Cross-modal auditory priors drive the perception of bistable visual stimuli with reliable differences between individuals

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Abstract

Background: It is a widely held assumption that the brain performs perceptual inference by combining sensory information with prior expectations, all being weighted by their uncertainty. Perception of ambiguous stimuli is influenced by higher- and lower-level priors, which can be manipulated with associative learning and sensory priming, respectively. Here, we investigate the differential effect of auditory vs. visual associative cues on perception of illusory visual motion, and we also take lower-level priming effects into account. Furthermore, we examine the test-retest reliability of individual differences and their correlates.

Methods: Healthy individuals (N=29; 13 men, mean (SD) age = 27.8 (9.6) years) performed a perceptual inference task (640 trials) twice with a one-week delay. They reported the perceived direction of (illusory) motion of dot pairs, which were preceded by a visuo-acoustic cue that probabilistically predicted the direction of the motion. In 30% of the trials, motion direction was ambiguous, and in half of these trials, the auditory vs. the visual cue predicted opposing directions. Cue-stimulus contingency could change every 40 trials. To explore the relationship with self-reported alterations in perception and thought, schizotypal traits were measured with the short Oxford–Liverpool Inventory of Feelings and Experiences questionnaire.

Results: Importantly, on ambiguous trials where the visual and the auditory cue predicted conflicting directions of motion, participants made more decisions consistent with the prediction of the acoustic cue. Increased predictive processing under stimulus uncertainty was indicated by slower responses to ambiguous (vs. non-ambiguous) stimuli. Associative learning influenced perceptual decisions: we observed slower responses to less (vs. more) predictable non-ambiguous stimuli and an above-chance rate of cue-congruent decisions on ambiguous trials. Furthermore, priming effects were also observed in that perception of ambiguous stimuli was influenced by perceptual decisions on the previous ambiguous and unambiguous trials as well. Critically, all the above effects had substantial inter-individual variability which showed high test-retest reliability (intraclass correlation coefficient (ICC) > 0.78). Finally, indicators reflecting the dominance of associative learning vs. sensory priming (higher- vs. lower-level priors, respectively) clustered together, these sets of variables were inversely related to each other, and some task-derived indicators showed stable and meaningful associations with schizotypal traits .

Discussion: Overall, higher-level priors based on auditory (as compared to visual) information seem to have greater influence on the perception of illusory visual motion, replicating the sensory conditioning effect. The influence of lower-level priors was evident as well, suggesting that sensory priming was also in action. Importantly, we observed large and stable differences in various aspects of task performance. Computational modelling combined with neuroimaging could allow testing hypotheses regarding the potential mechanisms causing these behavioral effects (e.g. characteristics of visual vs. auditory processing, perceptual organisation and attention, and uncertainty). The reliability of the behavioural differences implicates that such perceptual inference tasks could be valuable tools during large-scale biomarker and neuroimaging studies.

Introduction

Perception can be understood as an unconscious inferential process that estimates the state of the environment by combining prior expectations with incoming sensory data, weighted by their uncertainty (de Lange et al., 2018; Fiser et al., 2010; Friston, 2009; Helmholtz, 1867): the less informative sensory data becomes, the more observers will rely on their prior expectations that are influenced by their previous experiences (Corn-Becker et al., 1949; Ellson, 1941; Powers et al., 2017; Weilhhammer et al., 2018). Behavioural evidence robustly supports these principles: Ellson were among the first to demonstrate sensory conditioning and induced perception in the absence of sensory stimulation (i.e. conditioned hallucinations) in healthy humans (1941). In addition, Brogden's sensory pre-conditioning experiment in dogs revealed that associative learning can operate on multisensory representations (also see Deroy et al., 2016; Macaluso & Driver, 2005 for more recent reviews of multisensory integration): a light and a sound were repeatedly presented together and by subsequently associating one but not the other stimulus with a shock, the latter still triggered a conditioned response (Brogden, 1939). Furthermore, simple frequency statistics of previous sensory input and percepts, and even internally generated mental images (i.e. imagery) also affect perception (de Lange et al., 2018; Klüver, 1928; Pear, 1925; Pearson, 2019). For instance, repetition priming refers to the well-established phenomenon that exposure to perceptual objects facilitates their subsequent processing (Schacter, 1992) and mental images alone (in the absence of sensory stimulation) can drive the perception of ambiguous stimuli (Bergmann et al., 2016; Pearson et al., 2008). Importantly, the above mentioned phenomena can be derived from the idea that the brain is an organ of inference (Helmholtz, 1867) that actively optimises a probabilistic model of its environment and uses it to select actions (Fiser et al., 2010; Friston, 2009).

The neural correlates of perceptual inference have been extensively studied. The influence of prior beliefs on perception is implemented by top-down feedback signals arriving from higher-level multimodal association areas to sensory areas, mirrored by the modulation of posterior alpha by frontal delta (Helfrich et al., 2017) or parietal beta activity (Richter et al., 2017). These signals seem to carry information as prior expectations induced by sensory conditioning activate feature-specific stimulus representations in the human primary visual cortex (Kok et al., 2014). On the other hand, bottom-up processing of sensory data in unimodal sensory areas (e.g. visual cortex) is assumed to be implemented by gamma-band oscillations (Richter et al., 2017). As mentioned above (Friston, 2009), prior expectations have a stronger weight when sensory input is uncertain and at the neural level, increased frontal theta and fronto-parietal and occipital-parietal beta power have been observed when processing ambiguous stimuli (Maksimenko et al., 2020), while the precision of lower-level priors in the primary visual cortex was reduced if the environment was inconsistent (Varrier et al., 2020). Finally, lower-level priming effects co-occur with reductions in neural activity - termed 'repetition suppression' (Henson & Rugg, 2003) or 'expectation suppression' (de Lange et al., 2018) - which may reflect top-down effects of expectations based on stimulus frequency statistics (Summerfield et al., 2008). Critically, there are differences between individuals in terms of the weighting of sensory information vs. prior beliefs during perceptual inference, and evidence suggests that this variation might be of clinical relevance. A number of studies have examined the alterations of perceptual inference in association with psychosis-spectrum conditions or their extended phenotypes in the general population. For instance, delusions may emerge to explain anomalies that arise due to weaker lower-level predictions while stronger higher-level priors might be responsible for the rigidity of delusional beliefs. In an experiment, where participants were shown bistable binocular stimuli, the percept changed more frequently in patients with schizophrenia who experienced delusions and also in healthy participants prone to delusions; furthermore, they were more prone to the effect of expectation manipulations influencing their perception of ambiguous stimuli (wearing 'special' glasses) (Schmack et al., 2013, 2015). Additionally, hallucinations can be explained by stronger top-down priors overwriting sensory evidence and indeed, voice-hearing individuals (independently of a diagnosable psychotic disorder) are more prone to conditioned hallucinations (Powers et al., 2017). Davies (Davies et al., 2018) has shown that people prone to

delusions vs. hallucinations differ in terms of extracting sensory evidence (on the task of deciding whether dots are inside or outside of previously seen, but noisy shapes): those who were prone to hallucinations were more able to extract sensory evidence, and this was especially true if they were not prone to delusions. In turn, those who were prone to delusions, especially those who were not prone to hallucinations, performed worse, suggesting that lower- vs. higher-level expectations are differentially associated with aspects of psychosis. In summary, carefully designed paradigms that reliably capture individual differences are needed to provide mechanistic explanations for hallucinations and delusions in the psychosis spectrum.

Here, we build upon the paradigm of Weinhhammer and colleagues (2018) who implemented an audiovisual sensory conditioning task to study the hierarchical neural representation of perceptual states in a changing environment. In their task, motion directions were probabilistically associated with auditory cues. Following the presentation of a cue, participants had to make predictions based on conditional expectations. Then, they made perceptual decisions about disambiguated or ambiguous target stimuli (sensory uncertainty, see Bach & Dolan, 2012). In order to induce associative learning, most trials followed an underlying cue-target association rule (e.g. high tone - counter-clockwise tilt). On some trials, however, the presented tilt violated expectations (e.g. high tone - clockwise tilt) and cue-target contingency changed from time to time (rule uncertainty, see Bach & Dolan, 2012). Computations underlying perceptual decisions were inferred with hierarchical Bayesian models. According to the best fitting model, higher-level predictions based on cue-target contingency (associative learning) had greater weight, relative to lower-level predictions based on previous sensory data (sensory priming). At the neural level, higher-level predictions correlated with activity in the orbitofrontal cortex and the hippocampus, while lower-level predictions correlated with activity in the retinotopic visual cortex.

This elegant study motivates several intriguing research questions that demand careful analysis at the level of behaviour (Krakauer et al., 2017). First, the experiment of Weinhhammer et al. was designed to maximize the effect of associative learning, by explicitly asking participants to report their expectations right after the presentation of the associative cues. One may reason that such subjective reports trigger causal metacognition and explicit memory which may interfere with task performance (Deroy et al., 2016). To examine interactions between higher- and lower-level prior expectations within the same task, we aimed to increase the effect of sensory priming, therefore, we shortened the time frame available to respond and did not ask participants to make their predictions explicit. Following Lawson et al. (2017), we argue that despite the latter modification, data from this adapted design contains sufficient information for the assessment of predictive processes (i.e. these can be inferred from responses and reaction times). Additionally, this way participant burden (i.e. the overall time needed for the experiment) was drastically reduced, which may facilitate data quality. Second, the experimental setting of Weinhhammer et al. consisted of auditory cues and visual targets, thus, associative learning relied on cross-modal integration. Using multimodal cues (from both the acoustic and visual domain), we examine whether auditory vs. visual associative cues dominantly influence perceptual decisions about uncertain visual targets. One could reason that if visual sensations are uncertain, sounds will become more important to infer the state of the world, and thus, one may expect the dominance of auditory cues during the perception of ambiguous visual stimuli (Deroy et al., 2016; Friston, 2009). Last but not least, although individual differences were evident in the data of Weinhhammer et al., no systematic investigation of these were reported in their study. The reliability of behavioural tasks as indicators of individual differences is often overlooked (Dang et al., 2020; Enkavi et al., 2019) despite the crucial importance of accurate measurement in the study of personality (Clark & Watson, 2019; Montag et al., 2020) and endophenotypes (Chan & Gottesman, 2008). Strikingly, despite the growing interest in perceptual inference in clinical neuroscience (Sterzer et al., 2018), to our best knowledge, relatively little information is available on the reliability of indicators derived from perceptual inference tasks. To estimate the reliability of differences in task performance as trait markers, individuals performed our experiment twice.

Methods

Participants

Based on an a priori power calculation (Faul et al., 2009), we aimed to obtain analysable data from at least 28 participants (expected minimum test-retest effect size $r = 0.5$, power = 90%, $\alpha = 0.05$). Accounting for potential exclusion and dropout, we recruited 34 young adults to take part in the study. Of this initial sample, 2 participants were excluded due to self-reported previous or concurrent psychiatric disorder or any disease affecting the central nervous system. Following inspection of raw data, data of 3 participants were excluded because their behaviour suggested that they did not follow the instructions and we excluded data from two participants only from the first and the second session due to their anomalous behaviour (see details in Results/Ensuring that participants followed task instructions and generated reliable data). The final sample comprised 29 individuals (13 men, mean (SD) age = 27.8 (9.6) years, mean (SD) education = 17.3 (1.6) years). Participants repeated the experiment after one week. The study was conducted in accordance with the Declaration of Helsinki and it was approved by the United Ethical Review Committee for Research in Psychology (Egyesített Pszichológiai Kutatásetikai Bizottság; EPKEB, 2016/032).

Perceptual inference paradigm

The paradigm was based on the work of Weinhhammer et al. (2018). In this task, participants had to pay attention to vertical point pairs which tilted to a horizontal state and they were asked to indicate the perceived direction of the movement with a button press. In our study, participants most probably were shown a tilting illusion which made the percept unambiguous but on 30% of the trials, the stimulus was ambiguous and only the initial (vertical) and the final (horizontal) state were shown (see Figure 1B). Before every tilt, multimodal cues were presented which consisted of a higher (576 Hz) or lower (352 Hz) sound and a yellow disk moving upwards or downwards. On unambiguous trials, the cues were congruent in that the acoustic and the visual cue always predicted the same movement direction. In order to facilitate learning of the underlying rule, on 86% of unambiguous trials (60% of all trials), congruent cues were followed by one type of tilt (*regular* trials). However, on 14% of unambiguous trials (10% of all trials), congruent cues were followed by the other type of tilt (*irregular* trials). Furthermore, on one half of the ambiguous trials, the cues were congruent (auditory and visual cues predict the same tilt), while on the other half, they were incongruent (auditory and visual cues predict opposite tilts) cues were presented. The task included 640 trials which were presented in 16 randomly ordered consecutive blocks, without any break. The probability distribution of conditions was balanced in each block of 40 trials and during the entire experiment too. The probabilistic rule predicting one particular direction (e.g. combination of high pitch and upward movement before a clockwise tilt) could change from block to block. Participants were informed that the cues are related to the direction of the motion, but the association between cues and motions may change from time to time.

Procedure

The experiment lasted about 30 minutes and was performed in a room with closed windows, artificially and evenly lit. Participants listened to the auditory stimuli through headphones. Visual stimuli were presented on a computer screen (generic PnP monitor) with 60 Hz refresh rate. The task was built in and presented with Psychopy 3.2.3. under Python v3.7. First, we estimated hearing thresholds (using 464 Hz sounds with varying volume [10 levels] in a randomly presented order) in order to individually ensure the audibility of the acoustic cues. Then, participants were trained to appropriately respond to the tilting directions (clockwise tilt - right arrow button, counterclockwise tilt - left arrow button) as fast as possible, but at maximum within 1200 ms. Please note that we aimed to reduce the influence of conscious, top-down processing by providing a shorter time window for

responses, as compared to Weilhammer et al. (For task timing information see Figure 1A.) After the perceptual inference paradigm, participants were asked to complete a short questionnaire that assessed schizotypal traits.

A TIME COURSE

B TRIAL CONDITIONS

B/1 Incidence rate

B/2 Congruent cues followed by more/less predictable unambiguous target

B/3 Congruent/incongruent cues followed by ambiguous target

C DATA QUALITY

C/1 Response rate [%]

C/2 Accuracy on unambiguous trials [%]

C/3 Percentage of 'left tilt' responses [%]

C/4 Median reaction time of correct responses on regular unambiguous trials [ms]

Figure 1. Experimental paradigm and data quality. [A] Time course. At the beginning of every trial, a multimodal cue pair was presented for 300 ms consisting of a yellow dot moving up or down and a higher or lower tone. This was followed by a 500 ms interstimulus interval, during which a fixation cross attracted attention to the middle of the screen. Then we presented dot pairs in vertical, then in horizontal position for 600-600 ms. Between these for 33 ms a motion strike indicated a turning illusion, disambiguating the stimuli, or on ambiguous trials we showed nothing (just the gray background), keeping the stimuli bistable. Participants were asked to indicate the perceived direction of the motion, their button presses were detected in the time interval from the presentation of the horizontal dotpair, until maximum 1200 ms later. We used a 500 ms long intertrial interval. [B] Trial conditions. Throughout the experiment 30% of the trials were ambiguous (no motion illusion presented). The cues presented were congruent (high tone + top-down movement, low tone + bottom-up movement) when preceding the unambiguous stimuli, and on half of the ambiguous trials. On the other half of the ambiguous trials the cues were incongruent (low tone + top-down movement, high tone + bottom-up movement). Conditions were balanced in every block of 40 trials. In-block trial order was randomized. In 8 blocks the underlying rule associated 1-1 congruent cuepair with 1-1 (more predictable) direction ($0.6 = P(\text{left} \mid \text{high tone, top-down move}) = P(\text{right} \mid \text{low tone, bottom-up move}) > P(\text{left} \mid \text{low tone, bottom-up move}) = P(\text{right} \mid \text{high tone, top-down move}) = 0.1$), in the other 8 to the other ($0.6 = P(\text{right} \mid \text{high tone, top-down move}) = P(\text{left} \mid \text{low tone, bottom-up move}) > P(\text{right} \mid \text{low tone, bottom-up move}) = P(\text{left} \mid \text{high tone, top-down move}) = 0.1$). These blocks followed each other in random order. [C] Data quality. Within each panel of the figure, on the left side, dots represent participants, and the values from each session are connected along the x axis, a boxplot (median, 50% CI) is shown, and the distribution for each session can be seen. While on the right side of the panels, each dot represents a participant's performance in session 1 and 2 on the x and the y axis, respectively. Trend line shows linear fit with 95% confidence interval and the dashed line indicates the hypothetical perfect correlation. Please find test-retest statistics in Table 1. [C/1] Overall response rate was very high. Percentage of valid responses on 640 trials is presented. Test-retest stability was low, probably due to a ceiling effect. [C/2] Accuracy on unambiguous trials was very high. Percentage of correct answers on 448 unambiguous trials is shown. Test-retest stability was weak, which might be due to ceiling performance. [C/3] There was no general response tendency in the data. Percentage of 'left tilt' responses on 640 trials is shown. Test-retest stability was high. [C/4] Processing speed. Median RT of correct responses on 384 regular unambiguous trials. Test-retest stability was high and motor learning was evident.

Schizotypal traits

We were interested to see whether objectively assessed differences in perceptual inference are associated with self-reported variation in perception and cognition. Therefore, we measured positive, negative and disorganised dimensions of schizotypal traits (that is, personality traits resembling the signs and symptoms of schizophrenia) with the Oxford–Liverpool Inventory of Feelings and Experiences, short version (sO-LIFE) (Mason et al., 2005; Hungarian version: Kéri, 2011). Here, we used three subscales. Positive schizotypy was measured with the Unusual Experiences subscale (12 items, reliability in the sample Cronbach's $\alpha=0.82$ / 0.82 , test-retest reliability Spearman's $\rho = 0.92$, ICC = 0.96), negative schizotypy was measured with the Introverted Anhedonia subscale (10 items, reliability in the sample Cronbach's $\alpha=0.76$ / 0.74 , test-retest reliability Spearman's $\rho = 0.86$, ICC = 0.94), and disorganised schizotypy was assessed with the Cognitive Disorganisation subscale (11 items, reliability in the sample Cronbach's $\alpha=0.78$ / 0.84 , test-retest reliability Spearman's $\rho = 0.87$, ICC = 0.95). Studies have shown that the sO-LIFE has appropriate psychometric properties to assess schizotypal traits in the non-clinical population (except for the Impulsive Nonconformity dimension, which we therefore did not use in our study, reliability in the sample Cronbach's $\alpha=0.74$ / 0.70 , test-retest reliability Spearman's $\rho = 0.44$, ICC = 0.91) (Fonseca-Pedrero et al., 2015). Although the original questionnaire uses a binary response format, we decided on 5-level Likert-format in order to improve reliability (following Cohen et al., 2010), which was excellent in the present sample.

Statistical analyses

First, in order to ensure data quality, we explored raw data to identify potential anomalies in task performance (i.e. overall response rate and reaction times, accuracy on congruent regular unambiguous trials, severe response bias on all and/or ambiguous trials), and we excluded participants who suspectedly did not follow task instructions (see Participants section).

Then, we examined the effects of higher- and lower-level predictions on perceptual inference. The overall effect of higher-level predictions (sensory conditioning / associative learning) is reflected in perceptual decisions being consistent with the congruent cues on ambiguous trials. Moreover, we argued that if participants learned the associative rule, their responses on irregular unambiguous trials should be slower and less accurate. Critically, performance on ambiguous trials where the cues are incongruent allow the examination of unisensory vs. multisensory higher-level predictions: perceptual decisions consistent with the acoustic (vs. visual) cue indicate multisensory (vs. unisensory) dominance. Furthermore, lower-level predictions are mirrored in perceptual decisions consistent with the stimulus presented on the previous unambiguous trial (sensory priming) and with the perceptual decision on the previous ambiguous trial (perceptual priming). The above experimental effects were analysed with nonparametric Wilcoxon t-tests and $r (= Z/\sqrt{N})$ was computed as a measure of effect size. Finally, test-retest reliability was analysed with Spearman's rank order correlations and intraclass correlations (ICC(3,k), based on two-way mixed effects model, aiming for consistency in $k=2$ measures, following (Enkavi et al., 2019)). Visualisations were created following the excellent work of van Langen (Langen, 2020/2020).

Analyses were performed with R (R Core Team, 2019) and the R-packages *broom* (Robinson et al., 2020), *carData* (Fox, Weisberg, & Price, 2020), *corrplot* (Wei et al., 2017), *effects* (Fox, Weisberg, Price, et al., 2020), *effsize* (Torchiano, 2015/2020), *factoextra* (Kassambara & Mundt, 2020), *forcats* (Wickham, 2020), *Formula* (Zeileis & Croissant, 2020), *GGally* (Schloerke et al., 2020), *ggcorrplot* (Kassambara, 2019), *gg halves* (Tiedemann, 2019/2020), *ggstatsplot* (Patil, 2020), *gridExtra* (Auguie & Antonov, 2017), *Hmisc* (Harrell & others, 2020), *knitr* (Xie, 2011/2020), *lattice* (Sarkar et al., 2020), *papaja* (Aust, 2014/2020), *psych* (Revelle, 2020), *readr*

(Wickham et al., 2020), *readxl* (Wickham et al., 2019), *rmarkdown* (Allaire et al., 2020), *survival* (Therneau, 2016/2020), *tidystats* (Slegers, 2020), and *tidyverse* (Wickham, 2019).

Results

Ensuring that participants followed task instructions and generated reliable data

After the inspection of raw data, we decided to exclude data of 2 participants because their behaviour suggested that they did not follow the instructions (they had disproportionately fast responses on unambiguous trials (*median* RT < 230 ms vs. *median* RT [*IQR*] in the whole sample = 352 [323; 378] ms), and we also excluded another participant's data who at debriefing reported that they purposely adopted a strategy to respond 'left' on ambiguous trials, which was also reflected in their behaviour: proportion of 'left' responses on ambiguous trials = 91%). Furthermore, we excluded data from two participants only from the first and the second session due to their anomalous behaviour (one had a 77% response rate on all trials during the first session, while *median* [*IQR*] response rate in the whole sample = 99 [98; 99] %; and the other had a 83% accuracy on trials, where performance should be near 100%, as expected unambiguous stimuli are shown: *median* [*IQR*] accuracy on these trials in the whole sample = 97 [94, 98] %).

In the final sample, response rate (*mean* (*SD*)=99.2 (1.07) %) and accuracy (*mean* (*SD*)=96.5 (2.26)%) for unambiguous stimuli were very high, indicating that participants followed task instructions (See Figure 1C/2,3). Then, we evaluated whether there was any indication of response tendency. Proportion of 'left' responses did not differ from 50%, as calculated with one-sample Wilcoxon T-test, which is perfectly reasonable given the balanced design of the task and high accuracy for unambiguous stimuli (See Figure 1C/3 and Table 1). Finally, we inspected cognitive-perceptual processing speed. We calculated participants' median RT of accurate responses on regular unambiguous trials (*median* (*SD*) = 370 (39) ms). Motor learning was indicated by shorter reaction times in the second session, relative to the first session. (See Figure 1C/4.)

Ambiguous stimuli takes more time to process

To measure the effect of stimulus uncertainty, we performed Wilcoxon T-tests comparing median reaction times on unambiguous vs. ambiguous trials (target stimuli containing visible tilting illusion or not). We found significant differences in both sessions. Reaction times were significantly higher on ambiguous than on unambiguous trials, suggesting slower processing of uncertain stimuli (See Figure 2A and Table 1.).

Lower-level priors effects influence perception of ambiguous stimuli - evidence of sensory and motor priming

We examined three indicators of lower-level priors. First, we considered the priming effects of sensory data encountered on the previous unambiguous trial. Second, we evaluated the influence of the preceding perceptual inference under uncertainty on the previous ambiguous trial. Third, we examined whether participants demonstrated motor memory/priming as reflected in their tendency to repeat a certain response (this can also be interpreted as simple response/decision tendency). These are represented by the perceived tilting direction on the previous unambiguous trial, decisions made on the previous ambiguous trial and tendency towards a certain response (independent of experimental manipulation), respectively. We performed one-sample Wilcoxon T-tests to measure the effect of lower level priors (i.e. sensory priming) on ambiguous trials (see Table 1.). The proportion of decisions participants made on ambiguous trials consistent with the decision they made on the previous ambiguous trial was significantly higher than what would be expected by chance ($\mu=50\%$). In addition, the proportion of decisions on ambiguous trials consistent with the decision on the previous unambiguous trial was also significantly higher than chance level ($\mu=50\%$). We found no significant general response tendency towards any direction at the group level, but there was large variability across individuals (See Figure 2B/1-3.).

Figure 2. Processing of ambiguous stimuli and the influence of lower- and higher-level expectations Within each panel of the figure, on the left side, dots represent participants, and the values from each session are connected along the x axis, a boxplot (median, 50% CI) is shown, and the distribution for each session can be seen. While on the right side of the panels, each dot represents a participant's performance in session 1 and 2 on the x and the y axis, respectively. Trend line shows linear fit with 95% confidence interval and the dashed line indicates the hypothetical perfect correlation. Please find test-retest statistics in Table 1. **[A] Processing of ambiguous stimuli takes more time.** On the y axis, median reaction times differences on unambiguous-ambiguous trials (the target stimuli was made unambiguous with motion streaks). If there was no difference between these conditions, dots should be around 0 ms (level shown with dashed line). Test-retest stability was high and general motor learning was also observed. **[B] Effects of lower-level priors captured by response tendency on ambiguous trials.** [B/1] Response tendency in ambiguity. Along the y axis, we present the percentage of 'left' decisions in ambiguity. If there were no tendency, participants should perform around chance level (50%, shown with dashed line). Test-retest stability was high. [B/2] Sensory priming effect in ambiguity. Along the y axis, we present the percent of decisions consistent with the previous decision made in unambiguity. If there were no sensory priming, participants should perform around chance level (50%, shown with dashed line). Test-retest stability was high. [B/3] Effect of perceptual priming in ambiguity. Along the y axis, we present the percentage of decisions consistent with the previous decision made in ambiguity. If there were no perceptual priming, participants should perform around chance level (50%, shown with dashed line). Test-retest stability was high. **[C] Effects of higher-level priors captured by reaction time and accuracy on unambiguous trials and by response tendency on ambiguous trials.** [C/1] Slowing down to unexpected (vs. expected) targets. On the y axis, median reaction times differences between irregular - regular unambiguous trials (when cues were followed by less vs more predictable tilting illusion according to the probabilistic rule). If there was no difference between these conditions, dots should lie around 0 ms (level shown with dashed line). Test-retest stability was high and motor learning was indicated by shorter reaction times in session 2. [C/2] Decreased accuracy to unexpected vs. expected targets. On the y axis, the difference between the % of correct responses to irregular - regular unambiguous stimuli are presented. If there was no difference between these conditions, dots should be around 0 ms (level shown with dashed line). Test-retest stability was poor, probably due to a ceiling effect. [C/3] Cues influence responses to ambiguous targets. Along the y axis, we present the percentage of decisions consistent with the direction associated with the cues in ambiguity when the cues were congruent. If there were no effect of

associative learning on perceptual decisions, participants should perform around chance level (50%, shown with dashed line). Test-retest stability was high. [C/4] Auditory cues dominantly influence responses to ambiguous targets. Along the y axis, we present the percentage of decisions consistent with the direction associated to the acoustic cue in *ambiguity* after *incongruent* cues (where the acoustic and visual cues were associated with different directions). If there were no dominance of any modality, participants should perform around chance level (50%, shown with dashed line). Test-retest stability was high.

Higher-level priors based on associative learning also influence perceptual inference - evidence of sensory conditioning

We performed several Wilcoxon T-tests to investigate the effect of associative learning (See Table 1.). First, we compared median reaction times on regular vs. irregular unambiguous trials (when cues were followed by a more vs. less predictable tilt) with paired Wilcoxon T-tests in each session and found that participants reacted slower on irregular, than on regular trials (See Figure 2C/1 and Table 1.). Second, we compared the rate of correct responses on regular vs. irregular unambiguous trials in each session and found that participants made more errors on irregular trials than on regular trials (See Figure 2C/2 and Table 1.). Third, we performed one-sample Wilcoxon T-tests to measure if decisions differed from chance level ($\mu=50\%$) on ambiguous trials when cues were congruent. We found that participants responded more consistently with the direction associated with the cues (See Figure 2C/3 and Table 1.). These results suggest that participants developed expectations (higher-level priors) consistent with the cues' prediction regarding tilting direction, and this resulted in slower responses and more errors when the expectation was violated by the presented tilt, relative to when their expectations were met by the stimulus. Furthermore, these expectations shaped their perceptual decisions when they were faced with ambiguous target stimuli.

When the cues are conflicting, auditory cues dominate the perception of ambiguous visual stimuli

To examine whether the modality of the cues caused behavioral differences in participants, we focused on those trials where after an incongruent cue ambiguous target was presented, because here the cues from the acoustic and the visual domain were associated with different directions. We performed a one-sample Wilcoxon T-test, comparing chance level ($\mu=50\%$) to the proportions of decisions consistent with auditory cues in both sessions, on *incongruent ambiguous* trials. Importantly, we found that decisions were significantly more likely to be in line with the direction associated with the acoustic cue (See Table 1. and Figure 2C/4.).

Individual differences in behavioural effects have robust test-retest stability

All the above effects were relatively subtle at the group level. However, we observed substantial variation between individuals in terms of the magnitude of these effects. Now, we turn to evaluate whether these reflect temporally stable, trait-like differences between participants. To measure the reliability of our metrics, we performed a test-retest analysis using Spearman's rank correlation across sessions, which tests whether the ranking of individuals within the group was similar at the two sessions for a given variable. Furthermore, we calculated the intraclass correlation coefficient (ICC), which reflects both the degree of correlation and the agreement between measurements (see details in Table 1 and in the scatterplots in the right side of Figure 1 and 2.).

First of all, cognitive-perceptual processing speed was reliable, which allowed further testing of reaction time differences. Slowing down on ambiguous (vs. unambiguous) trials had high test-retest reliability. This suggests that although participants demonstrated motor learning (i.e. they became faster) throughout the experiment, in-group ranks stayed relatively consistent.

Indicators of lower-level priors were based on response tendencies deviating from chance level (50%) towards consistency with previously made perceptual decisions. As can be seen from the histograms (Figure 2B), the extent of these effects varied greatly between participants. Importantly, this variation across individuals in sensory and

perceptual priming were both stable over the test-retest interval. When examining motor memory, we did not find a tendency towards any direction at the group level (neither on all trials nor in ambiguity), but individual scores varied highly here too. These differences were stable throughout the sessions, as shown by high test-retest *rho* and ICC values.

Variables reflecting associative learning (see Figure 2C) were calculated in multiple ways. First, on unambiguous trials, we examined the behavioural effects of expectation violation. Differences in the extent of slowing down on irregular (vs. regular) trials was reliable, but differences in the degree of reduced accuracy were not. Second, we examined response tendencies on ambiguous trials. The proportion of cue-consistent decisions were reliable, and so was the dominance of the acoustic domain on trials with incongruent cues.

Interestingly, individual differences in the behavioural effects of expectation violation and in the measures of attention were reliably captured by reaction time but not by decision accuracy, further strengthening our rationale that reaction times not only carry important information but they may provide a more sensitive form of measurement. Low reliabilities were observed for average response rate and weakened accuracy of responses on irregular unambiguous trials, which could be explained by almost perfect performance (i.e. ceiling effects) resulting in low and uninformative variability.

Overall, we argue that the found high variability captures a substantial amount of true variance (and is not due to error variance), because those variables all showed individual stability. Participants consistently reacted slower/faster and if they were less/more affected in the first session, they behaved similarly in the second session.

	Session	Wilcoxon T-test			Effect size			Spearman's correlation			Intraclass correlation		
		M1 or M	M2 or μ	diff	r	CI lower	CI higher	ρ	CI lower	CI higher	ICC	CI lower	CI higher
Resp[%]	1	98.4	-	-	-	-	-	0.35	-0.04	0.64	0.44	-0.08	0.71
	2	99.1											
AccResp[%]	1	95.6	-	-	-	-	-	0.43	0.06	0.70	0.65	0.33	0.82
	2	96.6											
Gen RespTend[%]	1	48.9	50	-1.1	-0.24	-0.58	0.11	0.64	0.35	0.82	0.88	0.75	0.93
	2	48.6	50	-1.4	-0.28	-0.63	0.07						
ProcSpeed[ms]	1	360	-	-	-	-	-	0.67	0.38	0.83	0.78	0.57	0.88
	2	345											
AmbSlow[ms]	1	422	360	62	0.82	0.70	0.87	0.81	0.63	0.91	0.88	0.77	0.94
	2	389	344	45	0.86	0.80	0.88						
Amb RespTend[%]	1	46.7	50	-3.3	-0.17	-0.54	0.22	0.64	0.34	0.82	0.88	0.77	0.94
	2	47.4	50	-2.6	-0.20	-0.56	0.17						
SensPrim[%]	1	54.9	50	4.9	0.67	0.42	0.83	0.65	0.36	0.83	0.80	0.62	0.90
	2	57.6	50	7.6	0.65	0.38	0.81						
PercPrim[%]	1	57.5	50	7.5	0.75	0.56	0.86	0.79	0.58	0.90	0.91	0.83	0.95
	2	53.7	50	3.7	0.48	0.16	0.72						
AssocLearn IrregSlow[ms]	1	386	360	26	0.76	0.60	0.86	0.39	0.02	0.67	0.80	0.61	0.89
	2	368	342	26	0.68	0.45	0.85						
AssocLearn IrregInacc[%]	1	94.0	97	-3	-0.60	-0.81	-0.31	0.07	-0.31	0.44	0.24	-0.47	0.60
	2	97.0	97	0	-0.48	-0.76	-0.17						
AssocLearn AmbCue[%]	1	55.7	50	5.7	0.81	0.67	0.88	0.55	0.22	0.77	0.83	0.68	0.91
	2	54.2	50	4.2	0.48	0.14	0.72						
AssocLearn AmbTone[%]	1	53.3	50	3.3	0.70	0.49	0.83	0.35	-0.04	0.64	0.81	0.64	0.90
	2	52.6	50	2.6	0.62	0.33	0.77						

Table 1. Group level tendencies. Individual differences in task performance have high temporal stability over a 1-week interval. In the first group of columns, the results of paired Wilcoxon T-tests results are shown, with the null hypothesis being that populations' mean ranks are equal ($N = 27$). In the case of one sample comparisons ($N = 29$), we tested the null hypothesis that the median is equal to a theoretical value, namely 50% (as chance level). In the middle, we show the effect size of the difference ($r = Z/\sqrt{N}$) and its 95% confidence interval. In the last group of columns we show Spearman's rank order correlation coefficients (ρ), intraclass correlation coefficients (ICC_{3,k}) and their 95% confidence intervals ($N = 27$; $df = 26$). In a frequentist framework, a 95%CI should be interpreted as follows: if the true value is smaller (larger) than the lower (upper) bound, only 2.5% of the time would we expect a test-retest correlation as large (small) as we have found (*Language for Communicating Frequentist Results about Treatment Effects*, 2018). Thus, true values of 1-week test-retest reliability outside these intervals are contradicted by the data (with an error rate of 5%). Variable labels: Resp[%]. Response rate (%); AccResp[%]. Accurate responses under certainty (% of correct responses);

GenRespTend[%]. General response tendency (% of 'left' response); ProcSpeed[RT]. General perceptual speed (RT to expected certain stimuli, ms); AmbSlow[RT]. Perceptual inference speed under uncertainty (RT to unexpected minus expected, ms); AmbRespTend[%]. Response tendency under uncertainty (% of 'left' response); SensPriming[%]. Sensory priming effect under uncertainty (% consistent with perceptual decision on previous unambiguous trial); PercPriming[%]. Perceptual decision priming effect under uncertainty (% consistent with perceptual decision on previous ambiguous trial); AssocLearnIrregSlow[RT]. Associative learning effect under certainty - cost of irregularity (ms RT); AssocLearnIrregInacc[%]. Associative learning effect under certainty - cost of irregularity (% accurate responses); AssocLearnAmbCue[%]. Associative learning effect under uncertainty - cue-consistency (congruent cues); AssocLearnAmbAuditory[%]. Associative learning effect under uncertainty - auditory dominance (incongruent cues).

$p < 0.05$; $p < 0.01$; $p < 0.001$

Exploratory analyses: internal structure of perceptual inference indicators and their relationship with schizotypal traits

We conducted Spearman's rank order correlation analyses using age, gender, task-derived indicators and self-reported alterations of perception and cognition (i.e. schizotypal traits) (See Figure 3.) Given that our sample is rather low in the context of cross-method individual difference research (Eisenberg et al., 2019; Owens et al., 2020), these analyses are highly exploratory; nevertheless, if consistent patterns emerge across sessions, it may facilitate the generation of hypotheses.

First, we found moderate positive correlations between measures of higher-level priors (the extent of slowing down to less predictable unambiguous targets, the proportion of cue-consistent decisions on ambiguous trials, and the proportion of decisions consistent with the acoustic cue on ambiguous trials where the cues were conflicting) in both sessions. These variables seemed to positively correlate with the extent of slowing down when faced with ambiguous (vs. unambiguous) targets. Additionally, we observed strong positive correlations between some of the indicators of lower-level priors: sensory and perceptual priming (proportion of decisions on ambiguous trials consistent with the decision on the previous unambiguous and ambiguous trial, respectively) were positively associated across individuals. Furthermore, it is noticeable that these two sets of variables (that putatively indicate the effects of higher- vs. lower-level priors) were weakly and negatively correlated with each other. There was a particularly strong and consistent negative association between perceptual priming and the effect of congruent cues on perceptual decisions in ambiguity.

Although we considered response tendency in ambiguity as an additional form of lower-level priors, it was not related neither to sensory nor to perceptual priming. Instead, a tendency towards 'left' responses on ambiguous trials had a trivial association with general response tendency. Neither age or gender demonstrated any consistent and robust association with individual differences in task performance.

Finally, disorganised, positive and negative schizotypy all were both consistently and negatively correlated with slowing down to irregular (vs. regular) unambiguous targets and they also negatively correlated with response accuracy on unambiguous trials, which may suggest a general tendency to rely more on expectations and less on sensory input. These associations seem to be the most pronounced for disorganisation. Additionally, disorganisation was also positively related to sensory and perceptual priming. In contrast, negative schizotypy was positively associated with indicators of higher-level priors (based on associative learning) while it was negatively linked to indicators of lower-level priors (sensory and perceptual priming).

Figure 3. Correlations between task performance, schizotypal traits and demographics. Spearman's rank order correlation of each variable. Lower triangle: session 1, upper triangle: session 2, diagonal: test-retest. Variable labels: 1: age; 2: gender (higher [blue] = males score higher); 3: Resp[%]. Response rate (%); 4: AccResp[%]. Accurate responses under certainty (% of correct responses); 5: GenRespTend[%]. General response tendency (% of 'left' response); 6: ProcSpeed[RT]. General perceptual speed (RT to expected certain stimuli, ms); 7: AmbSlow[RT]. Perceptual inference speed under uncertainty (RT to unexpected minus expected, ms); 8: AmbRespTend[%]. Response tendency under uncertainty (% of 'left' response); 9: SensPriming[%]. Sensory priming effect under uncertainty (% consistent with perceptual decision on previous unambiguous trial); 10: PercPriming[%]. Perceptual decision priming effect under uncertainty (% consistent with perceptual decision on previous ambiguous trial); 11: AssocLearnIrregSlow[RT]. Associative learning effect under certainty - cost of irregularity (ms RT); 12: AssocLearnIrregInacc[%]. Associative learning effect under certainty - cost of irregularity (% accurate responses); 13: AssocLearnAmbCue[%]. Associative learning effect under uncertainty - cue-consistency (congruent cues); 14: AssocLearnAmbAuditory[%]. Associative learning effect under uncertainty - auditory dominance (incongruent cues); 15: CogDis. Cognitive disorganisation - O-Life subscale sum; 16: UnEx. Unusual experiences - O-Life subscale sum; 17: IntAnh. Introvertive anhedonia - O-Life subscale sum

Discussion

Perception can be seen as an unconscious inference that combines sensory input with prior expectations in an uncertainty-weighted manner: when input is impoverished, prior knowledge of the observer will play a greater role in determining what is perceived (de Lange et al., 2018; Fiser et al., 2010; Friston, 2009). Such prior expectations may have multiple sources (de Lange et al., 2018): one may distinguish between lower-level expectations based on frequency statistics of the environment (e.g. in general, some stimuli might be more common than others) and higher-level expectations based on conditional probabilities (e.g. some stimuli are more likely to occur in certain temporal or spatial contexts). In the present study, we demonstrated within a single experiment that perception of ambiguous visual stimuli in a changing, multimodal setting is simultaneously influenced by higher- and lower-level prior expectations. Interestingly, when higher-level priors from different modalities were conflicting, auditory (as compared to visual) cues had a stronger influence on the perception of ambiguous visual stimuli. There was substantial variability across individuals in behavioural performance and this variation was temporally stable. This suggests that such perceptual inference tasks might be suitable tools for large-scale biomarker studies (Chan & Gottesman, 2008) and personality neuroscience research (Clark & Watson, 2019; Montag et al., 2020).

Our study adds to the growing knowledge about how different expectations shape perceptual decisions under ambiguity. Here, building upon an elegant experimental paradigm (Weilnhhammer et al., 2018), we found that auditory information had a dominant influence on perception of ambiguous stimuli when the cues were conflicting. This may reflect the brain's tendency to infer that the visual target stimuli and the auditory (but not

the visual) cue preceding were caused by a common source, so it may integrate them into a single perceptual object representation (Deroy et al., 2016). Alternatively, the representation of the overall precision of the visual modality might be reduced by the presence of ambiguous visual targets, thereby ultimately downweighting the salience of visual information in learning and predictive processing (Friston, 2009). Indeed, unreliable feedback reduces accuracy and deteriorates representation of visual stimuli in the visual cortex (Varrier et al., 2020). Furthermore, we show that perceptual decisions are comparably influenced by expectations of multiple origin (see effect sizes in Table 1.). How such different expectations interact to shape perception and imagery is an outstanding question in cognitive science (de Lange et al., 2018; Pearson, 2019). We found that sensation and perception on the preceding unambiguous and ambiguous trial, respectively, both had an impact on perception of subsequent ambiguous stimuli. It has been argued that such forms of expectations may rely on relatively simple computations implemented within sensory areas (in this case, the visual system) (de Lange et al., 2018). In addition, we demonstrated that multisensory associative learning also influenced the perception of ambiguous stimuli, and such audio-visual integration is likely to be implemented by higher-order multimodal brain regions (de Lange et al., 2018). Relatedly, Weinhhammer et al (2018) have found that lower-level expectations correlated with activation in the retinotopic visual cortex, while higher-level expectations correlated with activation in the orbitofrontal cortex and the hippocampus. It has been suggested that the orbitofrontal cortex is anatomically well-suited to encode the actual task state with high complexity (Wilson et al., 2014). Although state representations encoded in the activation patterns of lower-order sensory areas can be utilised by more elementary reinforcement learning or decision making mechanisms, more complex representations and their integration in the higher-order orbitofrontal cortex might support finely-tuned learning and behavioural adaptation (Walton et al., 2010). In addition, pattern completion in the hippocampus may support the reinstatement of activation patterns representing the expected visual stimuli in the early visual cortex (Hindy et al., 2016).

Individual differences in perceptual inference were highly stable over a one-week interval (median ICC = 0.83, range: 0.80 - 0.91, range of 95% CIs: 0.61 - 0.95)¹. The reliability of behavioural tasks as indicators of individual differences is often overlooked (Dang et al., 2020; Enkavi et al., 2019) despite the crucial importance of accurate measurement in the study of personality (Clark & Watson, 2019; Montag et al., 2020) and endophenotypes (Chan & Gottesman, 2008). Even well-established cognitive paradigms may have poor reliability due to a critical trade-off affecting their design (Hedge et al., 2018): differences between participants increase noise in the data when effects of experimental manipulations are of interest (Cronbach, 1957). Crucially, reliability values in our task are comparable to the highest literature standards for indicators derived from single tasks. Similarly high reliabilities have been documented for oculomotor control (mean ICC of the most reliable indicators from the antisaccade and the smooth pursuit tasks = 0.77, Ettinger et al., 2003; antisaccade error rate ICC = 0.90, Wöstmann et al., 2013), visual (mean r = 0.76, Xu et al., 2018), verbal (r 's range: 0.52 - 0.81, G. S. Waters & Caplan, 2003), and complex working memory capacity (r 's range: 0.67 - 0.81, Klein & Fiss, 1999) or response inhibition and interference control (mean ICC = 0.74, Wöstmann et al., 2013). Although we observed somewhat higher test-retest stabilities for the self-report schizotypy scores (ICC's range: 0.94 - 0.96, also see the diagonal in Figure 3), the reliability of the performance-based indicators of perceptual inference in our study is even comparable to that of self-report measures of self-regulation (ICC = 0.67, Enkavi et al., 2019). Importantly, our findings stand in strong contrast with the poor reliability of behavioural measures of self-regulation (median ICC = 0.31, Enkavi et al., 2019; stop-signal reaction time ICC = 0.03, Wöstmann et al., 2013), implicit learning of statistical structures in the perceptual, cognitive and motor domains (mean r = 0.32, Kalra et al., 2019), and task-related brain activation (mean ICC = 0.4, Elliott et al., 2020). These contrasting findings highlight how essential it is to establish the reliability of behavioural tasks prior to their application in clinical and personality

¹ The only exception was the increase in error rate when congruent cues were followed by an unexpected unambiguous stimulus (ICC = 0.24), however, this is not that surprising given that the increase in errors for unexpected vs. expected unambiguous stimuli was minuscule (3% and 0% for session 1 and 2, respectively), in line with the notion that expectations are less likely to influence perceptual decisions when stimuli are certain (de Lange et al., 2018).

neuroscience (Chan & Gottesman, 2008; Clark & Watson, 2019; Montag et al., 2020). Strikingly, to our best knowledge, relatively little information is available on the reliability of indicators derived from perceptual inference tasks, despite the growing interest towards them in clinical neuroscience (Sterzer et al., 2018). Although simulations can be used to estimate the accuracy of parameter recovery with a given number of trials (i.e. internal consistency reliability within a single session) (Wilson & Collins, 2019), they are uninformative whether the indicator captures a temporally stable, trait-like feature. Nevertheless, some data suggested that individual differences in perceptual inference can be reliably measured. For instance, a behavioural measure of visual imagery strength has been found to have outstanding test-retest reliability ($r = 0.86$ over 2 weeks) (Bergmann et al., 2016). Others have shown that individuals are characterised by a unique profile of switching between percepts of multistable auditory stimuli and that switching patterns correlate not only with cognitive control and ego resiliency (a personality trait reflecting flexible adaptation) (Farkas et al., 2016) but also with glutamate–glutamine (Glx) and gamma-aminobutyric acid (GABA) concentrations in sensory and frontal areas, respectively (Kondo et al., 2017). Although these preliminary findings are encouraging and perceptual inference tasks seem to capture variation relevant to the psychosis-spectrum (Sterzer et al., 2018), lack of knowledge about the reliability of the measures and the stability of individual differences may limit the progress of this promising avenue of research. Thus, future studies should assess the temporal stability of perceptual inference and its neural correlates over longer intervals and in other populations². Establishing stability in clinical individuals would be crucial prior to the application of the paradigm in longitudinal observational and intervention studies.

Drawing on brain imaging studies, one may formulate hypotheses about the potential neurobiological correlates of our behavioural findings. There is evidence that perceptual decisions in ambiguity are governed by neural representations in the primary visual cortex: seeing the first element of a learned sequence of moving dots induces retinotopically specific but temporally compressed replaying of visual sequences in the early visual cortex, which may cause the experience of illusory motion (Ekman et al., 2017). Relatedly, imagery strength is negatively related to the surface of the primary and the secondary visual cortices, while imagery precision shows an opposite association (Bergmann et al., 2016). As imagery strength may reflect strong influence of priors while imagery precision could indicate increased sensory precision (i.e. likelihood) (see Pearson, 2019), we are tempted to speculate that stronger influence of higher-level priors in our task might be caused by a smaller surface of the primary and secondary visual cortices. Furthermore, sensory priming, mirroring the effect of lower-level priors, might be mediated by the activation of sensory representations in visual areas, which can occur even in the absence of sensory stimulation (de Lange et al., 2018). For instance, in individuals with the ‘visual snow’ syndrome (who repeatedly see miniscule, flickering dots), hypermetabolism of the right lingual gyrus and the left cerebellar anterior lobe has been reported (Schankin et al., 2014). Interestingly, such individuals also report various additional lower-level, non-meaningful perceptual experiences (e.g. seeing afterimages or photopsia). Another study suggests that the surface area of the primary visual cortex predicts the distinctiveness of subtle differences in orientation, but it is negatively related to modulation by the global context (Song et al., 2013). Based on the above studies, we predict that individuals in whom higher-level priors largely influenced perception of ambiguous stimuli, the visual cortices have reduced volume and decreased resting activation. On the other hand, individual variation in the effects of lower-level priors might be associated with structural and functional differences within the visual system.

² Reaction times on unambiguous trials where target stimuli are unambiguous were also highly reliable. This variable may reflect processing speed, a core aspect of intelligence (Redick et al., 2012). A study has found that perceptual speed was specifically related to increased task-related activation in various visual areas, the left thalamus and precentral gyrus, and the right insula, while it predicted decreased activation in the precuneus, the insula, the angular gyrus and some frontal and temporal areas (Habeck et al., 2014). Others have shown that white matter integrity in the parietal and temporal lobes bilaterally and in the left middle frontal gyrus predicted processing speed (Turken et al., 2008). We speculate that differences in perceptual speed in our task might covary with neural indicators of processing efficiency in the visual and the motor system and in their efficient top-down control by the dorsal attentional system (Petersen & Posner, 2012).

In addition, variation in perceptual inference might be related to differences in neuromodulation, that are known to be partially genetically determined. The glutamatergic (NMDA), dopaminergic and cholinergic systems can be of particular relevance here. Neuropharmacological and neuropathological studies on psychosis spectrum suggest abnormal neuromodulation (e.g. NMDA-R hypofunction) of superficial cortical neurons, which cells are responsible for the encoding of precision of prediction errors (Adams et al., 2013). NMDA modulation is composed of several parts and occurs on different timescales (postsynaptic excitatory potential induction, synaptic coincidence detection, synaptic input integration, plasticity and role in long-term synaptic depression or potentiation). However, neurotransmitter systems do not operate in isolation: NMDA-receptor inhibition (e.g. by ketamine) might lead to dopamine dysregulation. Relatedly, dopaminergic neurotransmission is essential for adaptive learning as it modulates the precision of prediction errors in the cortex (Haarsma et al., 2020), and in the midbrain and the striatum, it is associated with goal-relevant belief updating (Nour et al., 2018). In addition, the precision of sensory representations is enhanced by cholinergic (but not dopaminergic or noradrenergic) stimulation, which ultimately increases weighting of sensory evidence during perceptual inference that is behaviourally reflected in enhanced perceptual discrimination performance and attenuated psychotic symptoms. In contrast, cholinergic blockade reduces the precision of sensory representations and reduces tendency toward sensory evidence, which causes hallucinatory experiences and enhances conditioned hallucinations (reviewed by Corlett & Powers, 2018). Finally, increased noradrenergic (but not cholinergic) neurotransmission was shown to destabilise the perception of ambiguous stimuli by increasing cortical excitability and altering cortical connectivity (Pfeffer et al., 2018), while increased GABAergic activity seems to stabilise bistable perception (Kondo et al., 2018; van Loon et al., 2013). As our results indicate that our task reliably captures stable differences, it could be a suitable tool in future psychopharmacological studies of perceptual inference.

Furthermore, based on the predictive coding accounts of psychosis, one may also speculate how the observed differences in task performance would relate to psychosis-spectrum traits and symptoms. Some studies have implicated that psychotic phenomena are related to the dominance of expectations in perceptual inference (i.e. strong reliance on priors) (Corlett et al., 2019; Davies et al., 2018; Teufel et al., 2015) while others have found that perceptual anomalies and hallucinations in patients with schizophrenia are related to increased sensitivity to sensory evidence (i.e. likelihood) (Weilnhhammer et al., 2020). Disturbances of auditory and visual perception were found in patients with schizophrenia and also among their unaffected first-degree relatives, suggesting a familial/genetic liability behind these alterations (Force et al., 2008; P. Li et al., 2017; Ramsay et al., 2020; Sponheim et al., 2013). In line with the idea that activation of sensory areas are involved in the representation of perceptual experiences (Pearson, 2019), auditory hallucinations were found to correlate with activation in the associative auditory cortex and the superior temporal gyrus (Horga & Abi-Dargham, 2019), while visual hallucinations seem to be accompanied by increased activity of the visual association cortex (F. Waters et al., 2014). In individuals with schizotypal personality disorder, imagery strength is enhanced while early visual perception appears intact (Maróthi & Kéri, 2018). The formation of prior expectations and prediction errors is also altered along the psychosis-spectrum, as indicated by impaired mismatch negativity, a brain response to violation of sensory regularities (Farkas et al., 2015; Fitzgerald & Todd, 2020; Koshiyama et al., 2020; Michie et al., 2002; Näätänen et al., 2016; Stefanics et al., 2014), that may reflect precision-weighted prediction errors (Stefanics et al., 2018). Relatedly, nonclinical individuals reporting psychotic-like experiences demonstrate deficient learning of regularities and inference on a sensory task, and this deficit was associated with impaired mismatch negativity (Dzafic et al., 2020).

We conducted exploratory analyses to investigate the association between task performance and schizotypal traits that may facilitate hypothesis generation. Interestingly, individuals showing high levels of schizotypy were less likely to respond slower on ambiguous trials and to make more errors on unambiguous trials, which may indicate increased reliance on priors and reduced sensory precision. As all dimensions of schizotypy showed these associations, one may speculate that this tendency is related to disorganisation, a core feature of the psychosis-spectrum phenotype (Polner et al., 2019). On a related note, disorganisation has been linked to a deficit of visual

perceptual organisation, probably indicating impaired modulation by contextual expectations (Uhlhaas et al., 2005). Interestingly, negative schizotypy was related to increased reliance on higher-level priors and reduced influence of lower-level priors. Although this finding is preliminary, it may indicate that predictive coding accounts of psychosis (Sterzer et al., 2018) should consider going beyond psychosis and consider the motivational, hedonic and social impairment that lie at the core of negative schizotypy (Chang et al., 2020). Finally, differences in multimodal sensory integration have previously been linked to variation in the functioning of the cerebellum. Reduced cerebellar activity and disrupted connectivity during auditory-visual integration was found in patients with schizophrenia and, to an intermediate extent, in their non-clinical siblings (Z. Li et al., 2020). Together with twin data suggesting its heritability, multisensory integration deficit may serve as an endophenotype of schizophrenia. Relatedly, auditory cue dominance in our task arguable reflects multisensory integration (Deroy et al., 2016; Weinhhammer et al., 2018). High-powered future studies should establish how multisensory integration in our task relates to psychosis-spectrum traits and symptoms.

Conclusions and future directions

Overall, we conducted an experiment where higher- and lower-level effects (associative learning and priming) on perceptual inference were both present. We found that predictive processes can be captured by response tendencies and reaction times, furthermore, that for some auditory (but not visual) associative cues dominantly influence perceptual decisions about uncertain visual targets. Individual differences were evident in the data and the reliability of such differences were very high. We conducted exploratory analyses regarding association with schizotypal traits, which may open up novel research directions.

Prior to moving forward to combining the paradigm with neuroimaging and administering it to individuals facing mental health problems, a next logical step would be the explicit mathematical modelling of the underlying computational processes (e.g. uncertainty-weighting or multisensory integration). The idea that perception is the inferred posterior estimate of expectations and sensory evidence makes it possible to model the underlying calculations, based on prior and likelihood distributions. Uncertainty, precision and volatility are properties of the environment which can be characterized in a Bayesian framework. It has been shown that the Hierarchical Gaussian Filter (Mathys et al., 2014) is suitable for accessing individual parameters of associative learning in perceptual decision tasks with varying levels of uncertainty (Lawson et al., 2017; Weinhhammer et al., 2018). Now that we established that this paradigm is capable of identifying trait-like differences at the behavioural level, the next step is to see whether they can be explained by diverse computational mechanisms, which are based on detailed temporal information. Furthermore, this will also allow examining the temporal stability of computational parameters.

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References

- Adams, R. A., Stephan, K. E., Brown, H. R., Frith, C. D., & Friston, K. J. (2013). The computational anatomy of psychosis. *Frontiers in Psychiatry*, 4, 47. <https://doi.org/10.3389/fpsyt.2013.00047>
- Allaire, J. J., Xie [aut, Y., cre, McPherson, J., Luraschi, J., Ushey, K., Atkins, A., Wickham, H., Cheng, J.,

- Chang, W., Iannone, R., Dunning, A., filter), A. Y. (Number sections L., Schloerke, B., Dervieux, C., Aust, F., Allen, J., Seo, J., Barrett, M., ... filter), A. K. (pagebreak L. (2020). *rmarkdown: Dynamic Documents for R* (2.5) [Computer software]. <https://CRAN.R-project.org/package=rmarkdown>
- Auguie, B., & Antonov, A. (2017). *gridExtra: Miscellaneous Functions for 'Grid' Graphics* (2.3) [Computer software]. <https://CRAN.R-project.org/package=gridExtra>
- Aust, F. (2020). *Crsh/papaja* [R]. <https://github.com/crsh/papaja> (Original work published 2014)
- Bach, D. R., & Dolan, R. J. (2012). Knowing how much you don't know: A neural organization of uncertainty estimates. *Nature Reviews Neuroscience*, 13(8), 572–586. <https://doi.org/10.1038/nrn3289>
- Bergmann, J., Genç, E., Kohler, A., Singer, W., & Pearson, J. (2016). Smaller Primary Visual Cortex Is Associated with Stronger, but Less Precise Mental Imagery. *Cerebral Cortex*, 26(9), 3838–3850. <https://doi.org/10.1093/cercor/bhv186>
- Brogden, W. J. (1939). Sensory pre-conditioning. *Journal of Experimental Psychology*, 25(4), 323.
- Calkins, M. E., Iacono, W. G., & Curtis, C. E. (2003). Smooth pursuit and antisaccade performance evidence trait stability in schizophrenia patients and their relatives. *International Journal of Psychophysiology*, 49(2), 139–146. [https://doi.org/10.1016/S0167-8760\(03\)00101-6](https://doi.org/10.1016/S0167-8760(03)00101-6)
- Chan, R. C. K., & Gottesman, I. I. (2008). Neurological soft signs as candidate endophenotypes for schizophrenia: A shooting star or a Northern star? *Neuroscience and Biobehavioral Reviews*, 15.
- Chang, W. C., Strauss, G. P., Ahmed, A. O., Wong, S. C. Y., Chan, J. K. N., Lee, E. H. M., Chan, S. K. W., Hui, C. L. M., James, S. H., Chapman, H. C., & Chen, E. Y. H. (2020). The Latent Structure of Negative Symptoms in Individuals With Attenuated Psychosis Syndrome and Early Psychosis: Support for the 5 Consensus Domains. *Schizophrenia Bulletin*, sbaa129. <https://doi.org/10.1093/schbul/sbaa129>
- Clark, L. A., & Watson, D. (2019). Constructing validity: New developments in creating objective measuring instruments. *Psychological Assessment*, 31(12), 1412–1427. <https://doi.org/10.1037/pas0000626>

- Cohen, A. S., Matthews, R. A., Najolia, G. M., & Brown, L. A. (2010). Toward a more psychometrically sound brief measure of schizotypal traits: Introducing the SPQ-Brief Revised. *Journal of Personality Disorders*, 24(4), 516–537. <https://doi.org/10.1521/pedi.2010.24.4.516>
- Corlett, P. R., Horga, G., Fletcher, P. C., Alderson-Day, B., Schmack, K., & Powers, A. R. (2019). Hallucinations and Strong Priors. *Trends in Cognitive Sciences*, 23(2), 114–127. <https://doi.org/10.1016/j.tics.2018.12.001>
- Corlett, P. R., & Powers, A. R. (2018). Conditioned hallucinations: Historic insights and future directions. *World Psychiatry*, 17(3), 361–362. <https://doi.org/10.1002/wps.20557>
- Corn-Becker, F., Welch, L., Fisichelli, V., & Toback, E. (1949). Factors Productive of Conditioned Images or Sensations. *The Pedagogical Seminary and Journal of Genetic Psychology*, 75(2), 149–164. <https://doi.org/10.1080/08856559.1949.10533515>
- Cronbach, L. J. (1957). The two disciplines of scientific psychology. *American Psychologist*, 12(11), 671–684. <https://doi.org/10.1037/h0043943>
- Dai, M., Li, Y., Gan, S., & Du, F. (2019). The reliability of estimating visual working memory capacity. *Scientific Reports*, 9(1), 1155. <https://doi.org/10.1038/s41598-019-39044-1>
- Dang, J., King, K. M., & Inzlicht, M. (2020). Why Are Self-Report and Behavioral Measures Weakly Correlated? *Trends in Cognitive Sciences*, 24(4), 267–269. <https://doi.org/10.1016/j.tics.2020.01.007>
- Davies, D. J., Teufel, C., & Fletcher, P. C. (2018). Anomalous Perceptions and Beliefs Are Associated With Shifts Toward Different Types of Prior Knowledge in Perceptual Inference. *Schizophrenia Bulletin*, 44(6), 1245–1253. <https://doi.org/10.1093/schbul/sbx177>
- de Lange, F. P., Heilbron, M., & Kok, P. (2018). How Do Expectations Shape Perception? *Trends in Cognitive Sciences*, 22(9), 764–779. <https://doi.org/10.1016/j.tics.2018.06.002>
- Deroy, O., Spence, C., & Noppeney, U. (2016). Metacognition in Multisensory Perception. *Trends in Cognitive Sciences*, 20(10), 736–747. <https://doi.org/10.1016/j.tics.2016.08.006>

- Dzafic, I., Randeniya, R., Harris, C. D., Bammel, M., & Garrido, M. I. (2020). Statistical Learning and Inference Is Impaired in the Nonclinical Continuum of Psychosis. *Journal of Neuroscience*, 40(35), 6759–6769. <https://doi.org/10.1523/JNEUROSCI.0315-20.2020>
- Eisenberg, I. W., Bissett, P. G., Zeynep Enkavi, A., Li, J., MacKinnon, D. P., Marsch, L. A., & Poldrack, R. A. (2019). Uncovering the structure of self-regulation through data-driven ontology discovery. *Nature Communications*, 10(1), 2319. <https://doi.org/10.1038/s41467-019-10301-1>
- Ekman, M., Kok, P., & de Lange, F. P. (2017). Time-compressed preplay of anticipated events in human primary visual cortex. *Nature Communications*, 8(1), 15276. <https://doi.org/10.1038/ncomms15276>
- Elliott, M. L., Knodt, A. R., Ireland, D., Morris, M. L., Poulton, R., Ramrakha, S., Sison, M. L., Moffitt, T. E., Caspi, A., & Hariri, A. R. (2020). What Is the Test-Retest Reliability of Common Task-Functional MRI Measures? New Empirical Evidence and a Meta-Analysis. *Psychological Science*, 31(7), 792–806. <https://doi.org/10.1177/0956797620916786>
- Ellson, D. G. (1941). Hallucinations produced by sensory conditioning. *Journal of Experimental Psychology*, 28(1), 1–20. <https://doi.org/10.1037/h0054167>
- Enkavi, A. Z., Eisenberg, I. W., Bissett, P. G., Mazza, G. L., MacKinnon, D. P., Marsch, L. A., & Poldrack, R. A. (2019). Large-scale analysis of test–retest reliabilities of self-regulation measures. *Proceedings of the National Academy of Sciences*, 116(12), 5472–5477. <https://doi.org/10.1073/pnas.1818430116>
- Ettinger, U., Kumari, V., Crawford, T. J., Davis, R. E., Sharma, T., & Corr, P. J. (2003). Reliability of smooth pursuit, fixation, and saccadic eye movements. *Psychophysiology*, 40(4), 620–628.
- Farkas, D., Denham, S. L., Bendixen, A., Tóth, D., Kondo, H. M., & Winkler, I. (2016). Auditory Multi-Stability: Idiosyncratic Perceptual Switching Patterns, Executive Functions and Personality Traits. *PLOS ONE*, 11(5), e0154810. <https://doi.org/10.1371/journal.pone.0154810>
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, 41(4), 1149–1160.

<https://doi.org/10.3758/BRM.41.4.1149>

Fiser, J., Berkes, P., Orbán, G., & Lengyel, M. (2010). Statistically optimal perception and learning: From behavior to neural representations. *Trends in Cognitive Sciences*, 14(3), 119–130.

<https://doi.org/10.1016/j.tics.2010.01.003>

Fonseca-Pedrero, E., Ortuño-Sierra, J., Mason, O. J., & Muñiz, J. (2015). The Oxford–Liverpool Inventory of Feelings and Experiences short version: Further validation. *Personality and Individual Differences*, 86, 338–343. <https://doi.org/10.1016/j.paid.2015.06.041>

Force, R. B., Venables, N. C., & Sponheim, S. R. (2008). An Auditory Processing Abnormality Specific to Liability for Schizophrenia. *Schizophrenia Research*, 103(0).

<https://doi.org/10.1016/j.schres.2008.04.038>

Fox, J., Weisberg, S., & Price, B. (2020). *carData: Companion to Applied Regression Data Sets* (3.0-4) [Computer software]. <https://CRAN.R-project.org/package=carData>

Fox, J., Weisberg, S., Price, B., Friendly, M., Hong, J., Andersen, R., Firth, D., Taylor, S., & R Core Team. (2020). *effects: Effect Displays for Linear, Generalized Linear, and Other Models* (4.2-0) [Computer software]. <https://CRAN.R-project.org/package=effects>

Friston, K. (2009). The free-energy principle: A rough guide to the brain? *Trends in Cognitive Sciences*, 13(7), 293–301. <https://doi.org/10.1016/j.tics.2009.04.005>

Haarsma, J., Fletcher, P. C., Griffin, J. D., Taverne, H. J., Ziauddeen, H., Spencer, T. J., Miller, C., Katthagen, T., Goodyer, I., Diederer, K. M. J., & Murray, G. K. (2020). Precision weighting of cortical unsigned prediction error signals benefits learning, is mediated by dopamine, and is impaired in psychosis. *Molecular Psychiatry*. <https://doi.org/10.1038/s41380-020-0803-8>

Habeck, C., Steffener, J., Barulli, D., Gazes, Y., Razlighi, Q., Shaked, D., Salthouse, T., & Stern, Y. (2014). Making Cognitive Latent Variables Manifest: Distinct Neural Networks for Fluid Reasoning and Processing Speed. *Journal of Cognitive Neuroscience*, 27(6), 1249–1258.

https://doi.org/10.1162/jocn_a_00778

Harrell, F. E., & others, with contributions from C. D. and many. (2020). *Hmisc: Harrell Miscellaneous* (4.4-2)

[Computer software]. <https://CRAN.R-project.org/package=Hmisc>

Hedge, C., Powell, G., & Sumner, P. (2018). The reliability paradox: Why robust cognitive tasks do not produce reliable individual differences. *Behavior Research Methods*, 50(3), 1166–1186.

<https://doi.org/10.3758/s13428-017-0935-1>

Helfrich, R. F., Huang, M., Wilson, G., & Knight, R. T. (2017). Prefrontal cortex modulates posterior alpha oscillations during top-down guided visual perception. *Proceedings of the National Academy of Sciences*, 114(35), 9457–9462. <https://doi.org/10.1073/pnas.1705965114>

Helmholtz, H. von. (1867). *Concerning the perceptions in general*. In *Treatise on physiological optics, vol. III, 3rd edn* (translated by J. P. C. Southall 1925 *Opt. Soc. Am. Section 26*, reprinted New York: Dover, 1962).

Henson, R. N. A., & Rugg, M. D. (2003). Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia*, 41(3), 263–270. [https://doi.org/10.1016/S0028-3932\(02\)00159-8](https://doi.org/10.1016/S0028-3932(02)00159-8)

Hindy, N. C., Ng, F. Y., & Turk-Browne, N. B. (2016). Linking pattern completion in the hippocampus to predictive coding in visual cortex. *Nature Neuroscience*, 19(5), 665–667. <https://doi.org/10.1038/nn.4284>

Hockey, A., & Geffen, G. (2004). The concurrent validity and test–retest reliability of a visuospatial working memory task. *Intelligence*, 32(6), 591–605. <https://doi.org/10.1016/j.intell.2004.07.009>

Horga, G., & Abi-Dargham, A. (2019). An integrative framework for perceptual disturbances in psychosis. *Nature Reviews Neuroscience*, 20(12), 763–778. <https://doi.org/10.1038/s41583-019-0234-1>

Kalra, P. B., Gabrieli, J. D. E., & Finn, A. S. (2019). Evidence of stable individual differences in implicit learning. *Cognition*, 190, 199–211. <https://doi.org/10.1016/j.cognition.2019.05.007>

Kassambara, A. (2019). *ggcorrplot: Visualization of a Correlation Matrix using 'ggplot2'* (0.1.3) [Computer

software]. <https://CRAN.R-project.org/package=ggcorrplot>

Kassambara, A., & Mundt, F. (2020). *factoextra: Extract and Visualize the Results of Multivariate Data Analyses* (1.0.7) [Computer software]. <https://CRAN.R-project.org/package=factoextra>

Klein, K., & Fiss, W. H. (1999). The reliability and stability of the turner and Engle working memory task. *Behavior Research Methods, Instruments, & Computers*, 31(3), 429–432.
<https://doi.org/10.3758/BF03200722>

Klüver, H. (1928). Studies on the eidetic type and on eidetic imagery. *Psychological Bulletin*, 25(2), 69–104.
<https://doi.org/10.1037/h0070849>

Kok, P., Failing, M. F., & de Lange, F. P. (2014). Prior Expectations Evoke Stimulus Templates in the Primary Visual Cortex. *Journal of Cognitive Neuroscience*, 26(7), 1546–1554.
https://doi.org/10.1162/jocn_a_00562

Kondo, H. M., Farkas, D., Denham, S. L., Asai, T., & Winkler, I. (2017). Auditory multistability and neurotransmitter concentrations in the human brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1714), 20160110. <https://doi.org/10.1098/rstb.2016.0110>

Kondo, H. M., Pressnitzer, D., Shimada, Y., Kochiyama, T., & Kashino, M. (2018). Inhibition-excitation balance in the parietal cortex modulates volitional control for auditory and visual multistability. *Scientific Reports*, 8(1), 14548. <https://doi.org/10.1038/s41598-018-32892-3>

Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., & Poeppel, D. (2017). Neuroscience Needs Behavior: Correcting a Reductionist Bias. *Neuron*, 93(3), 480–490.
<https://doi.org/10.1016/j.neuron.2016.12.041>

Langen, J. van. (2020). *Jorvlan/open-visualizations* [Jupyter Notebook]. <https://github.com/jorvlan/open-visualizations> (Original work published 2020)

Language for communicating frequentist results about treatment effects. (2018, November 13). Datamethods Discussion Forum. <https://discourse.datamethods.org/t/language-for-communicating-frequentist->

- Lawson, R. P., Mathys, C., & Rees, G. (2017). Adults with autism over-estimate the volatility of the sensory environment. *Nature Neuroscience*, 20(9), 1293–1299. <https://doi.org/10.1038/nn.4615>
- Li, P., Fan, T.-T., Zhao, R.-J., Han, Y., Shi, L., Sun, H.-Q., Chen, S.-J., Shi, J., Lin, X., & Lu, L. (2017). Altered Brain Network Connectivity as a Potential Endophenotype of Schizophrenia. *Scientific Reports*, 7(1), 5483. <https://doi.org/10.1038/s41598-017-05774-3>
- Li, Z., Huang, J., Hung, K. S. Y., Deng, Y., Wang, Y., Wang, Y., Lui, S. S. Y., Mak, H. K. F., Sham, P. C., Cheung, E. F. C., Öngür, D., Dazzan, P., & Chan, R. C. K. (2020). Cerebellar hypoactivation is associated with impaired sensory integration in schizophrenia. *Journal of Abnormal Psychology*, No Pagination Specified-No Pagination Specified. <https://doi.org/10.1037/abn0000636>
- Macaluso, E., & Driver, J. (2005). Multisensory spatial interactions: A window onto functional integration in the human brain. *Trends in Neurosciences*, 28(5), 264–271. <https://doi.org/10.1016/j.tins.2005.03.008>
- Maksimenko, V. A., Kuc, A., Frolov, N. S., Khramova, M. V., Pisarchik, A. N., & Hramov, A. E. (2020). Dissociating Cognitive Processes During Ambiguous Information Processing in Perceptual Decision-Making. *Frontiers in Behavioral Neuroscience*, 14. <https://doi.org/10.3389/fnbeh.2020.00095>
- Maróthi, R., & Kéri, S. (2018). Enhanced mental imagery and intact perceptual organization in schizotypal personality disorder. *Psychiatry Research*, 259, 433–438. <https://doi.org/10.1016/j.psychres.2017.11.015>
- Mason, O., Linney, Y., & Claridge, G. (2005). Short scales for measuring schizotypy. *Schizophrenia Research*, 78(2), 293–296. <https://doi.org/10.1016/j.schres.2005.06.020>
- Mathys, C. D., Lomakina, E. I., Daunizeau, J., Iglesias, S., Brodersen, K. H., Friston, K. J., & Stephan, K. E. (2014). Uncertainty in perception and the Hierarchical Gaussian Filter. *Frontiers in Human Neuroscience*, 8. <https://doi.org/10.3389/fnhum.2014.00825>
- Montag, C., Ebstein, R. P., Jawinski, P., & Markett, S. (2020). Molecular genetics in psychology and personality

neuroscience: On candidate genes, genome wide scans, and new research strategies. *Neuroscience & Biobehavioral Reviews*, 118, 163–174. <https://doi.org/10.1016/j.neubiorev.2020.06.020>

Nour, M. M., Dahoun, T., Schwartenbeck, P., Adams, R. A., FitzGerald, T. H. B., Coello, C., Wall, M. B., Dolan, R. J., & Howes, O. D. (2018). Dopaminergic basis for signaling belief updates, but not surprise, and the link to paranoia. *Proceedings of the National Academy of Sciences*, 115(43), E10167–E10176. <https://doi.org/10.1073/pnas.1809298115>

Owens, M. M., Potter, A., Hyatt, C., Albaugh, M., Thompson, W. K., Jernigan, T., Yuan, D., Hahn, S., Allgaier, N., & Garavan, H. (2020). *Recalibrating expectations about effect size: A multi-method survey of effect sizes in the ABCD study*. PsyArXiv.

Pailian, H., & Halberda, J. (2015). The reliability and internal consistency of one-shot and flicker change detection for measuring individual differences in visual working memory capacity. *Memory & Cognition*, 43(3), 397–420. <https://doi.org/10.3758/s13421-014-0492-0>

Patil, I. (2020). *ggstatsplot: 'ggplot2' Based Plots with Statistical Details* (0.6.6) [Computer software]. <https://CRAN.R-project.org/package=ggstatsplot>

Pear, T. H. (1925). Modern Investigations of Mental Imagery. *Nature*, 115(2900), 853–853. <https://doi.org/10.1038/115853a0>

Pearson, J. (2019). The human imagination: The cognitive neuroscience of visual mental imagery. *Nature Reviews Neuroscience*, 20(10), 624–634. <https://doi.org/10.1038/s41583-019-0202-9>

Pearson, J., Clifford, C. W. G., & Tong, F. (2008). The Functional Impact of Mental Imagery on Conscious Perception. *Current Biology*, 18(13), 982–986. <https://doi.org/10.1016/j.cub.2008.05.048>

Petersen, S. E., & Posner, M. I. (2012). The Attention System of the Human Brain: 20 Years After. *Annual Review of Neuroscience*, 35(1), 73–89. <https://doi.org/10.1146/annurev-neuro-062111-150525>

Pfeffer, T., Avramiea, A.-E., Nolte, G., Engel, A. K., Linkenkaer-Hansen, K., & Donner, T. H. (2018). Catecholamines alter the intrinsic variability of cortical population activity and perception. *PLoS*

Biology, 16(2), e2003453. <https://doi.org/10.1371/journal.pbio.2003453>

- Polner, B., Faiola, E., Urquijo, M. F., Meyhöfer, I., Steffens, M., Rónai, L., Koutsouleris, N., & Ettinger, U. (2019). The network structure of schizotypy in the general population. *European Archives of Psychiatry and Clinical Neuroscience*. <https://doi.org/10.1007/s00406-019-01078-x>
- Polner, B., Simor, P., & Kéri, S. (2018). Insomnia and intellect mask the positive link between schizotypal traits and creativity. *PeerJ*, 6. <https://doi.org/10.7717/peerj.5615>
- Powers, A. R., Mathys, C., & Corlett, P. R. (2017). Pavlovian conditioning–induced hallucinations result from overweighting of perceptual priors. *Science*, 357(6351), 596–600. <https://doi.org/10.1126/science.aan3458>
- R Core Team. (2019). *R: The R Project for Statistical Computing* [Methodology Reference]. <https://www.eea.europa.eu/data-and-maps/indicators/oxygen-consuming-substances-in-rivers/r-development-core-team-2006>
- Ramsay, I. S., Schallmo, M.-P., Biagianti, B., Fisher, M., Vinogradov, S., & Sponheim, S. R. (2020). Deficits in Auditory and Visual Sensory Discrimination Reflect a Genetic Liability for Psychosis and Predict Disruptions in Global Cognitive Functioning. *Frontiers in Psychiatry*, 11. <https://doi.org/10.3389/fpsy.2020.00638>
- Redick, T. S., Unsworth, N., Kelly, A. J., & Engle, R. W. (2012). Faster, smarter? Working memory capacity and perceptual speed in relation to fluid intelligence. *Journal of Cognitive Psychology*, 24(7), 844–854. <https://doi.org/10.1080/20445911.2012.704359>
- Revelle, W. (2020). *psych: Procedures for Psychological, Psychometric, and Personality Research* (2.0.9) [Computer software]. <https://CRAN.R-project.org/package=psych>
- Richter, C. G., Thompson, W. H., Bosman, C. A., & Fries, P. (2017). Top-Down Beta Enhances Bottom-Up Gamma. *Journal of Neuroscience*, 37(28), 6698–6711. <https://doi.org/10.1523/JNEUROSCI.3771-16.2017>

- Robinson, D., Hayes [aut, A., cre, Couch, S., Patil, I., Chiu, D., Gomez, M., Demeshev, B., Menne, D., Nutter, B., Johnston, L., Bolker, B., Briatte, F., Arnold, J., Gabry, J., Selzer, L., Simpson, G., Preussner, J., Hesselberth, J., ... Wiernik, B. M. (2020). *broom: Convert Statistical Objects into Tidy Tibbles* (0.7.2) [Computer software]. <https://CRAN.R-project.org/package=broom>
- Sarkar, D., Andrews, F., Wright (documentation), K., Klepeis, N., & Murrell, P. (2020). *lattice: Trellis Graphics for R* (0.20-41) [Computer software]. <https://CRAN.R-project.org/package=lattice>
- Schacter, D. L. (1992). Priming and Multiple Memory Systems: Perceptual Mechanisms of Implicit Memory. *Journal of Cognitive Neuroscience*, 4(3), 244–256. <https://doi.org/10.1162/jocn.1992.4.3.244>
- Schankin, C. J., Maniyar, F. H., Sprenger, T., Chou, D. E., Eller, M., & Goadsby, P. J. (2014). The Relation Between Migraine, Typical Migraine Aura and “Visual Snow”. *Headache: The Journal of Head and Face Pain*, 54(6), 957–966. <https://doi.org/10.1111/head.12378>
- Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., Elberg, A., Toomet, O., Crowley, J., Hofmann, H., & Wickham, H. (2020). *GGally: Extension to 'ggplot2'* (2.0.0) [Computer software]. <https://CRAN.R-project.org/package=GGally>
- Schmack, K., Castro, A. G.-C. de, Rothkirch, M., Sekutowicz, M., Rössler, H., Haynes, J.-D., Heinz, A., Petrovic, P., & Sterzer, P. (2013). Delusions and the Role of Beliefs in Perceptual Inference. *Journal of Neuroscience*, 33(34), 13701–13712. <https://doi.org/10.1523/JNEUROSCI.1778-13.2013>
- Schmack, K., Schnack, A., Priller, J., & Sterzer, P. (2015). Perceptual instability in schizophrenia: Probing predictive coding accounts of delusions with ambiguous stimuli. *Schizophrenia Research: Cognition*, 2(2), 72–77. <https://doi.org/10.1016/j.scog.2015.03.005>
- Slegers, W. (2020). *tidystats: Save Output of Statistical Tests* (0.5) [Computer software]. <https://CRAN.R-project.org/package=tidystats>
- Song, C., Schwarzkopf, D. S., & Rees, G. (2013). Variability in visual cortex size reflects tradeoff between local orientation sensitivity and global orientation modulation. *Nature Communications*, 4(1), 2201.

<https://doi.org/10.1038/ncomms3201>

Sponheim, S. R., Sass, S. M., Noukki, A. L., & Hegeman, B. M. (2013). Fragile Early Visual Percepts Mark Genetic Liability Specific to Schizophrenia. *Schizophrenia Bulletin*, 39(4), 839–847.

<https://doi.org/10.1093/schbul/sbs041>

Sterzer, P., Adams, R. A., Fletcher, P., Frith, C., Lawrie, S. M., Muckli, L., Petrovic, P., Uhlhaas, P., Voss, M., & Corlett, P. R. (2018). The Predictive Coding Account of Psychosis. *Biological Psychiatry*, 84(9), 634–643. <https://doi.org/10.1016/j.biopsych.2018.05.015>

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M.-M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, 11(9), 1004–1006.

<https://doi.org/10.1038/nn.2163>

Teufel, C., Subramaniam, N., Dobler, V., Perez, J., Finnemann, J., Mehta, P. R., Goodyer, I. M., & Fletcher, P. C. (2015). Shift toward prior knowledge confers a perceptual advantage in early psychosis and psychosis-prone healthy individuals. *Proceedings of the National Academy of Sciences of the United States of America*, 112(43), 13401–13406. <https://doi.org/10.1073/pnas.1503916112>

Therneau, T. (2020). *Therneau/survival* [R]. <https://github.com/therneau/survival> (Original work published 2016)

Tiedemann, F. (2020). *Erocoar/gghalves* [R]. <https://github.com/erocoar/gghalves> (Original work published 2019)

Torchiano, M. (2020). *Mtorchiano/effsize* [R]. <https://github.com/mtorchiano/effsize> (Original work published 2015)

Turken, U., Whitfield-Gabrieli, S., Bammer, R., Baldo, J. V., Dronkers, N. F., & Gabrieli, J. D. E. (2008). Cognitive processing speed and the structure of white matter pathways: Convergent evidence from normal variation and lesion studies. *NeuroImage*, 42(2), 1032–1044.

<https://doi.org/10.1016/j.neuroimage.2008.03.057>

- Uhlhaas, P. J., Phillips, W. A., & Silverstein, S. M. (2005). The course and clinical correlates of dysfunctions in visual perceptual organization in schizophrenia during the remission of psychotic symptoms. *Schizophrenia Research*, 75(2), 183–192. <https://doi.org/10.1016/j.schres.2004.11.005>
- Unsworth, N., Miller, A. L., & Robison, M. K. (2020). Are individual differences in attention control related to working memory capacity? A latent variable mega-analysis. *Journal of Experimental Psychology: General*, No Pagination Specified-No Pagination Specified. <https://doi.org/10.1037/xge0001000>
- van Loon, A. M., Knapen, T., Scholte, H. S., St. John-Saaltink, E., Donner, T. H., & Lamme, V. A. F. (2013). GABA Shapes the Dynamics of Bistable Perception. *Current Biology*, 23(9), 823–827. <https://doi.org/10.1016/j.cub.2013.03.067>
- Varrier, R. S., Rothkirch, M., Stuke, H., Guggenmos, M., & Sterzer, P. (2020). Unreliable feedback deteriorates information processing in primary visual cortex. *NeuroImage*, 214, 116701. <https://doi.org/10.1016/j.neuroimage.2020.116701>
- Walton, M. E., Behrens, T. E. J., Buckley, M. J., Rudebeck, P. H., & Rushworth, M. F. S. (2010). Separable Learning Systems in the Macaque Brain and the Role of Orbitofrontal Cortex in Contingent Learning. *Neuron*, 65(6), 927–939. <https://doi.org/10.1016/j.neuron.2010.02.027>
- Waters, F., Collerton, D., Ffytche, D. H., Jardri, R., Pins, D., Dudley, R., Blom, J. D., Mosimann, U. P., Eperjesi, F., Ford, S., & Larøi, F. (2014). Visual Hallucinations in the Psychosis Spectrum and Comparative Information From Neurodegenerative Disorders and Eye Disease. *Schizophrenia Bulletin*, 40(Suppl_4), S233–S245. <https://doi.org/10.1093/schbul/sbu036>
- Waters, G. S., & Caplan, D. (2003). The reliability and stability of verbal working memory measures. *Behavior Research Methods, Instruments, & Computers*, 35(4), 550–564. <https://doi.org/10.3758/BF03195534>
- Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., & Zemla, J. (2017). *corrplot: Visualization of a Correlation Matrix* (0.84) [Computer software]. <https://CRAN.R-project.org/package=corrplot>
- Weilnhammer, V. A., Röd, L., Eckert, A.-L., Stuke, H., Heinz, A., & Sterzer, P. (2020). Psychotic Experiences

in Schizophrenia and Sensitivity to Sensory Evidence. *Schizophrenia Bulletin*, sbaa003.

<https://doi.org/10.1093/schbul/sbaa003>

Weilnhammer, V. A., Stuke, H., Sterzer, P., & Schmack, K. (2018). The Neural Correlates of Hierarchical Predictions for Perceptual Decisions. *Journal of Neuroscience*, 38(21), 5008–5021.

<https://doi.org/10.1523/JNEUROSCI.2901-17.2018>

Wickham, H. (2019). *tidyverse: Easily Install and Load the 'Tidyverse'* (1.3.0) [Computer software].

<https://CRAN.R-project.org/package=tidyverse>

Wickham, H. (2020). *forcats: Tools for Working with Categorical Variables (Factors)* (0.5.0) [Computer software]. <https://CRAN.R-project.org/package=forcats>

Wickham, H., Bryan, J., attribution), Rs. (Copyright holder of all R. code and all C. code without explicit copyright, code), M. K. (Author of included R., code), K. V. (Author of included libxls, code), C. L. (Author of included libxls, code), B. C. (Author of included libxls, code), D. H. (Author of included libxls, & code), E. M. (Author of included libxls. (2019). *readxl: Read Excel Files* (1.3.1) [Computer software]. <https://CRAN.R-project.org/package=readxl>

Wickham, H., Hester, J., Francois, R., R), R. C. T. (Date time code adapted from, RStudio, implementation), J. J. (grisu3, & implementation), M. J. (grisu3. (2020). *readr: Read Rectangular Text Data* (1.4.0) [Computer software]. <https://CRAN.R-project.org/package=readr>

Wilson, R. C., & Collins, A. G. (2019). Ten simple rules for the computational modeling of behavioral data. *ELife*, 8, e49547. <https://doi.org/10.7554/eLife.49547>

Wilson, R. C., Takahashi, Y. K., Schoenbaum, G., & Niv, Y. (2014). Orbitofrontal Cortex as a Cognitive Map of Task Space. *Neuron*, 81(2), 267–279. <https://doi.org/10.1016/j.neuron.2013.11.005>

Wöstmann, N. M., Aichert, D. S., Costa, A., Rubia, K., Möller, H.-J., & Ettinger, U. (2013). Reliability and plasticity of response inhibition and interference control. *Brain and Cognition*, 81(1), 82–94. <https://doi.org/10.1016/j.bandc.2012.09.010>

Xie, Y. (2020). *Yihui/knitr* [R]. <https://github.com/yihui/knitr> (Original work published 2011)

Xu, Z., Adam, K. C. S., Fang, X., & Vogel, E. K. (2018). The reliability and stability of visual working memory capacity. *Behavior Research Methods*, 50(2), 576–588. <https://doi.org/10.3758/s13428-017-0886-6>

Zeileis, A., & Croissant, Y. (2020). *Formula: Extended Model Formulas* (1.2-4) [Computer software]. <https://CRAN.R-project.org/package=Formula>