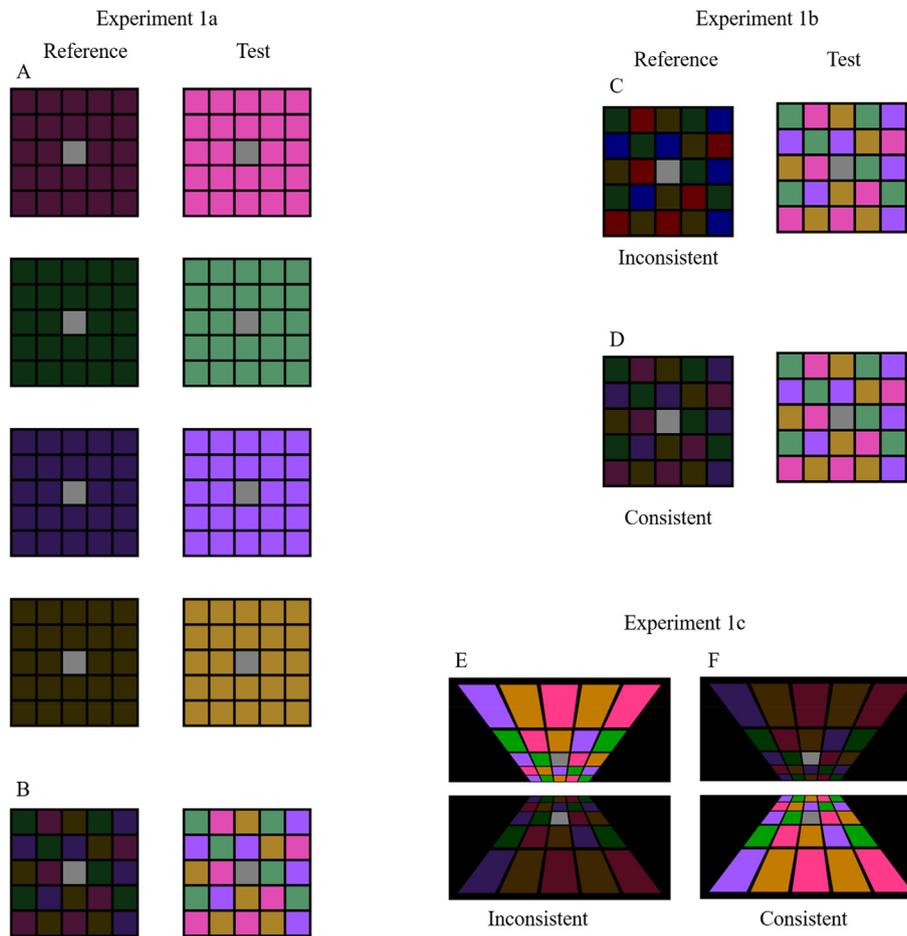


Fig. 1. Brightness contrast illusion. Experiment 1a: We tested whether the central grey *test* square embedded in a high luminance surround appeared comparatively darker than the equiluminant central grey *reference* square embedded in a low luminance surround under (A) unicoloured and (B) multicoloured surround conditions. Experiment 1b: We tested whether the perceived difference in luminance between the equiluminant *test* and *reference* squares is greater when the spectral returns in the array are inconsistent with a “shadow” interpretation (D) compared to when they are consistent (C). Experiments 1c: We tested whether the perceived difference in luminance between the equiluminant *test* and the *reference* is greater when the spectral returns in the array are consistent with the natural direction of light (F) compared to when they are inconsistent (E).

pairs (i.e., Fig. 1A: red, green, blue and yellow) and one multicoloured pair (Fig. 1B). Lotto and Purves (1999) have previously shown that the test square embedded in a multicoloured array requires greater adjustment compared to the unicoloured array (i.e., compared to the grey test and reference squares in 1A, the grey test square in 1B appears relatively darker than the reference square in 1B). They discussed this in terms of a stronger dependence on the shadow prior for the multicoloured arrays due to an increased probability that they were the same stimulus under two different lighting conditions. Thus, in this experiment we looked to see whether the average adjustments in *test* luminance were in the direction consistent with use of the shadow prior (i.e., and positive increase in PSE grey value). We also examined whether the test square in the multicoloured array required a greater adjustment compared to the test square in the unicoloured array. Our main interest was to examine whether patients would rely less on the shadow prior compared to controls, and thus report brightness judgements that are less affected by the above manipulations.

1b Testing effects of incompatibility with the shadow prior

Here we tested how colour information that is *inconsistent* with a shadow prior influences brightness judgments. Fig. 1C & D shows the stimuli used. The pair of arrays in C and D is the same, however the saturation of red and blue tiles on the left side of C is greater, making C less *consistent* with the shadow interpretation. Under these experimental

conditions, it has been reported that participants make a smaller average adjustment to equalize the appearance of test and reference squares in C (*inconsistent*) compared to D (*consistent*), due to less reliance on the shadow prior (Lotto and Purves, 1999). If patients with schizophrenia form weaker priors, we would expect brightness perception to be less affected by *consistent vs inconsistent* manipulations.

1c Testing priors for illumination direction

Here we tested the integrity of priors for illumination direction. Fig. 1E & F shows the stimuli used. It is statistically more probable that illumination comes from above, however the spectral returns in E are inconsistent with this interpretation. When the same stimulus is rotated, as shown in F, it is more consistent with the light-from-above prior. As a result, the two grey squares of equal luminance (i.e., reference and test) are typically perceived to differ in brightness more in F compared to E (Lotto and Purves, 1999). Again, if patients with schizophrenia form weak priors, we expect brightness perception judgments (and thus adjustments to the test square) to be less affected by *consistent vs inconsistent* manipulations.

General Hypothesis. If patients with schizophrenia form weaker priors as a result of a failure to learn environmental contingencies, then their perception of brightness should be unaffected by experimental manipulations that are *consistent* or *inconsistent* with prior knowledge about

light sources. This would be observed in terms of evidence for a group * condition (*consistent vs inconsistent*) interaction.

2. Line length illusion

It has been shown that psychophysical measurements of the apparent line length are a function of the line's orientation (Cormack and Cormack, 1974; Pollock and Chapanis, 1952; Shipley et al., 1949). That is, the same straight line appears progressively longer when presented at increasing angles away from horizontal. The maximum length perceived by observers occurs when the line is oriented 70–80° from the horizontal axis, at which point it appears about 10–15% longer than the same line when oriented horizontal. Howe and Purves (2002) explain this illusion in terms of the brain using priors in accordance with the probability distribution of possible real-world 3D physical sources of oriented lines on the retina. Specifically, the statistics of natural images reveal that a 2D vertically oriented line on the retinal image is seen as longer than the same line oriented horizontally due to its possible real-world 3D sources being, on average, physically longer (i.e., the physical sources of vertical or near-vertical lines on the retina tend to be more inclined in depth and thus longer).

To examine whether patients with schizophrenia make accurate use of priors about the sources of oriented lines on the retina, we tested apparent line length as a function orientation in patients and controls. We replicated the original method described in Craven (1993). On every trial, participants were presented with two straight lines (a test and a reference) and decided whether the left or right line was longer, by pressing the appropriate arrow key (Fig. 2). We used an adaptive staircase procedure, where the length of the test line was updated after each trial. The reference was always horizontal, while the test was oriented away from horizontal at one of the following angles: 10, 30, 50, 70, 90°. The PSE was determined as the length at which the test line appeared equal to the horizontal reference line. Previous research shows that participants typically report perceptual biases consistent with prior knowledge of natural scene statistics. That is, they show an increase in PSE with increasing orientation from the horizontal axis with a peak at 70–80° from horizontal.

Hypothesis. If patients with schizophrenia form weak priors, we would expect their judgments of line length to not be a function of line orientation. This would be observed in terms of evidence for a group * orientation interaction.

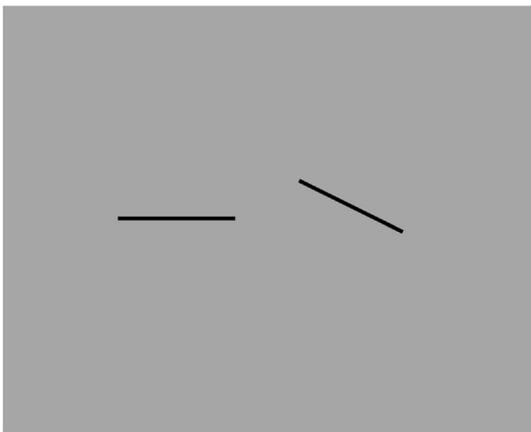


Fig. 2. Line length illusion. Participants indicated which of the two lines was longer. We measured apparent line length as a function of orientation. These lines are the same length, however the *test* line on the right appears longer than the *reference* line on the left.

3. Aperture effect

When a moving line is seen through an aperture (e.g., a circle) its perceived direction is constrained by the orientation of the line and the shape of the aperture. For example, an angled line moving behind a circular aperture typically appears to move in a direction orthogonal to its orientation. Like the above illusions, Sung et al. (2008) have proposed an empirical explanation based on natural scene statistics. They demonstrate that the direction of perceived motion corresponds to the most frequently occurring 2D retina projections of moving objects generated from real-world 3D sources, constrained by the geometry of the aperture. That is, the illusion reflects the use of priors formed in response to experience with moving objects in the natural world.

To examine whether patients with schizophrenia make use of priors in the same way as healthy controls, we replicated the psychophysical experiment detailed in Sung et al. (2008). Participants viewed a solid line, oriented at one of seven orientations (30, 35, 40, 45, 50, 55 and 60°), travelling across the screen from left to right at a constant speed (6°/s). The line was viewed through a circular aperture (Fig. 3). Participants indicated the perceived direction of motion by adjusting an arrow on the screen. Participants typically indicate the direction of motion as being orthogonal to the line orientation, consistent with prior knowledge of natural scene statistics.

Hypothesis. If patients with schizophrenia form weak priors about the sources of perceived motion, they will not systematically report a perceived motion direction that is orthogonal to the line orientation (i.e., the direction normal to the line). This would be observed in terms of evidence for a group * orientation interaction.

2.4. Data analysis

We first used a classical frequentist approach to analyse our results. We then applied Bayesian statistics in order to determine whether our null effects were genuine evidence for the null hypothesis relative to the alternative hypotheses. All analyses were performed using JASP (JASP Team, 2018, Version 0.9) and R (<https://www.R-project.org>) software.

3. Results

1. Brightness contrast illusion

For experiments 1a–b we report results from 19 patients and 21 controls. Results are reported as the average adjustment required to match

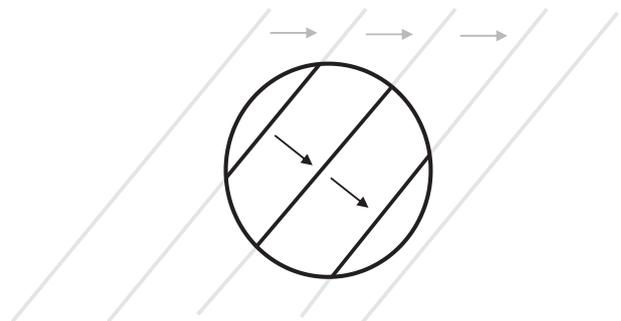


Fig. 3. Aperture effect. A moving line viewed through a circular aperture appears to translate in a direction orthogonal to its orientation (i.e. the direction normal). Participants indicate the direction of the moving line. Here, the grey arrows indicate the actual motion direction of the oriented line. The black arrows indicate the perceived direction typically reported. The grey lines are for illustrative purposes (i.e., not seen by the participant).

the perceived brightness of *test* to the brightness of the *reference*, calculated as a percentage of the *reference* luminance.

1a Testing priors for light and shadow

Consistent with a use of priors for light sources (Lotto and Purves, 1999), both groups showed strong effects of the shadow manipulation (i.e., means were >100 , $ps < 0.001$). The mean adjustment made by patients was 147.1% (SD = 23.7%) and the mean adjustment made by controls was 142.1% (SD = 24.4%). A two sample one-tailed *t*-test was performed collapsing across the surround colour conditions, with the hypothesis that control participants will make larger adjustments. There was no effect of group ($t(38) = 0.71$, $p = 0.76$, Cohen's $d = 0.22$), further confirmed by moderate evidence for the null with a Bayes Factor (BF) of 0.2. All participants perceived the grey *test* square embedded in high luminance tiles to be darker than the grey *reference* square, which was observed for all five colour conditions (Fig. 4). This is a replication of previous results from neurotypical subjects reported by Lotto and Purves, 1999 that have been explained in terms of a high statistical likelihood that the left side of the scene in Fig. 1 is in shadow and the right side is in light. Contrary to our hypothesis, we did not see a difference between our patient and control groups. The groups differed by $<6\%$ on average, with a tendency for patients to make larger adjustments (i.e., the opposite to what would be expected if patients had formed weak priors compared to controls). Thus, consistent with studies using a simple monochromatic version of this task (Tibber et al., 2013; Yang et al., 2013), the Brightness Contrast Illusion occurred robustly in individuals with schizophrenia.

An ANOVA with colour (red, green, blue, yellow, multicolour) as the within subject factor and group (patient, control) as the between subject factor yielded a main effect of colour ($F(4,152) = 38.1$, $p < 0.001$, $\eta_p^2 = 0.5$). Bonferroni-corrected post-hoc tests on the main effect of colour revealed that the multi-coloured tiles yielded significantly higher adjustments than the unicoloured tiles (all $t < -6.81$, all $p < 0.001$), except for the red unicoloured tile, for which PSEs did not differ from multi-coloured tiles ($t = -2.19$, $p = 0.35$). The result is consistent with previous reports by Lotto and Purves (1999) that showed a greater average adjustment required for multicoloured tiles explained by a

stronger dependence on the shadow prior (due to an increased probability that the left and right side of Fig. 1B were the same stimulus under different lights). No effect of group ($F(1,38) = 0.5$, $p = 0.48$, $\eta_p^2 = 0.013$) and no colour * group interaction ($F(4,152) = 1.06$, $p = 0.38$, $\eta_p^2 = 0.027$) was observed in our data. A Bayesian repeated measures ANOVA with a default Cauchy prior width of 1 revealed that the main effect of surround colour outperformed the null model best ($BF_{10} = 1.955e + 19$). This model was preferred over the colour * group interaction, suggesting sufficient ($BF = 0.09$) evidence against the hypothesis that brightness judgements in schizophrenia would be unaffected by the colour manipulation.

1b Testing effects of incompatibility with the shadow prior

Results are presented in Fig. 5. We replicated Lotto and Purves, 1999, showing that judgments of brightness are biased toward what is statistically more probable. A one-way repeated measures ANOVA comparing *consistent* and *inconsistent* conditions, with group (patients, controls) as a between-subject variable, yielded a significant and strong main effect of condition ($F(1,38) = 62.5$, $p < 0.001$, $\eta_p^2 = 0.62$, $BF > 1000$). All participants made larger adjustments to the luminance of the grey test square in the condition where the array tiles were arranged *consistent* with a shadow interpretation compared to the *inconsistent* condition. In contrast to our hypothesis, brightness judgments were similar in our patient and control groups ($F(1,38) = 0.006$, $p = 0.9$, $\eta_p^2 < 0.0001$; $BF = 0.38$). Importantly, we found no evidence of a group * condition interaction ($F(1,38) = 0.13$, $p = 0.7$, $\eta_p^2 = 0.003$, $BF = 0.17$), which one would expect if patients were not using the shadow prior (i.e., we'd expect no difference between *consistent* and *inconsistent* in this group). This Bayes Factor value indicates sufficient evidence against the interaction.

1c Testing priors for illumination direction

Data was not collected for one patient, we thus report results for 18 patients and 21 controls.

Results are presented in Fig. 6. Similar to the results above, we replicated Lotto and Purves, 1999, showing that judgments of brightness were consistent with reported probability distributions of natural

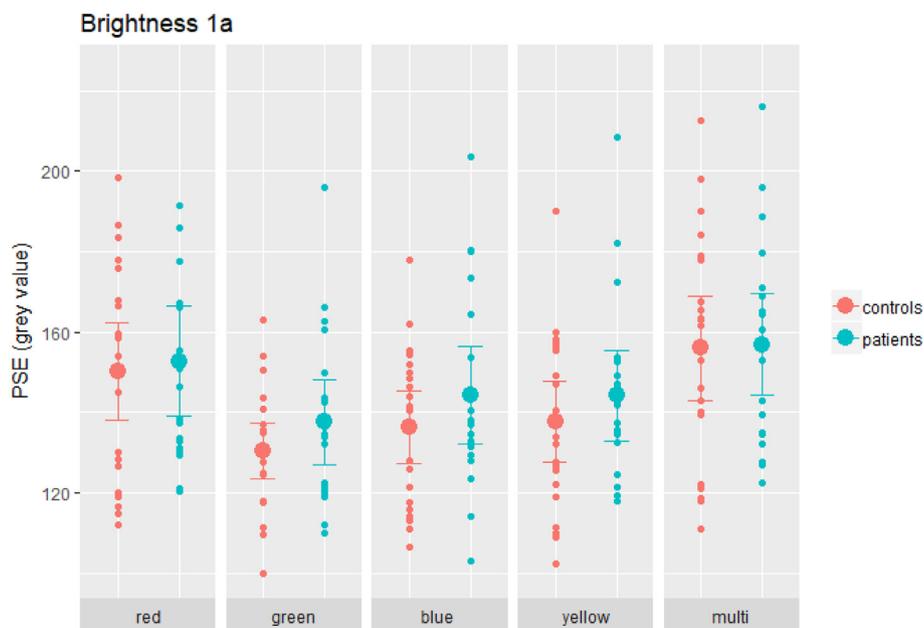


Fig. 4. Experiment 1a. Both groups perceived the grey test stimulus as being darker when embedded within a surround with greater luminance (i.e., average brightness adjustments were $>100\%$ of the reference). No significant group * condition interaction was found. Error bars represent the 95% confidence intervals.

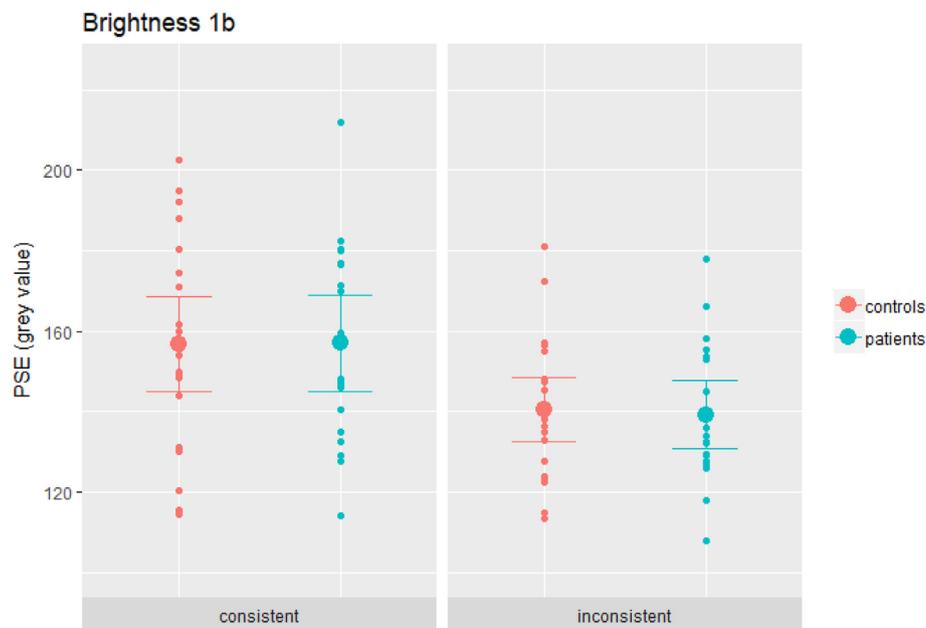


Fig. 5. Experiment 1b. Participants made relatively larger brightness adjustments in the condition that was *consistent* with a shadow interpretation, compared to the condition that was *inconsistent* a shadow interpretation. No significant group * condition interaction was found. Error bars represent the 95% confidence intervals.

scene characteristics. A one-way repeated measures ANOVA comparing *consistent* and *inconsistent* conditions, with group (patients, controls) as a between-subject variable, yielded a strong and significant main effect of condition ($F(1,37) = 34.3, p < 0.001, \eta_p^2 = 0.48, BF > 1000$). As predicted by natural scene statistics, participants made larger adjustments to the luminance of the grey test stimulus in the *consistent* condition compared to the *inconsistent* condition. Contrary to our hypothesis, we did not see a difference between our patient and control group ($F(1,37) = 1.08, p = 0.3, \eta_p^2 = 0.028, BF = 0.72$). Critically, there was no evidence for a group * condition interaction ($F(1,37) = 0.04, p = 0.85, \eta_p^2 = 0.001, BF = 0.17$), which would be expected if patients failed to use the “illumination comes from above” prior (i.e., we would expect no difference

between *consistent* and *inconsistent* in this group). This Bayes Factor indicates sufficient evidence against the interaction.

2. Line length illusion

An ANOVA on the PSE data with line orientation as a within subject variable and group as a between subject variable yielded a main effect of line orientation ($F(4,152) = 128.9, p < 0.001, \eta_p^2 = 0.77; BF > 1000$). There was no effect of group ($F(1,38) = 0.035, p = 0.85, \eta_p^2 = 0.001; BF = 0.22$). The interaction was significant ($F(4,152) = 2.86, p = 0.025, \eta_p^2 = 0.07$). Bonferroni-corrected post-hoc tests showed no differences in PSE between patients and controls for any of the line orientations tested (all t between -1.3 and 1.43 ; all $p = 1$). Further, both

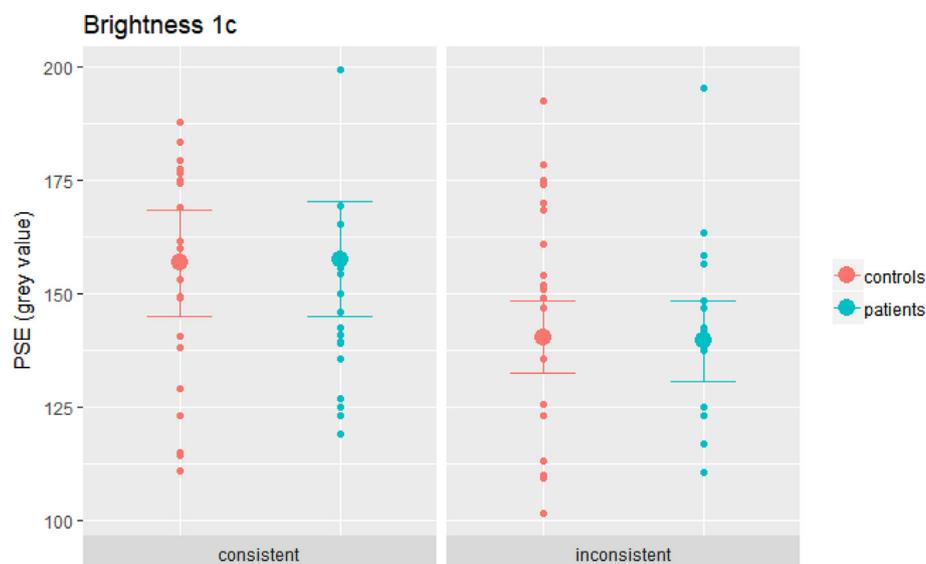


Fig. 6. Experiment 1c. Participants made relatively larger brightness adjustments in the condition that was *consistent* with the direction of natural light compared to the *inconsistent* condition. No significant group * condition interaction was found. Error bars represent the 95% confidence intervals.

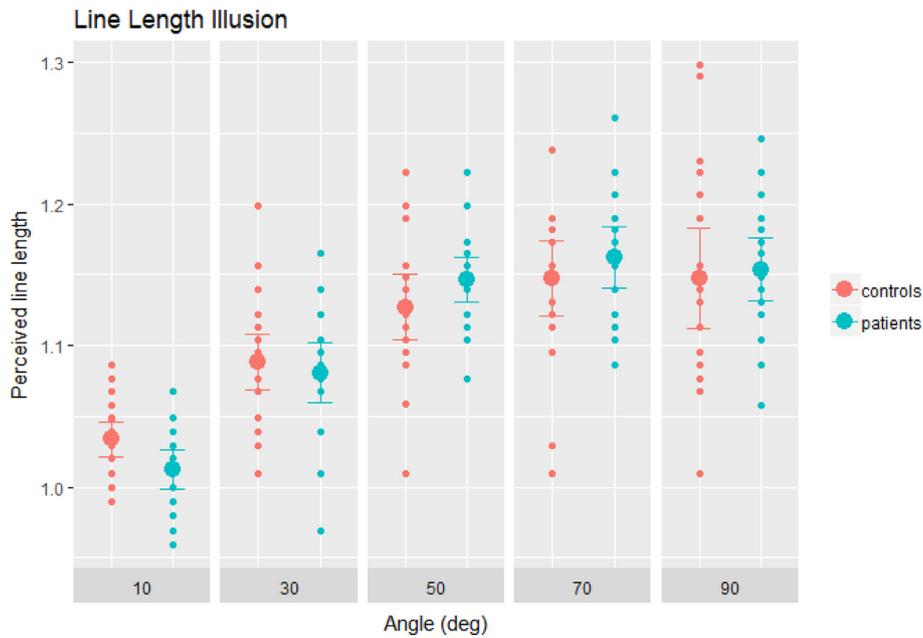


Fig. 7. Line length illusion. Participants perceived oblique lines as being longer than horizontal lines of the same physical length. The strongest effect of orientation occurred at 70° from the horizontal axis. No significant group × orientation interaction was found. Error bars represent the 95% confidence intervals.

groups showed a similar pattern of results, judging the line as progressively longer for 10 to 30° (controls $t = -5.6, p < 0.001$; patients $t = -6.7, p < 0.001$) and 30 to 50° (controls $t = -4, p = 0.004$; patients $t = -6.4, p < 0.001$). No difference was found comparing PSEs for 50 to 70° (controls $t = -2.1, p = 1$; patients $t = -1.5, p = 1$) and 70 to 90° (controls $t = 0.01, p = 1$; patients $t = 0.8, p = 1$) for either patients or controls. The BF showed anecdotal evidence for the null (0.6), when compared to the model yielding the best fit (i.e. the main effect of orientation) (Fig. 7).

3. Aperture effect

One patient and one control did not perform the task correctly and their data were excluded from the analysis. In addition, data from one

patient was not collected due to time constraints. We therefore report data for 17 patients and 20 controls.

Results are presented in Fig. 8. Firstly, we replicate Sung et al. (2008), showing that participants' judgements of motion direction are biased toward what is more statistically probable. That is, we found the direction of motion was most frequently judged as orthogonal to the line orientation (median deviation from the direction normal to the line orientation for patients: 1.97° SD = 3.5, and controls: 0.5° SD = 3.7). Note that all values are close to zero. A repeated measures ANOVA performed on the mode of responses revealed a significant effect of orientation ($F(6,210) = 2.9, p = 0.01, \eta_p^2 = 0.077, BF = 3.097$); post-hoc Bonferroni corrected tests revealed a single significant difference between estimates at 30° and 60° ($t = 3.8, p = 0.011$). This is in accordance with Sung et al. (2008) who reported a trend of increasing

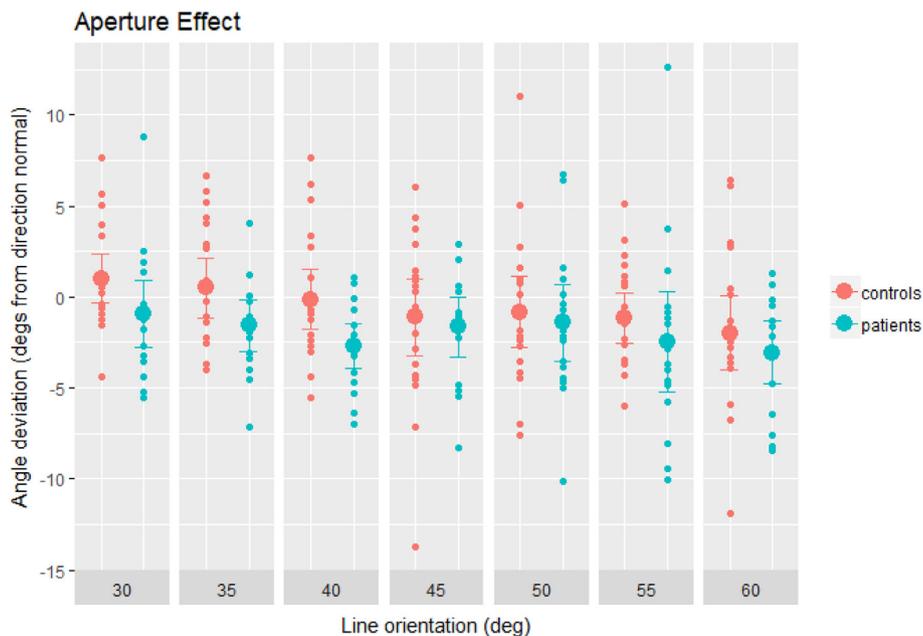


Fig. 8. Aperture effect. Results. A moving line viewed through a circular aperture appeared to translate in a direction orthogonal to its orientation (i.e. angle deviation from direction normal is equal to zero). No significant group × orientation interaction was found. Error bars represent the 95% confidence intervals.

deviation from the direction normal with an increase in line orientation. Importantly, this model was preferred over the orientation * group interaction ($F(6,210) = 0.62, p = 0.71, \eta_p^2 = 0.017$), with a $BF = 0.05$ indicating strong evidence against the interaction and suggesting that both groups showed the same effect of line orientation on perceived motion direction. Inconclusive evidence for a main effect of group ($F(1,35) = 3.06, p = 0.089, \eta_p^2 = 0.081, BF = 0.92$) could be ascertained from our data.

4. Discussion

The predictive coding framework applied to schizophrenia suggests a decreased precision in the encoding of prior beliefs relative to the sensory input, resulting in maladaptive or “false” inferences (Corlett et al., 2009; Fletcher and Frith, 2009; Sterzer et al., 2018; Sterzer et al., 2016; Voss et al., 2010). This framework has gained considerable interest in recent years as it provides a basis for linking the neurobiology of psychosis with positive symptom phenomenology (Adams et al., 2013; Corlett et al., 2009; K. J. Friston et al., 2014; Griffin and Fletcher, 2017). In this paper, we used classical methods from vision science as a tractable approach to assess whether the formation of priors at the lowest levels of sensory processing is abnormal in schizophrenia. A large body of evidence has previously shown that our perception of an ambiguous visual stimulus is generated in accordance with statistical regularities (i.e., priors) in natural scenes (Howe and Purves, 2002; Lotto and Purves, 1999; Sung et al., 2008; Wojtach et al., 2008). Here, we hypothesised that if schizophrenia is associated with the abnormal formation of priors, then patients should report percepts that are less in accordance with probability distributions of natural scene characteristics. Using an approach that examined visual biases (i.e., illusions) under a set of parametric manipulations previously employed to demonstrate agreement between perception and probability distributions of real-world sources of retinal images (Howe and Purves, 2002; Lotto and Purves, 1999; Sung et al., 2008; Wojtach et al., 2008), our study found no evidence for the abnormal formation or use of priors in schizophrenia. That is, both groups showed strong and robust evidence for the existence of priors based on natural scene statistics (as indicated by strong Bayes Factors). Although we acknowledge the small sample size may have reduced our power to detect a group difference (e.g., Grzeczowski et al., 2018), our data suggests that patients' percepts of brightness, line length, and motion direction are in accordance with what is statistically more probable in the visual world. Moreover, except for the line-length illusion, Bayesian statistics also provided strong evidence for the null hypothesis with regard to group differences, adding further support for our conclusions.

According to the predictive coding account of schizophrenia, a decreased precision in the formation of priors at lower levels of the visual hierarchy should result in biased percepts that are less in accordance with the learnt probability distributions of natural scene statistics. However, our data show no support for this. Instead, our patients exhibited perceptual biases that were in high agreement with previous accounts showing a strong relationship between perception and the probability distributions of natural scene statistics (Howe and Purves, 2002; Lotto and Purves, 1999; Sung et al., 2008; Wojtach et al., 2008). Similar to controls, patients with schizophrenia made subjective judgments of brightness based on how consistent the stimulus was with a shadow interpretation, thus in line with the use of priors about the appearance of surfaces under changing light levels (experiments 1a–c). Patients also made different judgments of line length as a function of line orientation, consistent with biases toward more probable real-world sources of lines on the retinal image (experiment 2). Finally, ambiguous motion viewed through an aperture was perceived in a direction that accords with priors for motion of objects in natural scenes (experiment 3). Together, the results provide no evidence for impaired priors in schizophrenia.

Predictive coding has been a well-regarded model for explaining psychosis as it suggests that positive symptoms result from an aberrant and pervasive style of processing that links all levels of processing. Importantly, current models assume that priors are embodied even at the lowest levels of sensory computation (Adams et al., 2013; K. Friston, 2005), where they can take effect automatically and without conscious introspection (Clark, 2013; Lee and Mumford, 2003; Notredame et al., 2014). The data reported in this paper, however, call for a refinement of the predictive coding account of schizophrenia, suggesting that the impairment may not generally affect early visual priors based on natural scene statistics. The neural representation of such priors is believed to exist at the earliest stages of the visual processing, including subcortical structures such as the retina and Lateral Geniculate Nucleus (LGN) (Atick and Redlich, 1992; Laughlin, 1981; Purves and Lotto, 2003; Ruderman, 1994; Schiller, 1992; Shapley and Enroth-Cugell, 1984; Simoncelli and Olshausen, 2001; Tadmor and Tolhurst, 2000; van Hateren, 1992). Thus, it is possible that the predictive coding impairments previously purported in schizophrenia are more evident at higher levels of the processing hierarchy. In support of this view, Tibber et al. (2013) who conducted a related study on the processing of low-level visual illusions, which included a variant of the brightness illusion used here, proposed a possible lower limit to visual dysfunction in schizophrenia, restricting the deficit to a predominantly cortical origin (Tibber et al., 2013). This constraint also supports findings from Yang et al. who examined a similar battery of center-surround illusions in a single patient group and showed no evidence for a generalized deficit (Yang et al., 2013). Many other studies can also attribute their findings of visual impairments to a cortical deficit (Chen et al., 2008; Dakin et al., 2005; Keane et al., 2012; Seymour et al., 2013; Silverstein, 2016; Tadin et al., 2006; Yang et al., 2013; Yoon et al., 2010; Yoon et al., 2009). Moreover, higher stages of perceptual inference (e.g., involving conscious top-down computations) have been shown to correlate with positive symptom and disorganisation phenomenology (Barbalat et al., 2012; Horga et al., 2014; Longevialle-Henin et al., 2005; Schenkel et al., 2005a; Schenkel et al., 2005b; Schmack et al., 2013; Schmack et al., 2015; Uhlhaas et al., 2006; Uhlhaas et al., 2005), while only limited evidence exists for a relationship between symptom severity and lower level deficits (Butler et al., 2003; O'donnell et al., 2002; W. A. Slaghuis, 1998; W. L. Slaghuis, 2004).

The findings reported in this paper are not in agreement with other reports of a reduced susceptibility to some visual illusions in schizophrenia (Butler et al., 2008; Notredame et al., 2014; Silverstein, 2016; Silverstein et al., 2013; Tibber et al., 2013; Yang et al., 2013). For instance, the Hollow Mask Illusion, which is arguably the most notable demonstration of the use of priors in early vision (Gregory, 1970), is reportedly reduced in schizophrenia (Dima et al., 2010; Dima et al., 2009; Keane et al., 2013; Keane et al., 2016). Dima et al. (2009) explained their findings of a reduced Hollow Mask illusion in terms of suboptimal learning of natural scene statistics during postnatal development. Our data provide no support for a general deficit associated with learning natural scene characteristics. Instead, it should be noted that a reduced susceptibility to the Hollow Mask illusion has most commonly been observed in patients with acute symptoms (Keane et al., 2013) (though see (Koethe et al., 2009) who found no difference between treated and prodromal patients). The severity of symptom expression in patients examined in the current study was relatively low and might therefore explain why a group differences were not observed in this study. However, such a dependence on illness *state* and symptom severity provides evidence against a general postnatal learning deficit. Moreover, it has been argued that statistical regularities such as those investigated in this study are represented within the human visual system (e.g., as functional anisotropies) through evolutionary processes rather than postnatal learning (Geisler and Diehl, 2002; Mannion et al., 2010; Patten et al., 2017; Purves and Lotto, 2003; Simoncelli and Olshausen, 2001). Thus, the priors assessed in the current study may be hardwired into the neural tissue (e.g., in utero) and therefore less susceptible to a

predictive coding deficit compared to the other higher-level visual illusions examined in previous studies (Crawford et al., 2010; Dima et al., 2010; Dima et al., 2009; King et al., 2017; Sanders et al., 2013; Uhlhaas et al., 2006) but see also (Palmer et al., 2018).

Finally, this study highlights the value of using classical well-validated experiments from vision science to test models of psychosis. Here, we examined a set of simple visual illusions not previously tested in patients that are thought to arise from empirically based associations instantiated in the nervous system according to the relative frequency of occurrence of the possible sources of the stimulus in question (Purves and Lotto, 2003; Purves et al., 2015; Purves et al., 2011). Recently, there has been an expansion of research in this field due to its tractable nature, its experimental precision, and our advanced understanding of the neural mechanisms involved in visual information processing. In an important review of the Bayesian framework of psychosis, Fletcher and Frith (2009) propose a link between aberrant sensory processing and positive symptom phenomenology. Using the rigorous approach employed here, we provide data that show no general abnormality in the formation of priors, at least at the earliest levels of the visual hierarchy. These data are in line with previous reports that failed to show a general impairment in the susceptibility to illusions in schizophrenia (Grzeckowski et al., 2018; King et al., 2017; Tibber et al., 2013; Yang et al., 2013). Together, these findings call for a refinement in the predictions of quantitative models of psychosis. For instance, Bayesian frameworks used to explain visual perception distinguish between priors that are *encoded* within neural tissue (Fischer and Peña, 2011; Ganguli and Simoncelli, 2014) and priors that become apparent at a *decoding* stage (Zemel et al., 1998). We believe we have examined the encoding phase here. Future research that addresses the distinction between the encoding and decoding of priors in schizophrenia may be fruitful.

Conflict of interest

The authors declare no conflict of interest.

Role of funding source

The funding sources had no role in the design of the study, nor during its execution, analyses, interpretation of results and drafting of the manuscript.

CRedit authorship contribution statement

Maria Kaliuzhna: Formal analysis, Funding acquisition, Writing - review & editing, Writing - original draft. **Timo Stein:** Conceptualization, Software, Writing - review & editing. **Tessa Rusch:** Data curation. **Maria Sekutowicz:** Data curation. **Philipp Sterzer:** Conceptualization, Resources, Writing - review & editing. **Kiley J. Seymour:** Conceptualization, Validation, Supervision, Software, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.schres.2018.12.027>.

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