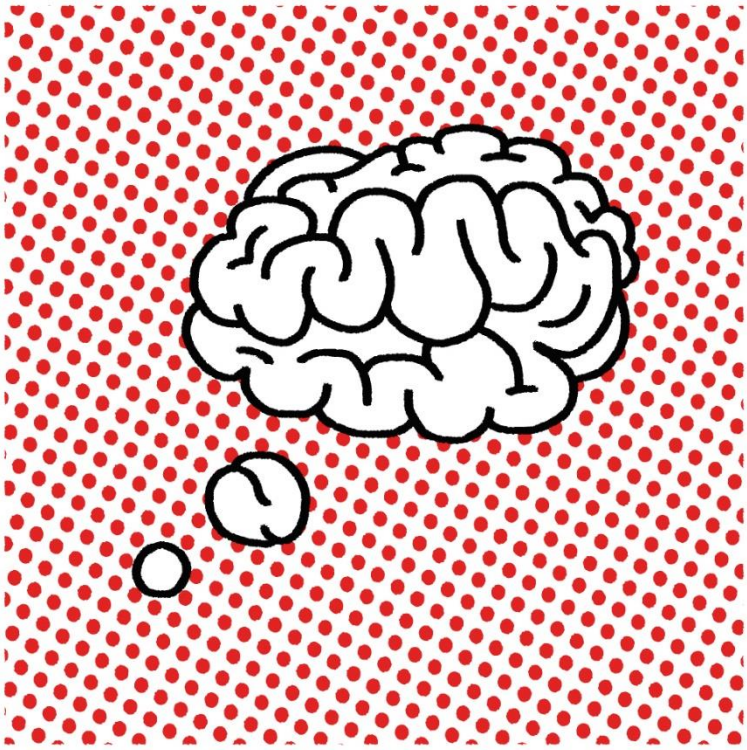
Hallucinations & Expectations

The influence of expectations on perception in relation to hallucination-proneness



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Abstract

Predictive processing accounts propose that the brain constructs perceptual inferences about our environment by combining prior expectations with incoming sensory information. Alterations in the precision-weighted balance between priors and sensory input have been related to the emergence of psychotic symptoms such as hallucinations. Specifically, both healthy individuals and psychotic patients who experience daily hallucinations have been found to over-rely on perceptual priors. However, it remains unknown whether hallucinations in the general population also relate to an increased usage of prior beliefs. With a Pavlovian learning task, the current study examined the effect of task-induced expectations on participants' susceptibility to report hearing tones that were in fact not presented, called conditioned hallucinations. Here, we found that hallucination-proneness in fifty-one healthy individuals was associated with greater susceptibility to report conditioned hallucinations. Moreover, delusion-proneness also nearly significantly predicted participants' likelihood to report hearing tones that were not presented. Thus, our findings indicate that hallucination-prone healthy individuals indeed rely more on prior expectations. Therefore, our study supports the notion that psychotic symptoms emerge due to a bias in predictive processing, and in particular indicates that hallucinations relate to strong priors.

Keywords: hallucinations, prior expectations, perception, predictive processing, psychosis, schizophrenia, delusions, Pavlovian conditioning.

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Introduction

Hallucinations are experiences of perceiving something that is in fact not present. Hallucinations occur in both healthy individuals and patients, for instance with schizophrenia or bipolar disorder (Sommer et al., 2010). In patients, hallucinations are intrusive experiences with negative emotional valence (Daalman et al., 2011), and lead to a lower quality of life, more incidents of self-harm (Haddock, Eisner, Davies, Coupe, & Barrowclough, 2013), violence (Bo, Abu-Akel, Kongerslev, Haahr, & Simonsen, 2011), and even suicide (Hor & Taylor, 2010). Although pharmacotherapy is effective in some patients, many hallucinations remain resistant to treatment, and for whom treatment does work it often induces severe side effects (DiBonaventura, Gabriel, Dupclay, Gupta, & Kim, 2012; Shergill, Murray, & McGuire, 1998). Currently, the cognitive mechanisms that underlie the emergence of hallucinations are still unknown. To address this issue, recent studies have focused on the influence of expectations (or *priors*) on the emergence of psychotic symptoms, such as hallucinations and delusions (Corlett et al., 2019; Sterzer et al., 2018). These studies are predominantly based on the *predictive processing theory*, which suggest that the brain is similar to a perfect scientist: both use predictions based on prior knowledge to interpret new information, and then test their hypotheses with new evidence (Yon, de Lange, & Press, 2019). In this view, perception results from a combination of new sensory information and prior expectations. In a Bayesian fashion, the brain maintains top-down hypotheses about the most likely causes of sensory input, which are then tested by bottom-up sensory information (Hohwy, 2020). In this account, a belief is a probability distribution over an unknown state or attribute that is centered around the most probable value, the prior expectation (Adams, Stephan, Brown, Frith, & Friston, 2013). If there is a mismatch between predictions and new input, a prediction error (PE) will update the prior beliefs (Clark, 2013). The posterior prior results from the initial prior that is adjusted by the PE signal (Figure 1, upper graph). In future situations, the posterior prior will function as the initial prior.

Importantly, the relative influence of predictions and sensory information on perception may differ across situations. For instance, a person may rely more on expectations when he searches for his lost glasses, whereas he might rely more on sensory information instead when he drives through a foreign city. The degree to which expectations and sensory information inform perception depends on their precision (Sterzer et al., 2018). That is, the prediction error will update the new prior to a greater extent when the sensory information is clear and has high precision (Figure 1, middle graph). Besides, an unprecise prior expectation will be stronger informed than a precise prior by relatively precise sensory information (Figure 1, lower graph). Accordingly, a stronger reliance on prior expectations could be caused both by increased prior precision relative to sensory evidence, and by reduced sensory precision compared to prior precision. Thus, perception could be considered as the precision-weighted balance between priors and sensory input (Hohwy, 2020).

There are several advantages to the predictive processing theory. Firstly, the usage of prior knowledge would lead to more efficient sensory perception (Tulver, Aru, Rutiku, & Bachmann, 2019).

Secondly, the theory can account for multiple perceptual anomalies simultaneously, while previous accounts rather describe individual symptoms (Sterzer et al., 2018). Thirdly, the theory can be translated into computational models that facilitate empirical testing (Sterzer et al., 2018).

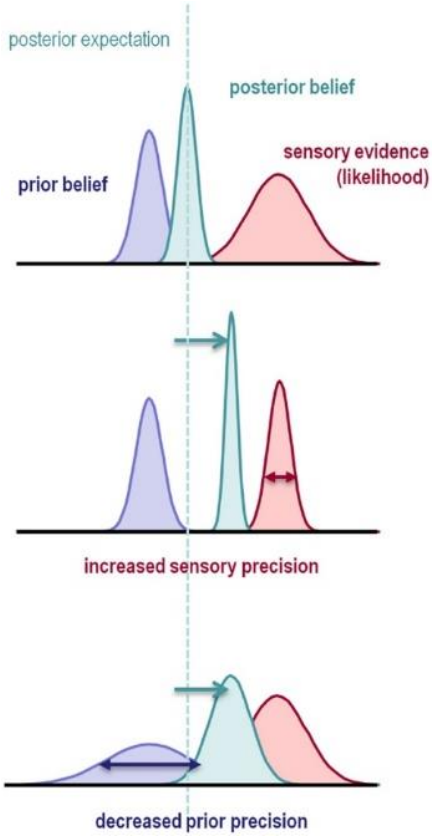

Figure 1. Illustration of the influence of prior and sensory precision on posterior expectations and beliefs. The graphs display the Gaussian probability distributions for prior beliefs, sensory evidence, and posterior beliefs. The width of the peaks indicates the variance, while the height of the peak signifies the precision of the distributions. The green line denotes the posterior expectation. The posterior prior shifts to the distribution with the greatest precision. Adapted from Adams, Stephan, Brown, Frith, & Friston, 2013.

Hallucinations and Strong Expectations

In general, predictive processing accounts agree that psychotic symptoms emerge due to a bias in information processing. However, there is an ongoing debate about whether psychosis in general, and hallucinations and delusions in particular, relate to over- or under-reliance on prior expectations (Corlett et al., 2019; Schmack, Rothkirch, Priller, & Sterzer, 2017; Stuke, Weilnhammer, Sterzer, & Schmack, 2018). Recent empirical studies support the account that hallucinations are associated with stronger priors (for a review, see Corlett et al., 2019). Specifically, hallucinations have been associated with stronger *perceptual* priors in a study by Powers, Mathys, and Corlett (2017). Powers et al. found that the presence of daily hallucinations rather than the diagnosis of a psychotic illness related to overreliance on perceptual expectations. In a Pavlovian conditioning task, the expectation that a sound would be heard when a visual checkerboard was on display was induced by repeated presentation of the visual checkerboard with a 1-kilo Hertz tone. Throughout the task, tone-intensity reduced from

clearly detectable to sub-threshold levels, and occasionally the tone was absent. If participants over-relied on prior expectations, they might report to hear a tone which was in fact not presented—this was considered a 'conditioned hallucination'. Powers, Mathys, and Corlett (2017) demonstrated that both psychotic patients and healthy participants with daily hallucinations were more susceptible to conditioned hallucinations than those without hallucinations. Moreover, participants with hallucinations showed greater confidence in their decisions than participants without hallucinations.

Perceptual Priors and Hallucination-proneness in the General Population

The association between hallucinations and increased reliance on perceptual expectation in the study by Powers, Mathys, and Corlett (2017) was found in a fairly specific sample: psychotic patients and non-diagnosed individuals with daily hallucinations. However, hallucinations also occur in the general population less frequently. For example, approximately 10% of the healthy individuals occasionally experiences hallucinations (Ohayon, 2000). Thus, the question remains whether also individuals with hallucinations in the general population show an increased reliance on perceptual expectations. Therefore, the current study assessed whether hallucination-proneness in healthy participants was associated with greater reliance on expectations. It was hypothesized that hallucination-proneness correlated with greater susceptibility for conditioned hallucinations, and greater confidence in decisions. In addition, as the conditioned hallucination task took approximately 50 minutes to complete, it was hypothesized that fatigue and reduced motivation would result in shorter response times and lower confidence ratings in the final four blocks than in the first four blocks.

Moreover, Powers and his colleagues (2017) employed the signal detection theory (SDT) to understand the processes that hallucinations and sensory processing may have in common. The SDT describes the process of stimulus detection, in which detection depends on the intensity of the stimulus and the background noise, and the internal state of the individual (Stanislaw & Todorov, 1999). Thus, deciding whether a stimulus is absent or present depends on the *sensitivity* or sensory quality, which is influenced by how well the individual perceives the stimulus, and on the *bias* or individuals' responsiveness, which is affected by prior knowledge and expectations. Powers, Mathys, and Corlett found that participants with hallucinations showed an increased bias—i.e. enhanced responsiveness—and decreased sensitivity—i.e. they perceived the stimulus less clearly—compared to the participants without hallucinations. Therefore, it was also hypothesized that hallucination-proneness in healthy participants would correlate with decreased sensitivity and increased bias.

Importance of Schizotypy Research

There are multiple incentives to study psychotic symptoms in healthy individuals. The presence of subclinical psychotic symptoms and other schizophrenia-related traits, e.g. aloofness and eccentric behaviour, in a non-clinical population is called *schizotypy*. Schizotypy is thought to reflect both a set of multidimensional personality traits, as well as the liability for schizophrenia (Lenzenweger, 2018).

As such, individuals with greater levels of schizotypy appear at greater risk for psychotic illnesses later in life (Lenzenweger, 2018). However, the exact relationship between schizotypy and psychotic illnesses remains unknown. For instance, do the same mechanisms underlie psychotic symptoms in healthy individuals and in psychotic patients? One argument that has been raised in favour a shared mechanism is the finding that presynaptic striatal hyperdopaminergic functioning relates to the severity of psychotic symptoms in both schizophrenia patients and to the degree of schizotypy in healthy individuals (Murray & Jones, 2012). Research on schizotypy and on whether there is a common mechanism underlying psychotic symptoms in clinical and non-clinical populations addresses the idea that psychosis is a continuum. According to the psychosis-continuum view, psychotic symptoms are a continuously distributed phenotype, with extreme expressions such as delusions (Schmack, Schnack, Priller, & Sterzer, 2015). In case research would support the idea of a psychosis-continuum, this might have implications for the diagnosis of psychotic illnesses, which is currently categorical in nature (Murray & Jones, 2012). Moreover, a psychosis-continuum would make healthy participants more relevant for patient research, as the same mechanism is also present in healthy individuals who do not bear potential confounds such as mediation, hospitalisation, and increased risk for drug and alcohol abuse (Steffens, Meyhöfer, Fassbender, Ettinger, & Kambeitz, 2018). Thus, the current study on information processing biases that underly hallucinations in healthy individuals might provide more insight in the notion of psychosis as a continuum and the cognitive mechanisms behind psychotic symptoms in schizotypy.

Furthermore, as psychotic symptoms also occur in other pathologies than schizophrenia and bipolar disorders, research on schizotypy might provide more insight into the relation between psychotic symptoms and other psychiatric disorders, such as depression and post-traumatic stress disorder. In fact, psychotic experiences in adolescents have been related more frequently to common mental disorders than to psychotic illnesses, and hence Murray and Jones (2012) have argued that psychotic symptoms in adolescents should not be considered as particularly predictive for psychotic disorders. Thus, although research on schizotypy has frequently focussed on the prevention of schizophrenia, schizotypy research might also provide insight in the identification of individuals at risk for other illnesses and prevention of additional disorders associated with psychotic symptoms.

Materials and Methods

Participants

Sixty-five healthy participants were recruited by online advertisements and word of mouth. The inclusion criteria were to be native English speakers and aged 18 years or older. Exclusion criteria were impairments in learning, language, movement, hearing or vision; history of any neurological disorder; schizophrenia or other psychotic illnesses. Table 1 provides the sample characteristics. Upon completion of two experimental sessions of two hours each, the participants were compensated with £30. The study was approved by the Cambridge Psychology Research Ethics Committee.

Materials

To assess whether hallucination-proneness correlated with increased likelihood to report hearing tones that were in fact not presented, participants performed a conditioned hallucination task (Powers, Mathys, & Corlett, 2017). Hallucination-proneness was measured with the 32-item Cardiff Anomalous Perception Scale (CAPS; Bell, Halligan, and Ellis 2006). Examples of CAPS items are 'Do you ever hear noises or sounds when there is nothing about to explain them?', and 'Do you ever see shapes, lights or colours even though there is nothing really there?'. To additionally analyse whether delusion-proneness and schizotypy could predict the susceptibility to conditioned hallucinations, the Peters Delusion Inventory (PDI; Peters, Joseph, and Garety 1999) was used to measure delusion-proneness, and the Schizotypy Personality Questionnaire was employed to assess schizotypy (SPQ; Raine 1991). The PDI measured individuals' proneness to hold bizarre and irrational beliefs in 21 items such as 'Do you ever feel as if you are being persecuted in some way?', and 'Do you ever feel as if there is a conspiracy against you?'. The SPQ measured in 74 items the presence of subclinical psychotic symptoms and other schizophrenia-related traits such as aloofness and eccentricity, with items as 'Some people think that I am a very bizarre person'.

Table 1.
Characteristics of the participants

	Total sample (n = 51)	Range of scores
Age	27.1 ± 11.2[a]	(18 – 65)
Gender	32 F – 19 M	
Ethnicity		
White	32 (63%)	
Asian	11 (22%)	
White and Asian	4 (8%)	
Black	1 (2%)	
Other	3 (6%)	
Education		
GCSE[b]	1 (2%)	
A-levels[c]	15 (30%)	
Higher education	18 (35%)	
Masters or doctoral degree	17 (33%)	
IQ[d]	122.4 ± 11	(83 – 139)
SPQ	20.5 ± 11.1	(1 – 50)
CAPS	3.7 ± 4.1	(0 – 16)
PDI		
Yes/No	3.6 ± 2.7	(0 – 11)
Distress	8.8 ± 7.9	(0 – 31)
Preoccupation	8.8 ± 7.3	(0 – 26)
Conviction	11 ± 8.5	(0 – 34)
Total	67.1 ± 20.4	(42 – 115)
SENS		
Hypersensitivity	28.1 ± 7.8	(9 – 43)

[a]Mean ± SD.
[b]General Certificate of Secondary Education.
[c]General Certificate of Education Advanced Level.
[d]Measured with the Wechsler Abbreviated Scale of Intelligence Vocabulary and Matrix Reasoning subscales

Moreover, to differentiate perceptual anomalies related to psychosis from those linked to autism spectrum conditions (ASC), the Sensory Perception Quotient-Revised Scale Hypersensitivity subscale (abbreviated here as SENS; Taylor, Holt, Tavassoli, Ashwin, & Baron-Cohen, 2020) was included. The 79-item SENS measured perceptual alterations linked to ASC with statements as 'I would be able to detect if a strawberry was ripe by smell alone'. Furthermore, to assess additional participants' characteristics that could serve as covariates in the analysis, an in-house demographic questionnaire and the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999) were employed. The WASI subscales Vocabulary and Matrix Reasoning were used to estimate participants' intelligence quotient (IQ).

Task Design

In the conditioned hallucination task, participants implicitly learned with Pavlovian conditioning the association between a visual checkerboard stimulus and an 1-kilo Hertz tone. Before the start of the experiment, subjects were instructed that there might be a tone embedded in the white background noise when the checkerboard flashed onscreen. Participants had to indicate as soon as possible whether the tone was present (press 'y' key for 'Yes, I heard a tone') or absent (press 'n' key for 'No, I did not hear a tone'). In addition, participants were instructed to indicate their confidence in the decisions by keeping the key pressed. Confidence was measured by the length of the keypress, and longer keypresses indicated higher confidence as was reflected on a simultaneously presented visual-analogue scale. The experiment started with two practice sessions, the first session with Yes/No responses only, and the second with additional confidence ratings. To ensure that every participant understood the task, a correct response rate of 85% was necessary before the participant could continue to the next part. Next, a QUEST maximum-likelihood-based procedure was used to determine the detection threshold (decibel signal-to-noise-ratio, abbreviated as dbSNR) at which participants were 75% likely to detect a tone embedded in white noise. The QUEST procedure was performed with Matlab 2018b (The MathWorks) and the Matlab Psychtoolbox Version 3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 2997). The threshold was based on the responses to a 40-trial staircase procedure that was run twice and which presented sounds at decreasing intensities. The 75% likelihood detection threshold was then used to compute individual psychometric curves and to estimate the sound intensities for the 25% and 50% likelihood detection conditions (Figure 2).

The goal of the main test phase was to assess how perception changed due to the conditioned expectation. Therefore, participants implicitly learned the association between the target tone and the visual checkerboard stimulus. To induce this expectation, the test phase consisted of 12 blocks of 30 trials each, in which at first clearly detectable tones were presented (75% likelihood detection condition). As the task progressed, tone intensities reduced to threshold tones (50% likelihood detection condition), subthreshold tones (25% likelihood condition), and absent tones (no-tone condition) (Figure 3). Note that 'yes' responses on no-tone trials were considered as conditioned

hallucinations, as the participant had reported hearing something that was not presented. Although the number of trials from each condition was fixed per block, the presentation of trials within each block was pseudorandomized.

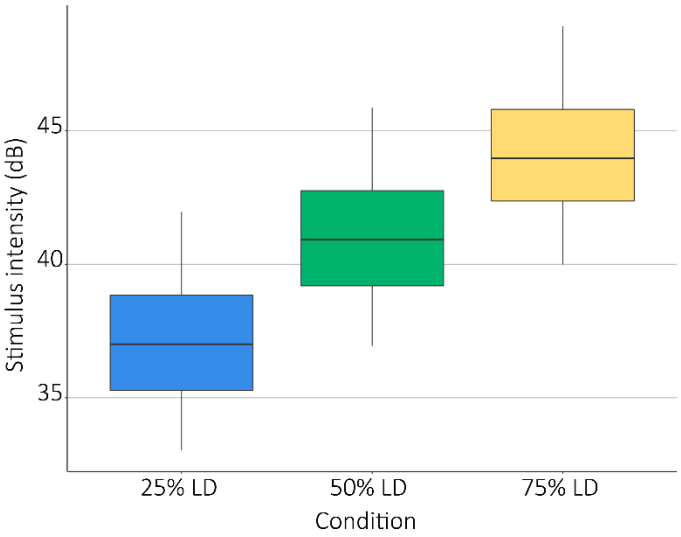

Figure 2. Average stimulus intensities (in decibel) across test phase conditions. Note that the no-tone condition is not presented since tones were absent in this condition. LD: likelihood detection.

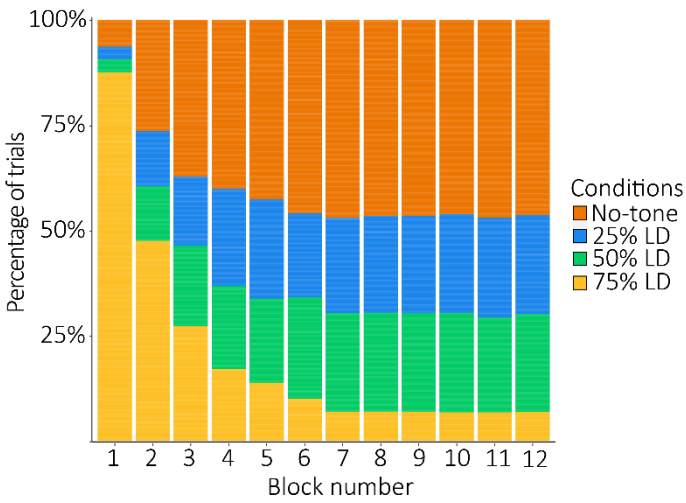

Figure 3. Distribution of conditions across blocks in the test phase. LD: likelihood detection.

The visual and auditory stimuli were the same in the practice, threshold-setting, and main test phases. Stimuli were displayed and responses were stored with the Matlab Psychtoolbox Version 3.0. Each trial consisted of the presentation for one second of a visual checkerboard pattern of 4 x 7 grey squares with 25% brightness on a black background, and an 1-kHz tone with 100 ms ramp-up at varying intensities (Figure 4). Task conditions differed in tone intensity, and tones were presented at 75%, 50%, and 25% likelihood detection, or the tone was absent (no-tone trials). White noise was presented throughout the experiment at 70 dB to ensure a consistent auditory background. The auditory stimuli were presented through on-ear headphones. Eight participants with uncalibrated auditory stimuli were excluded from the analysis. Throughout the task, a white fixation cross was presented on the checkerboard stimulus during a trial or on a black background between the trials.

Procedure

The conditioned hallucination task was part of a larger study. In two sessions of two hours each, participants completed six computerized cognitive tasks in a pseudo-randomised order and the WASI subscales Vocabulary and Matrix Reasoning. The sessions took place during working hours between 9 am and 7 pm and were situated in a testing room at the Behavioural and Clinical Neuroscience Institute, University of Cambridge. Before the first session, participants completed the online questionnaires. During the first session, participants first gave written informed consent, subsequently completed the WASI Vocabulary and Matrix Reasoning subscales, and then performed three

computerized tasks. In the second session, participants first filled out the payment form electronically and then performed three cognitive tasks, including the conditioned hallucination task of approximately 50 minutes. The conditioned hallucination task was run with Matlab 2018b and Psychtoolbox. Participants sat approximately 60 cm away from the screen. At the end of the second session, participants had the opportunity to ask questions about the study and were thanked for their participation.

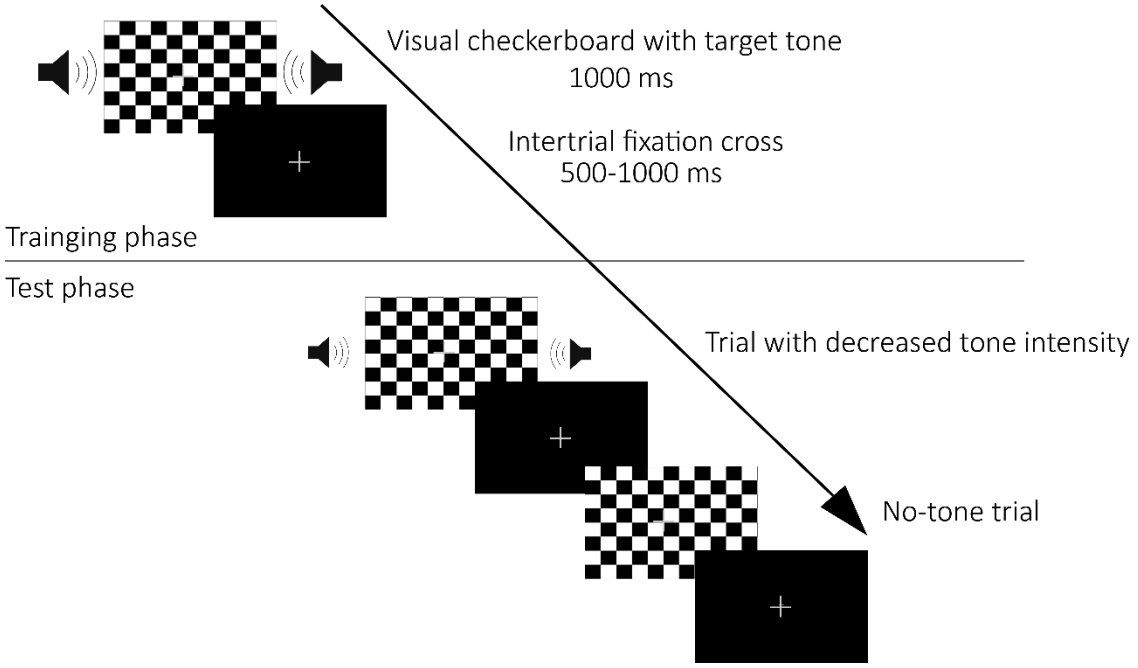

Figure 4. Illustration of practice and test phase trials with simultaneous presentation of a 1-kHz tone in white noise and a visual checkerboard.

Data Analysis

The behavioural measures from the test phase were binary responses ('yes' or 'no'), response times, and confidence ratings. Trials on which no key was pressed were removed from analysis. The average percentage of missed trials was 3.7%. Four participants missed more than 10% of the trials and were removed from the analysis. Furthermore, one participant with more than 140 practice trials, and one participant with a detection threshold of more than three standard deviations from the mean were excluded from the data analysis. Thus, the data analysis was performed on data of fifty-one participants. Removing the outliers did not affect the results. The response time was measured as the time in milliseconds between trial onset and the keypress. Confidence ratings were derived from the duration of the keypress and binned between 1 and 5, similar to the visual scale used in the test. Statistical analyses were performed in R (R Core Team, 2014). Data were processed with the packages Dplyr (Wickham, François, Henry, & Müller, 2020) and Magrittr (Bache & Wickham, 2014), and visualized with the packages Ggplot2 (Wickham, 2016), Scales (Wickham & Seidel, 2019), and RColorBrewer (Neuwirth, 2014). In case the assumption of normality was violated in any of the models, data were transformed to obtain a more normal distribution with the BestNormalize package

(Peterson & Cavanaugh, 2019). The correlations between the predictor variables are presented in Appendix A.

To analyse whether hallucination-proneness could predict the susceptibility to conditioned hallucinations, a logistic generalized linear mixed-effects model (GLMM) was performed on the probability to respond 'yes' with the Lme4 package (Bates, D., Maechler, M., Bolker, B. and Walker, 2015) (syntax and output are presented in Appendix B). The GLMM was fitted by the maximum likelihood procedure using the Adaptive Gauss-Hermite Quadrature. The dependent variable was the probability to respond 'yes' and consisted of a row vector of 1s and 0s (1 for 'tone present' and 0 for 'tone absent') with each row representing one trial. The predictor variables were CAPS scores, conditions, and the covariates age, detection threshold, SENS score, percentage of missed trials, and number of practice trials. Note that the number of practice trials was included as covariate because the number of training trials differed per person and these might have affected the strength of the expectation before the start of the test phase. Moreover, the model included random intercepts for participants. To additionally analyse whether PDI and SPQ scores could predict the susceptibility to conditioned hallucinations, the same GLMM was performed with PDI and SPQ as additional predictors (Appendix C). To assess GLMMs goodness of model fit, normality of residuals, overdispersion, and homoscedasticity, residuals were simulated with the DHARMa package (Hartig, 2020) and visualised with the Qwraps2 package (DeWitt, 2019). Multicollinearity between variables was tested with the Variance Inflation Factor (VIF) from the Car package (Fox & Weisberg, 2019).

Furthermore, to assess whether hallucination-proneness could predict the confidence in decisions, a linear mixed-effects model (LMM) was performed on the confidence ratings with the Lme4 package (Bates, D., Maechler, M., Bolker, B. and Walker, 2015) (Appendix D). The dependent variable was a row vector with each row representing the confidence rating on one trial. Predictor variables included CAPS scores, condition, response ('Yes, I heard the tone' or 'No, I did not hear the tone'), the covariates age, detection threshold and SENS scores, and participants as random intercepts. To additionally analyse whether delusion-proneness or schizotypy in general could predict confidence ratings, PDI and SPQ were included as predictors in a second LMM (Appendix E). The assumption of normality was checked by plotting the residuals, singularity was assessed with the Lmtest package (Zeileis & Hothorn, 2002), and multicollinearity was tested with VIF (Fox & Weisberg, 2019). To assess whether hallucination-proneness correlated with response times, the same LMMs as for confidence ratings were used with response times as dependent variable instead of confidence ratings.

Moreover, to assess whether hallucination-proneness was related to decreased sensitivity and increased bias, a linear regression model was performed with as dependent variable either sensitivity index or bias, and as predictors CAPS scores and covariates IQ, age, detection threshold, and SENS scores. In additional models, PDI and SPQ scores were added as predictors. Linear regression models were checked for homoscedasticity with the Breusch-Pagan test (Car package, Fox & Weisberg, 2019). Independence of residuals was assessed with the Durbin-Watson test (Lmtest package, Zeileis &

Hothorn, 2002), and normality was tested with the Shapiro-Wilkinson test. Finally, the effect of fatigue on response times and confidence ratings was tested by comparing the average RT and confidence ratings between the first four and last four test blocks with a two-sided paired t-test using the R Stats package (R Core Team, 2014). The assumption of normality was assessed with the Shapiro-Wilkinson test (R Core Team, 2014).

Results

In line with our hypothesis, hallucination-prone participants were more likely to respond 'yes' on no-tone trials (z = 2.179, p = 0.029). Even after correcting for age, detection thresholds, number of practice trials, sensory anomalies associated with ASC, and percentage of missed trials, hallucination-proneness remained a significant predictor for conditioned hallucinations (z = 2.485, p =0.013). Figure 5 illustrates the association between CAPS scores and the probability to respond 'yes' across conditions. The average probability to respond 'yes' on no-tone trials was 0.07, and the correlation between conditioned hallucinations and CAPS scores was 0.09. Interestingly, when PDI and SPQ scores were added to the model, PDI scores were nearly significantly correlated with the susceptibility to report conditioned hallucinations (z =1.783, p = 0.075). The correlation between PDI and conditioned hallucinations was 0.23 and is presented in Figure 6. When PDI was added to the model, hallucination-proneness did not relate significantly anymore to the likelihood to report conditioned hallucinations (z = 1.718, p = 0.086). The correlation between CAPS and PDI scores was 0.49 (Appendix A), and when CAPS was excluded from the model, PDI significantly predicted the likelihood to report conditioned hallucinations (z = 2.474, p = 0.013).

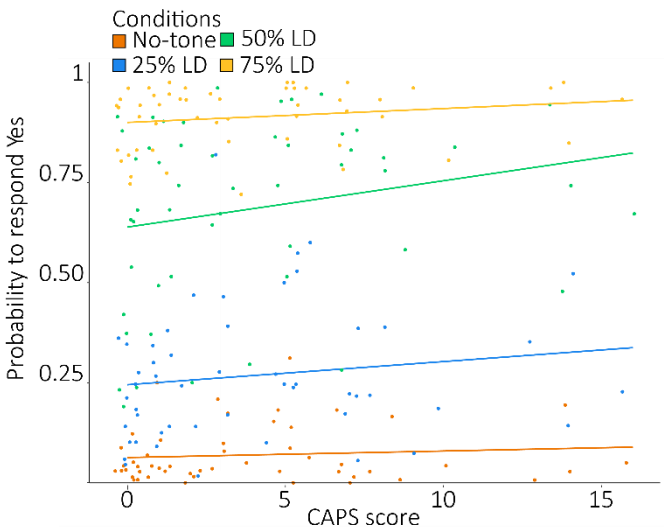

Figure 5. Associations between CAPS scores and the probability to respond 'yes' across conditions. LD: likelihood detection.

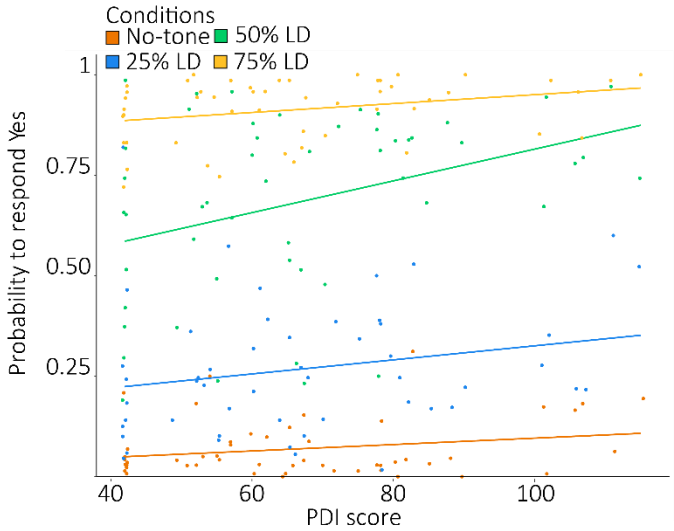

Figure 6. Relations between PDI scores and the probability to respond 'yes' across conditions. LD: likelihood detection.

Moreover, the probability to respond 'yes' on no-tone trials increased with greater detection thresholds (z = 2.792, p = 0.005) (Figure 7) and decreased with age (z = -2.977, p = 0.002) (Figure 8). As Figure 7 displays, detection thresholds seems most strongly related to the probability to respond 'yes' in the 25% and 50% likelihood detection conditions. Similar to the study by Powers et al. (2017), the probability to report tones differed between the no-tone and 25% likelihood detection conditions (z = -2.154, p = 0.031), but not between the no-tone versus 50% likelihood detection (z = -1.494, p = 0.135) and 75% likelihood detection (z = -0.976 , p = 0.329) (Figure 9). While the percentage of missed trials (Figure 10) and the number of practice trials (Figure 11) differed among participants, they did not affect the probability to respond 'yes'.

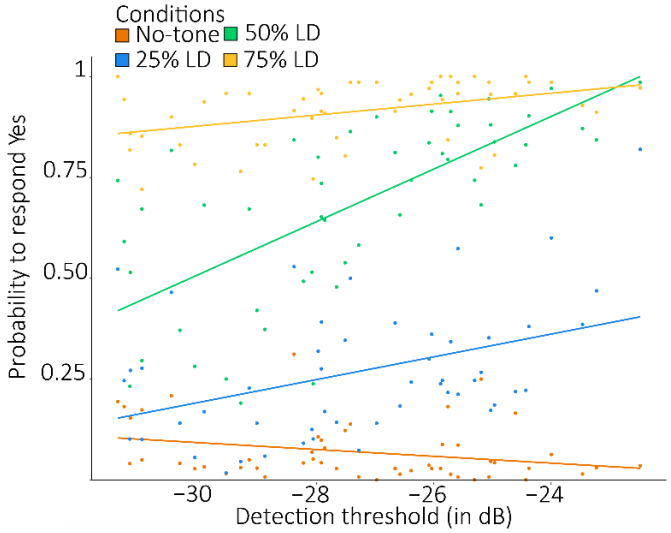

Figure 7. Associations between the probability to answer 'yes' and detection thresholds in decibel. LD: likelihood detection.

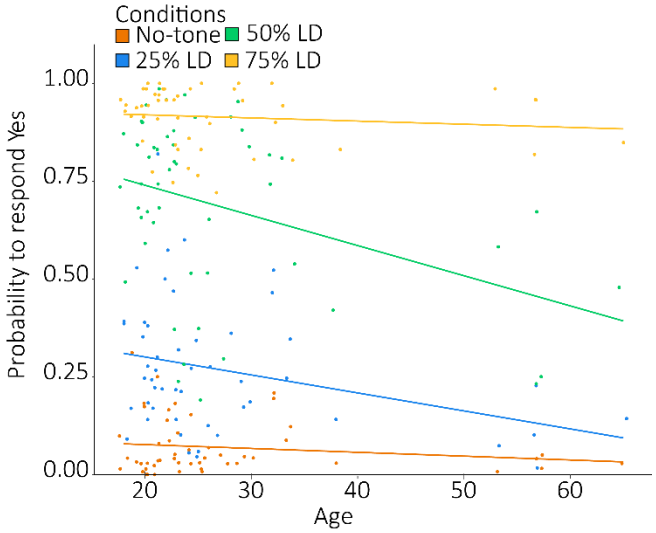

Figure 8. Associations between the probability to answer 'yes' and age. LD: likelihood detection.

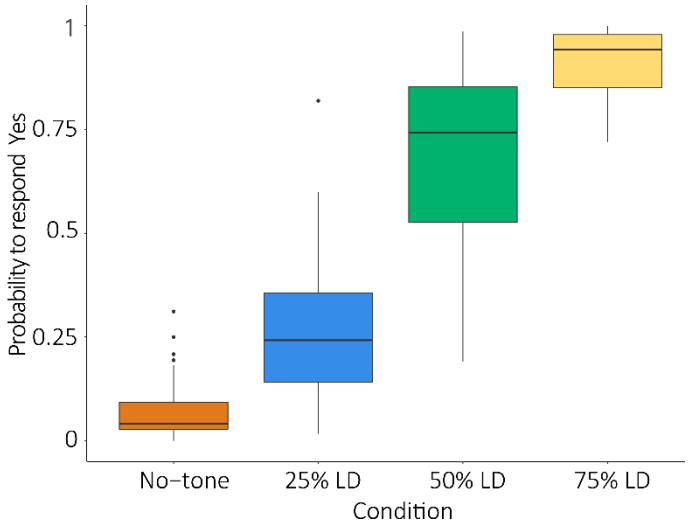

Figure 9. The average probability to respond 'yes' across conditions. LD: likelihood detection.

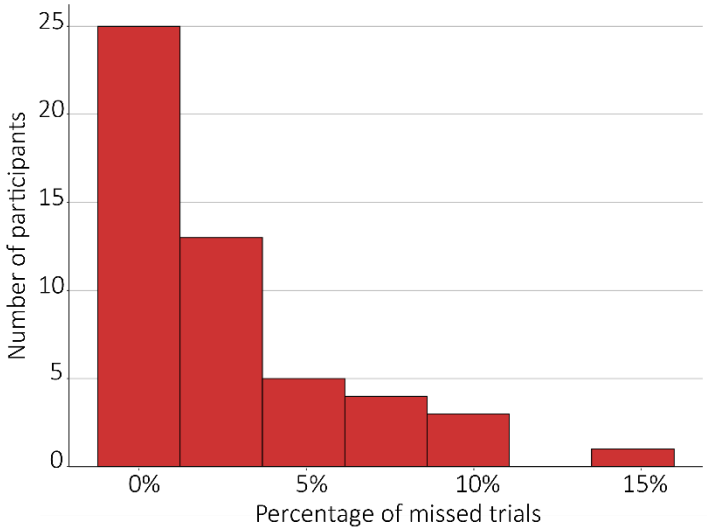

Figure 10. Distribution of the percentage of missed trails during the test phase.

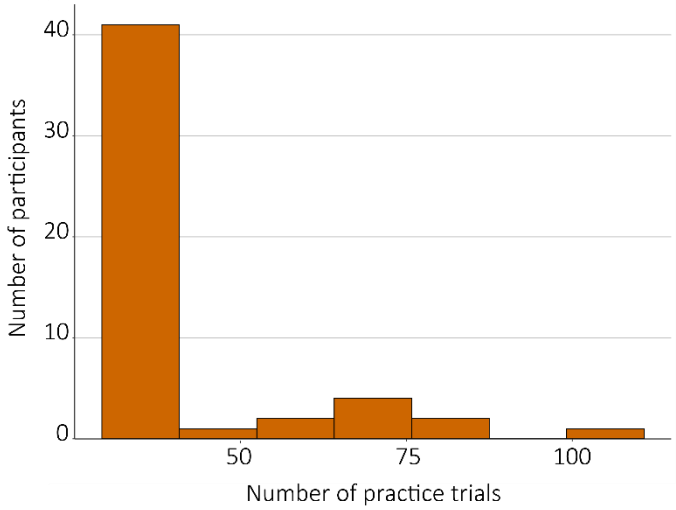

Figure 11. Distribution of the number of practice trials during the practice phase.

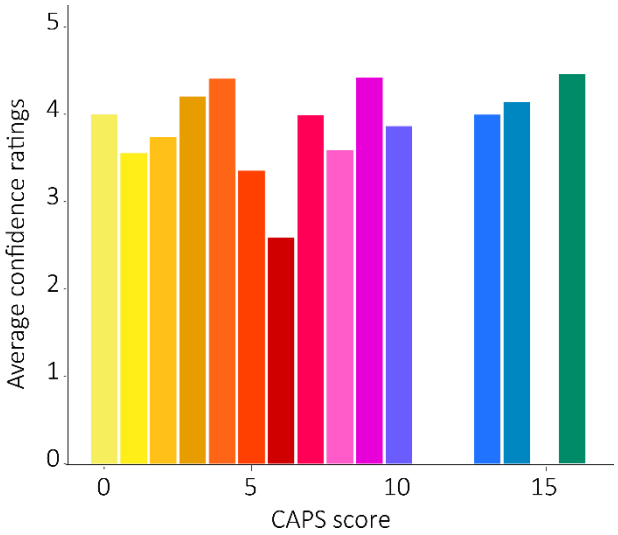

Figure 12. Association between the average individual confidence ratings and CAPS scores.

Confidence Ratings and Response Times

Hallucination-prone participants did not show greater confidence in their decisions (t = -0.240, p = 0.169) (Figure 12). When also adding PDI and SPQ to the model, neither delusion-proneness (t = -0.353, p = 0.726) nor schizotypy in general (t = 0.252, p = 0.802) could predict confidence ratings. Instead, confidence was greater for 'no' responses (t = -31.288, p < .000) (Figure 13), and increased with age (t = 2.762, p = 0.008). Figure 13 indicates that differences in confidence ratings between Yes and No responses were larger for target-absent and 25% likelihood detection trials than in the 50% and 75% likelihood detection conditions. Confidence on target-absent trials differed from the 25% likelihood detection condition (t = -2.053, p = 0.046), and nearly significantly from the 50% likelihood (t = -1.990, p = 0.052), and 75% likelihood detection (t = -1.7575, p = 0.085).

Furthermore, hallucination-proneness did not correlate with the speed of responding (t = 0.440, p = 0.662). When adding SPQ and PDI to the model, response times could neither be accounted for by delusion-proneness (t = 0.145, p = 0.886) or schizotypy (t = 0.338, p = 0.737). Instead, response times were on shorter for 'no' responses (t = 5.821, p < .000) (Figure 14). In addition, responses were nearly significantly faster for higher detection thresholds (t = -2.007, p = 0.051). Response times were faster on no-tone trials than 25% likelihood detection trials (t = 2.030, p 0.048), but did not differ between target-absent trails and 50% likelihood detection (t = 1.931, p =0.060) or 75% likelihood detection trials (t = 1.769, p = 0.084) (Figure 14)

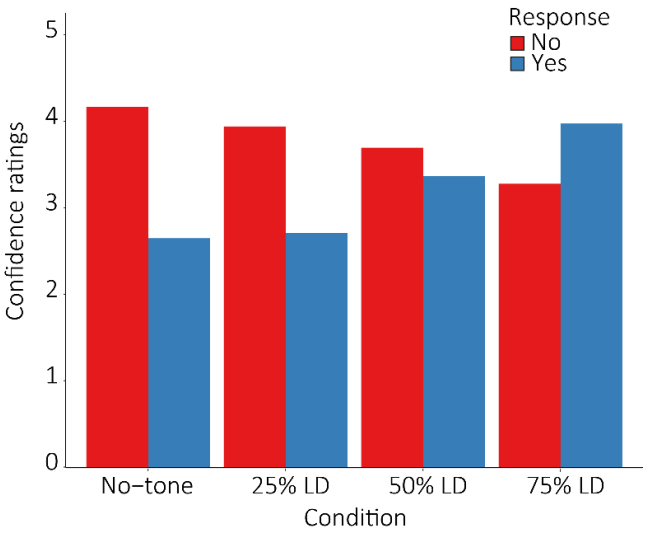

Figure 13. Average confidence ratings in 'yes' and 'no' responses across conditions. LD: likelihood detection.

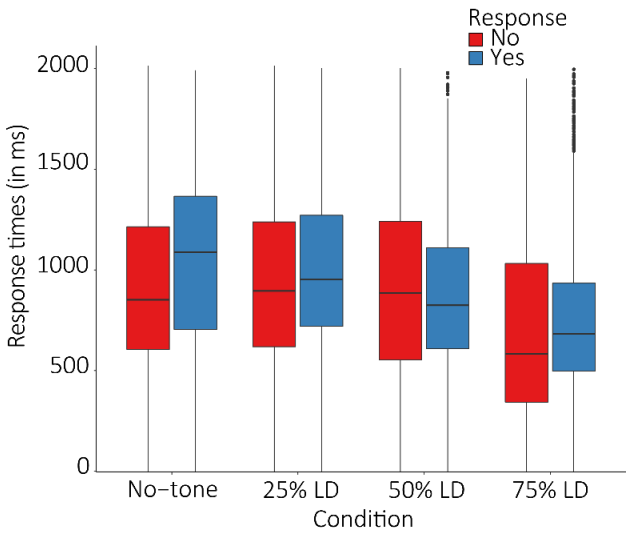

Figure 14. Distribution of response times (in ms) for 'yes' and 'no' responses across conditions. LD: likelihood detection.

Signal Detection Theory Parameters

Hallucination-proneness was not associated with increased bias (t = -0.926, p = 0.360) (Figure 15), but was nearly significantly associated with decreased sensitivity (t = 0.038, p = 0.069) (Figure 16). The correlation between CAPS scores and bias was 0.033, and the association between CAPS and sensitivity was 0.088. In addition, differences among participants in bias could also not be explained by delusion-proneness (t = -0. 545, p 0.589), or schizotypy (t = -0.005, p = 0.996). Similarly, variance in sensitivity could not be accounted for by delusion-proneness (t = 0.005, p 0.996), or schizotypy (t = -0.980, p = 0.333). Instead, bias increased with higher detection thresholds (t = 2.400, p = 0.021). Increased sensitivity could be predicted by higher IQ (t = 2.962, p = 0.005) and higher detection thresholds (t = 6.678, p < .000).

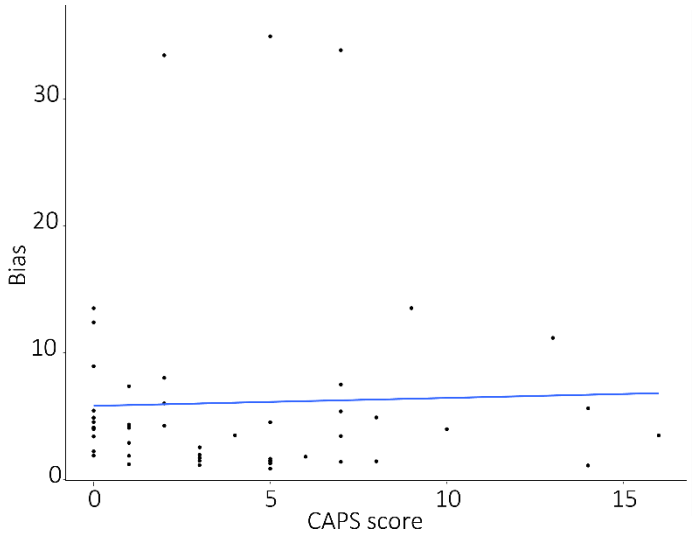

Figure 15. The relation between bias and CAPS scores.

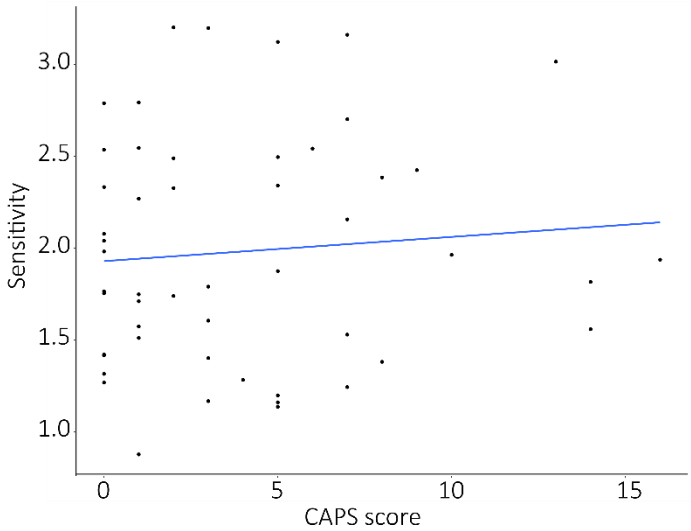

Figure 16. The relation between sensitivity and CAPS scores.

Fatigue

Contrary to the hypothesis, response times were on average lower in the first (853.219 ± 205.316 ms) than in the final four blocks (894.555 ± 225.431 ms) (t_{50} = -2.008, p = 0.05) (Figure 17). Confidence ratings did not differ between the first four (3.869 ± 0.602) and the last four (3.765 ± 0.708) blocks (t_{50} = -0.201, p = 0.106) (Figure 18).

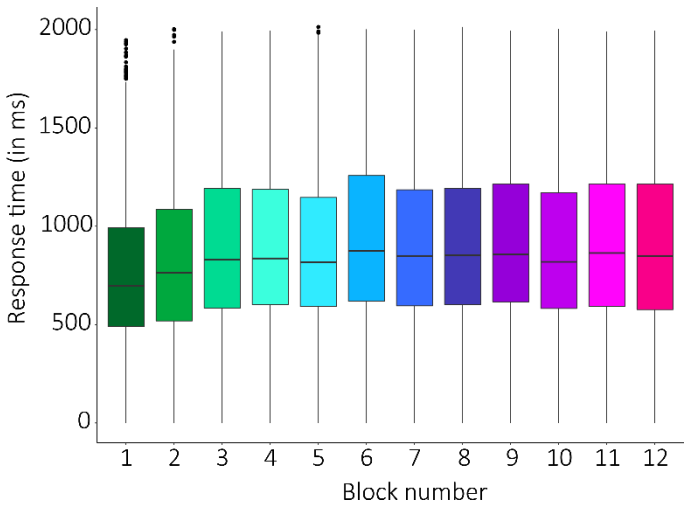

Figure 17. Response times in milliseconds across blocks in the test phase.

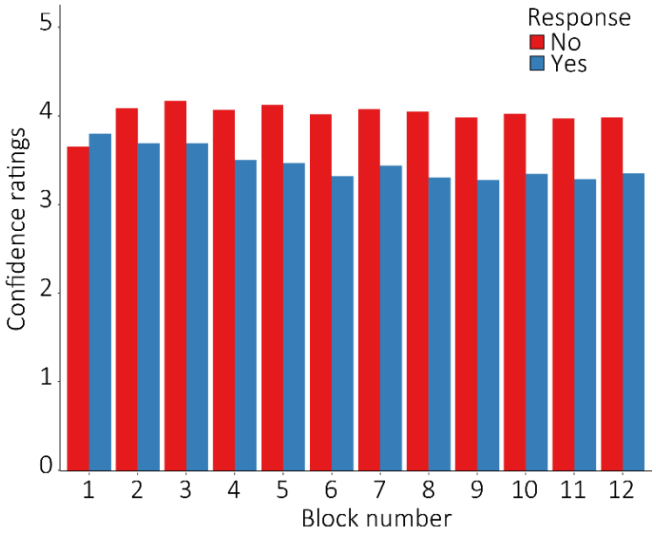

Figure 18. Confidence ratings for responses across blocks in the test phase.

Discussion

The current study tested whether hallucination-proneness in healthy participants was associated with greater reliance on prior expectations. The current study examined with a Pavlovian learning task the effect of task-induced expectations on participants' susceptibility to report conditioned hallucinations, i.e. hearing tones that were in fact not presented. Our results show that hallucination-proneness was indeed associated with greater susceptibility to report conditioned hallucinations. However, hallucination-proneness did not predict greater confidence in decisions. Interestingly, also delusion-proneness could nearly significantly predict the likelihood to answer 'yes' during no-tone trials. Thus, our findings indicate that hallucination-prone healthy individuals indeed rely more on prior expectations, and therefore support the notion that hallucinations relate to strong priors.

Two limitations of this study are worth mentioning. Firstly, it appeared difficult to disentangle the effects of hallucination- and delusion-proneness on the susceptibility to report conditioned hallucinations. In part, this may be due to the sample size, which was smaller than we initially aimed for because of the COVID19 outbreak. With a greater sample and a greater variety in CAPS and PDI scores, it might have been possible to better differentiate the effects of hallucination and delusion-proneness. Secondly, it appears difficult to determine whether participants actually perceived a tone and experienced a conditioned hallucination when they reported 'yes' on no-tone trials. This

challenges the validity of the study, as it raises the question of whether the task truly measured the effect of expectations on perception, or whether these 'yes' responses on no-tone trials could in fact be mere 'errors'. The 'yes' responses on no-tone trials could for instance reflect a failure to inhibit a motor response. Powers and his colleagues (2017) argue based on their fMRI study that participants did really hear a tone during conditioned hallucinations, because they found greater activation in tone-responsive regions in the right supplemental auditory cortex during conditioned hallucinations compared to correct rejections. However, this activation might also reflect the enhanced expectation to hear the tone or a prediction error, and hence does not necessarily indicate the perception of the tone. As an additional argument, Powers and his colleagues cite a 1963 study by Penfield and Perot, which showed that stimulation of the same area produced auditory verbal hallucinations. However, this study does not provide conclusive evidence, as laminar layers in this area might relate to multiple processing mechanisms.

Current Results & Previous Predictive Processing Research

Our finding that hallucination-proneness was associated with greater reliance on perceptual priors is in line with Powers et al.'s study (2017), the review by Corlett et al. (2019), and several other studies based on the predictive processing theory, such as Davies et al. (2018) and Teufel et al. (2015) who found that hallucinations correlated with stronger priors. However, the finding that also delusion-proneness nearly significantly predicted participants' susceptibility to report conditioned hallucinations is in contrast with multiple previous studies, such as Davies et al. (2018) and two studies by Katharina Schmack (Schmack et al., 2013, 2015), which found that delusions were instead associated with weaker perceptual priors in healthy participants and schizophrenia patients. On the contrary, Teufel et al. (2015) also found that PDI scores predicted greater reliance on prior expectations. These contradictory findings might in part be due to the different modalities and tasks that were employed in these studies, as the usage of expectations might be task- and modality-specific. Thus, a large study of both clinical and non-clinical samples with multiple tasks and modalities might provide more clarity. Fortunately, some aspects of such a study are underway in University of Cambridge and elsewhere (G. Murray 2020, personal communication).

Furthermore, hallucination-proneness was not associated with increased confidence in decisions in our sample with healthy participants, in contrast to the study by Powers et al. (2017) on psychotic patients and healthy individuals with daily hallucinations. Possibly, these contradictory results can be accounted for by one of the differences between our study and Powers et al. (2017). There are three main differences between these studies. Firstly, the average age was 27 years in our study and 40 years in Powers et al. (2017). Secondly, IQ scores were on average 100 in Powers et al. (2017), while participants had an average IQ of 122 in our study. Thirdly, none of our participants reported substance abuse, while drug and alcohol use disorders were present in every participant group in Powers et al.'s study (2017). Alternatively, the differences in confidence might be explained by the

idea that confidence in decisions increases with illness severity. This explanation appears in line with previous findings that schizophrenia patients can be overconfident in their decisions, and that patients hold delusions with greater conviction than healthy participants (Balzan, 2016). An example of this is shown in the so-called bead task, in which participants have to infer from which of the two jars a string of beads has been drawn. A characteristic finding from this task is that patients with schizophrenia or psychotic symptoms seem to 'jump-to-conclusions': they draw fewer beads to come to a decision and hold this choice greater confidence than healthy participants (Jardri, Duverne, Litvinova, & Deneve, 2017). To ascertain whether confidence indeed increases across psychotic illness stages, a longitudinal study on confidence, the development of psychotic symptoms, and reliance on prior beliefs might be employed. Hypothetically, if confidence indeed increases with psychotic illness progression, confidence might be used in clinical setting to detect individuals at risk for psychosis.

Possible Mechanisms & Clinical Implications

The findings from our study and Powers et al.'s 2017 article indicate that hallucination-prone healthy individuals, persons with daily hallucinations, and psychotic patients all show the same increased reliance on perceptual expectations. These results suggest that a common mechanism underlies hallucinations in both clinical and non-clinical populations, and thereby support the idea of psychosis as a continuum. The psychosis-continuum entails that psychotic symptoms are an extreme outcome of a continuous phenotype (Schmack et al., 2015), and may have several clinical implications. For instance, if psychotic symptoms are distributed continuously, should the diagnosis of psychotic illnesses still be categorical, or would a continuous scale prove a better option? Consequently, a continuous measurement scale would raise the question of where the cut-off point should lie that demarcates the distinction between 'healthy' and 'psychotic illness'.

Another clinical implication of the finding that strong priors associate with psychotic symptoms in both clinical and non-clinical populations, is whether great reliance on prior knowledge might function as a risk factor. As Murray and Jones (2012) stated, psychotic symptoms in young people do not specifically predict psychotic illnesses, since most psychiatric outcomes of psychotic experiences in adolescence are common disorders, such as depression or anxiety. Thus, additional risk factors for more specifically psychotic disorders might be beneficial to detect individuals at risk for psychosis. For this, further knowledge of the relation between priors usage and development of psychotic symptoms is required, and a longitudinal study with clinical and non-clinical samples in which priors and symptoms of various mental disorders are monitored would provide more clarity.

Unanswered Questions & Future Research

Although hallucinations are associated with stronger priors, further research is necessary to determine whether these strong priors result from increased prior precision or reduced sensory precision. As Schmack et al. (2015) note, an inadequate formation of predictions might be caused by impairments in

feedforward processes of sensory information, as well as by deficits in the generation of accurate feedback predictions. On the one hand, one argument in favour of the notion that strong priors result from an inadequate generation of feedback predictions is provided by Haarsma et al. (2020). They show that first-episode psychosis patients, unlike healthy participants, did not take into account the precision of the environment while updating prior beliefs. On the other hand, one finding that is in line with the account that strong priors are caused by reduced sensory precision, is the finding that people with hearing and vision impairments experience more frequently auditory and visual hallucinations respectively (Linszen et al., 2019). The frequency of experiencing hallucinations has even been found to increase with impairment severity. These results are also in line with our finding that higher auditory detection thresholds were associated with increased likelihood to report conditioned hallucinations. Thus, further research is necessary to determine the effects of these feedback and feedforward processes on the formation of priors in relation to psychotic symptoms.

Moreover, the exact mechanism by which priors relate to psychosis requires further research. For instance, do strong priors cause the emergence of delusions and hallucination, or are priors and psychotic symptoms caused by the same underlying mechanism, or are they triggered by distinct but related processes? Previous research has suggested that the usage of abstract and perceptual expectations differs across psychotic illness phases. For instance, Haarsma et al. (2018) showed that hallucination-proneness in healthy individuals was nearly significantly associated with greater reliance on perceptual priors, while hallucination-proneness in first-episode psychosis participants instead correlated with reduced reliance on perceptual priors, and hallucination-proneness did not correlate at all with prior usage in the at-risk mental state patients. Ideally, a large-scale longitudinal study might be employed with clinical and non-clinical samples to identify the relations between prior expectations, symptom severity, and the various stages of psychotic illness. Hypothetically, in case studies indicate that an increased usage of prior expectations renders individuals more vulnerable for psychosis, future research might focus on developing interventions that train individuals to rely more on sensory information and thereby reduce the risk of developing psychosis.

In conclusion, our results indicate that hallucination-prone healthy individuals rely more on perceptual priors, but do not hold greater confidence in their decisions. Furthermore, delusion-proneness was also nearly significantly related to greater reliance on perceptual priors. These results support the account that psychotic symptoms relate to a bias in predictive processing, and in particular, agree with the notion that hallucinations relate to strong priors. In addition, together with the findings of Powers et al. (2017), our results promote the view of psychosis as a continuum.

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Appendix A. Table with correlation coefficients between predictors

Table A1.
Pearson correlation coefficients and significance value of the predictor variables

	CAPS	*PDI*	*SPQ*	*SENS Hyper-sensitivity*	*Age*	*IQ*	*Detection threshold*	*Percentage missed trials*	*Number of practice trials*
CAPS		r = 0.490 p < .000 ***	r = 0.518 p = .000 ***	r = -0.400 p = 0.004 **	r = 0.316 p = 0.024 *	r = -0.069 p – 0.628	r = 0.060 p = 0.675	r = -0.244 p = 0.088	r = -0.168 p = 0.238
PDI	r = 0.490 p < .000 ***		r = 0.589 p < .000 ***	r = 0.117 p = 0.416	r = -0.060 p – 0.765	r = -0.115 p = 0.423	r = 0.196 p = 0.167	r = -0.244 p = 0.971	r = -0.120 p = 0.403
SPQ	r = 0.518 p < .000 ***	r = 0.589 p < .000 ***		r = -0.463 p = .001 ***	r = -0.005 p = 0.972	r = -0.201 p = 0.157	r = 0.215 p = 0.130	r = 0.076 p = 0.597	r = 0.026 p = 0.856
SENS Hyper-sensitivity	r = -0.400 p = 0.004 **	r = 0.117 p = 0.416	r = -0.463 p = .001 ***		r = -0.149 p = 0.298	r = 0.017 p = 0.907	r = 0.126 p = 0.379	r = 0.127 p = 0.376	r = -0.032 p = 0.824
Age	r = 0.316 p = 0.024 *	r = -0.060 p – 0.765	r = -0.005 p = 0.972	r = -0.149 p = 0.298		r = -0.014 p = 0.924	r = -0.279 p = 0.047	r = 0.068 p – 0.634	r = 0.008 p = 0.954
IQ	r = -0.069 p – 0.628	r = -0.115 p = 0.423	r = -0.201 p = 0.157	r = 0.017 p = 0.907	r = -0.014 p = 0.924		r = -0.257 p = 0.069	r = -0.267 p – 0.059	r = -0.308 p = 0.027*
Detection threshold	r = 0.060 p = 0.675	r = 0.196 p = 0.167	r = 0.215 p = 0.130	r = 0.126 p = 0.379	r = -0.279 p = 0.047	r = -0.257 p = 0.069		r = 0.244 p = 0.084	r = 0.040 p = 0.783
Percentage missed trials	r = -0.244 p = 0.088	r = -0.244 p = 0.971	r = 0.076 p = 0.597	r = 0.127 p = 0.376	r = 0.068 p – 0.634	r = -0.267 p – 0.059	r = 0.244 p = 0.084		r = 0.112 p = 0.436
Number of practice trials	r = -0.168 p = 0.238	r = -0.120 p = 0.403	r = 0.026 p = 0.856	r = -0.032 p = 0.824	r = 0.008 p = 0.954	r = -0.308 p = 0.027*	r = 0.040 p = 0.783	r = 0.112 p = 0.436	

Appendix B. Generalized logistic mixed-effects model with CAPS only syntax and results

Model information

The generalized linear mixed model was fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature). The family of data was binominal, and the *glmer()* optimizer bobyqa was used.

Syntax

glmer(Response ~ Condition + CAPS + SENS Hypersensitivity + Age + dbSNR +
Percentage missed trials + Number of practice trials + (1| Participant number),
family = binomial, nAGQ=0, control=glmerControl (optimizer = "bobyqa"))

Results

AIC	BIC	LogLik	deviance	df residual
12553.1	12638.3	-6265.6	12531.1	17114

Scaled residuals				
Min	1st Quantile	Median	3rd quantile	Max
-7.6868	-0.3170	-0.1797	0.3539	9.7711

Random effects		
Groups Name	Variance	Std.dev
Participant number (Intercept)	0.3873	0.6224
Number of observariongs: 17125, Groups: PTID Participant number 51		

Fixed effects				
	Estimate	**Std. Error**	***z* value**	**Pr(>|*z*|)**
Intercept	1.131570	1.277018	0.886	0.37556
Condition 25% LD	-5.898630	2.738251	-2.154	0.03123 *
Condition 50% LD	-4.337182	2.903212	-1.494	0.13520
Condition 75% LD	-2.957418	3.031569	-0.976	0.32929
CAPS	0.284939	0.114679	2.485	0.01297*
SENS Hypersensitivity	-0.006044	0.012928	-0.468	0.64013
Age	-0.026229	0.008810	-2.977	0.00291**
dbSNR	0.118613	0.042489	2.792	0.00524**
Percentage of missed trials	-0.001313	0.030308	-0.043	0.96545
No. practice trials	0.002747	0.005553	0.495	0.62083

Appendix C. Generalized logistic mixed-effects model with PDI and SPQ syntax and results

Model information

The generalized linear mixed model was fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature). The family of data was binominal, and the *glmer()* optimizer bobyqa was used.

Syntax

glmer(Response ~ Condition + CAPS + SENS Hypersensitivity + Age + PDI + SPQ + dbSNR + Percentage missed trials + Number of practice trials + (1| Participant number), family = binomial, nAGQ=0, control=glmerControl (optimizer = "bobyqa"))

Results

AIC	BIC	LogLik	deviance	df residual
12554.8	12655.5	-6264.4	12528.8	17112

Scaled residuals				
Min	1st Quantile	Median	3rd quantile	Max
-7.7210	-0.31768	-0.1789	0.3556	9.7418

Random effects		
Groups Name	Variance	Std.dev
Participant number (Intercept)	0.3688	0.6073
Number of observations: 17125, Groups: Participant number, 51		

Fixed effects				
	Estimate	**Std. Error**	***z* value**	**Pr(>|*z*|)**
Intercept	0.854248	1.478520	0.578	0.56342
Condition 25% LD	-6.262105	2.814537	-2.225	0.02609 *
Condition 50% LD	-4.722449	2.984123	-1.583	0.11353
Condition 75% LD	-3.360262	3.116132	-1.078	0.28088
PDI	0.011046	0.005995	1.843	0.06538 .
CAPS	0.044289	0.032217	1.375	0.16923
SPQ	-0.013481	0.012535	-1.075	0.28215
SENS Hypersensitivity	-0.014803	0.014432	-1.026	0.30502
Age	-0.025767	0.009248	-2.786	0.00533**
dbSNR	0.124255	0.043674	2.845	0.00444**
Percentage missed trials	-0.003737	0.032339	-0.116	0.90801
No. practice trials	0.003589	0.005468	0.656	0.51159

Appendix D. Linear mixed-effects model with CAPS only syntax and results

Model information

The linear mixed model was fitted by restricted maximum likelihood (REML). The REML criterion at convergence was 47330.3. The t-tests used Satterthwaite's method.

Syntax

lmer(Confidence ~ Condition + Response+ CAPS + SENS Hypersensitivity + Age +
dbSNR + (1|Participant number))

Results

Scaled residuals				
Min	1st Quantile	Median	3rd quantile	Max
-4.6382	-0.4904	0.1376	0.7099	3.0528

Random effects		
Groups Name	Variance	Std.dev
PTID (Intercept)	0.3360	0.5797
Residual	0.9133	0.9557
Number of observariongs: 17125, Groups: Participant number, 51		

Fixed effects					
	Estimate	**Std. Error**	**df**	***t*-value**	**Pr(>|*t*|)**
Intercept	5.437	0.9712	0.4700	5.598	> .000 ***
Condition 25% LD	-4.854	2.365	-0.4700	-2.053	0.04568 *
Condition 50% LD	-4.991	2.508	-0.4699	-1.990	0.05245 .
Condition 75% LD	-4.603	2.620	-0.4699	-1.757	0.08542 .
Response	-0.6763	0.02121	0.00017	-31.288	> .000 ***
CAPS	-0.005098	0.02121	0.4699	-0.240	0.16923
Age	0.0252	0.0008153	0.4702	2.762	0.00816 **
dbSNR	0.07047	0.03670	0.4699	1.920	0.06091 .

Appendix E. Linear mixed-effects model with PDI and SPQ syntax and results

Model information

The linear mixed model was fitted by restricted maximum likelihood (REML). The REML criterion at convergence was 42547.8. The t-tests used Satterthwaite's method.

Syntax

lmer(Confidence ~ Condition + Response+ CAPS + PDI + SPQ + SENS Hypersensitivity + Age + dbSNR + (1|Participant number))

Results

Scaled residuals				
Min	1st Quantile	Median	3rd quantile	Max
-5.1478	-0.3244	0.1996	0.6168	2.7536

Random effects		
Groups Name	Variance	Std.dev
Participant number (Intercept)	0.2164	0.4652
Residual	0.6901	0.8307
Number of observations: 17125, Groups: Participant number, 51		

Fixed effects					
	Estimate	**Std. Error**	**df**	***t*-value**	**Pr(>|*t*|)**
Intercept	1.357	1.004	0.4401	1.351	0.1837
Condition 25% LD	-3.539	1.980	0.4400	-1.787	0.0808 .
Condition 50% LD	-3.594	2.100	0.4399	-1.712	0.0940 .
Condition 75% LD	-3.240	2.194	0.4399	-1.477	0.1468
Response	-0.5989	00.1879	0.00017	-31.875	> .000 ***
PDI	-0.1559	0.02121	0.4399	-0.353	0.7258
CAPS	-0.005098	0.0008153	0.4400	-0.229	0.8198
SPQ	0.002223	0.004416	0.4400	0.252	0.8021
SENS Hypersensitivity	-0.002725	0.02193	0.4402	-0.260	0.7963
Age	0.01560	0.006719	0.4402	2.322	0.0249 *
dbSNR	0.05087	0.03670	0.4399	1.656	0.1049