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Neural Signatures of Predictive Strategies Track Individuals Along the Autism-Schizophrenia Continuum

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Background and Hypothesis: **Humans develop a constellation of different representations of the external environment, even in the face of the same sensory exposure. According to the Bayesian framework, these differentiations could be grounded in a different weight assigned to prior knowledge vs. new external inputs in predictive inference. Since recent advances in computational psychiatry suggest that autism (ASD) and schizophrenia (SSD) lie on the two diametric poles of the same predictive continuum, the adoption of a specific inferential style could be routed by dispositional factors related to autistic and schizotypal traits. However, no studies have directly investigated the role of ASD–SSD dimension in shaping the neuro-behavioral markers underlying perceptual inference.** *Study Design*: **We used a probabilistic detection task while simultaneously recording EEG to investigate whether neurobehavioral signatures related to prior processing were diametrically shaped by ASD and SSD traits in the general population (*n* = 80).** *Results*: **We found that the position along the ASD–SSD continuum directed the predictive strategies adopted by the individuals in decision-making. While proximity to the positive schizotypy pole was associated with the adoption of the predictive approach associated to the hyper-weighting of prior knowledge, proximity to ASD pole was related to strategies that favored sensory evidence in decision-making.** *Conclusions*: **These findings revealed that the weight assigned to prior knowledge is a marker of the ASD–SSD continuum, potentially useful for identifying individuals at-risk of developing mental disorders and for understanding the mechanisms contributing to the onset of symptoms observed in ASD and SSD clinical forms.**

Key words: alpha oscillations/perceptual decision-making/predictive coding/computational psychiatry

Introduction

The Bayesian approach conceptualizes the brain as an inferential organ[1] that optimizes perception by integrating sensory information coming from the outside world with prior knowledge structured through experience. This framework aids in understanding the generative mechanisms underpinning the constellation of predictive styles observable in the general and psychiatric populations, that would derive from a different weight each individual assigns to priors vs. new sensory information.[2,3] In a recent paper,[4] we shed light on these interindividual differences by identifying predictive styles marked by the tendency to overweight vs underweight prior information. Using a probabilistic detection task, we induced a perceptual expectation by informing the participants, on a trial-by-trial basis, about the probability of target occurrence. We demonstrated that prior knowledge does not affect objective performance (ie, sensitivity and drift rate). Instead, it induces a significant shift in response strategy, being more liberal for highly expected target trials and more conservative for low expected target trials. Crucially, we observed significant variations in the magnitude of bias shifting across participants, testifying that there is wide heterogeneity regarding the weight assigned to prior knowledge within the general population. At the neural level, the amplitude of the posterior alpha oscillations (8–14 Hz) allowed us to intercept these inter-individuals' differentiations: participants (*believers*) who exhibited a massive suppression in the amplitude of alpha oscillations in the high- probability vs low-probability condition showed a concurrent strong bias shift, whereas individuals (*empiricists*) who exhibited a reduced modulation of alpha amplitude showed a dampened criterion shifting. These findings are in the vein of recent studies revealing that alpha desynchronization is associated with decision-making confidence,[5] visual awareness,[6] and bias in reporting target-presence,[7] but is not associated with increased perceptual performance.[8–10]

However, we did not investigate which factors might drive the adoption of a particular predictive strategy. According to the autism-schizophrenia continuum model,[11] the cognitive-perceptual styles observable in the Autistic Spectrum Disorder (ASD) and in the Schizophrenic Spectrum Disorder (SSD), may represent one of the critical determinants in this process. ASD has been associated to overweighting of external evidence compared to prior knowledge.[12,13] For example, perception in individuals with high autistic traits is more constrained by the stimulus objectively displayed rather than expectations about its presence.[14] Moreover, ASD relies less on anticipatory neural response in multisensory integration tasks[15] and did not show posterior alpha desynchronization to behaviorally-relevant targets.[16] In contrast, in SSD, ill-adaptive perceptual inference would be due to overweighted priors over sensory evidence.[17,18] Powers et al.[19] identified that, in a visual-auditory conditioning task, the number and confidence of conditioned hallucinations were positively correlated with the severity of hallucinations, and that this inclination relies on the overweighting of priors' information in the perceptual process. A comparable result was obtained in individuals at high clinical risk for psychosis who showed behavioral performance consistent with the presence of hyper-precise priors.[20] Moreover, an abnormal modulation of alpha activity has been related to maladjustment expectation in social interaction in schizophrenic patients.[21]

Starting from these theoretical and empirical works, we explored whether the position along the ASD-SSD continuum could be associated with the predictive style adopted in a perceptual decision-making task. We hypothesize that the more individuals tend to adopt the believer's predictive style, associated with overweighting of prior knowledge, the more they should fall on the SSD side of the ASD-SSD continuum. In contrast, we assume that adherence to the empiricist style, characterized by behavioral and neural markers associated with the suppression of prior knowledge in perceptual inference, should be promoted by proximity to the ASD pole of the continuum.

Methods

Participants

80 participants (43 female, age range 18–35) completed a visual detection task (figure 1A) in which prior knowledge was manipulated by inducing expectations of target probability. All participants signed a written informed consent prior to take part in the study, which was approved by the Bioethics Committee of the University of Bologna. Part of the sample ($n = 66$) is drawn from a previously published dataset.[4]

Computational modeling on decision-making process

Both Signal Detection Theory (SDT)[22] and Drift Diffusion Model (DDM)[23] were used to unravel which decision-making parameter was influenced by prior information. The SDT measures d' (sensitivity) and c (criterion) were calculated based on the proportion of hits and false alarms separately for trials preceded by low, high, or medium probability cues (see Supplementary table S1). A rm-ANOVA was employed to investigate a cue-related effect on SDT indices. The following DDM parameters were allowed to vary according to conditions: drift rate, distance between decisional bounds, starting point of the accumulation process. Traces of model parameters and their autocorrelation have been inspected to evaluate that the models had properly converged (Supplementary figure S2).

EEG analysis

To confirm the central role of alpha oscillations in tracking the voluntary modulation of decision bias, we have replicated the EEG analyses strategy performed in our previous study[4] with this enlarged sample by 1) conducting a time-frequency analysis on the amplitude difference between high- and low-probability trials and 2) assessing whether the degree of criterion shifting due to prior knowledge was related to pre-stimulus alpha amplitude modulation (Supplementary figure S5). Moreover, building from the previous work, we separated the participants as a function of their prior-based pre-stimulus differentiation in alpha amplitude, to investigate whether large vs. small modulation of alpha could underlie the differences in the predictive style adopted. Specifically, for each individual, the mean alpha (~8–14 Hz) amplitude value in the pre-stimulus time (~-400–0 ms) was considered and the *Δ alpha amplitude* was computed by taking the difference between the alpha amplitude extracted in low- and high-probability trials. This metric was used to delineate two types of predictive styles: the *believers* (ie, individuals showing an above-median Δ alpha amplitude) and the *empiricists* (ie, individuals showing a below-median Δ alpha amplitude). To reconfirm that the two clusters of individuals showed specific differentiation related to bias-shift, we assessed with an independent-samples t-test whether the SDT and DDM indices were differently modulated by the group factor.

Autism-schizophrenic continuum

The autistic traits in our sample were measured using the Autism-Spectrum Quotient test (AQ),[24] while schizotypy was assessed using the Schizotypal Personality Questionnaire (SPQ).[25] An independent-samples t-test

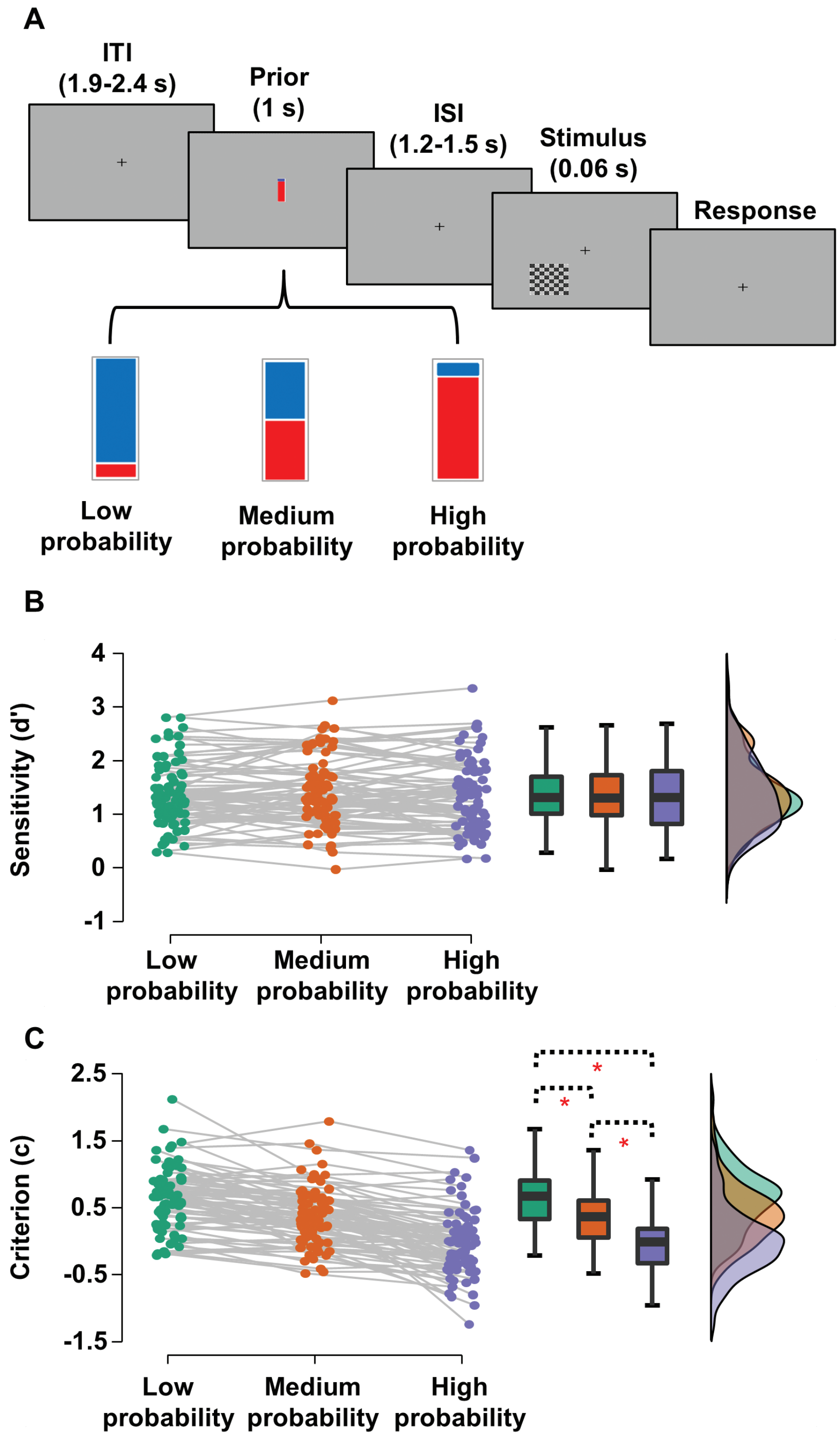

Figure 1. (A) Each trial started with the appearance of the cue presented at the center of the screen for 1 s. The cue was a bar with its bottom colored in red and its top colored in blue. The level of bar fill r indicated the probability of target's occurrence. High and low cue indicated the probability of target occurrence of 67% and 33%, respectively. Instead, the neutral cue equally predicted (50%) the target presence and absence. After a variable delay of 1.2–1.5 s a checkerboard containing (or not) grey circles appeared on the monitor. Participants pressed with the right hand the button associated with the choice. After response collection, the screen turned black for 1.9–2.4 s. The actual probability of target presentation was in accordance with the probability indicated by the cue, and participants were informed of this. (B) Prior information had no effect on perceptual sensitivity. (C) On the contrary, the probabilistic cue shaped the decision criterion that gradually became more liberal as the probability of target presentation increased.

was employed to explore which specific subscales of the AQ and SPQ had different magnitude between the group of believers and empiricists (see supplementary materials). Moreover, to identify where individuals on the autism-schizophrenia axis lay, a principal component analysis (PCA, see supplementary materials) was performed on the correlation matrix of the AQ and SPQ subscales. The first two principal components were extracted and the second one (PC2) was selected for subsequent analyses because, according to previous literature,[26–29] it is supposed to capture the diametric relationship between these two conditions. Then, to assess whether the predictive style adopted by the participants could be related to the individual position along the autism-schizophrenia axis, independent-sample *t*-tests were employed to investigate whether the individual PC2 score showed statistically significant differences between the believers and empiricists group. We checked that the results obtained from the median-split analysis remained valid even when using the continuous variables Δ alpha amplitude and Δ criterion as dependent variables and the PC2 score as a predictor. Finally, a mediation analysis was conducted to probe effects of ASD-SSD continuum factor on Δ criterion, mediated by any effects exerted by it on *Δ alpha amplitude* regulation. All the analyses were carried out with standardized values for all the variables, and we report 95% confidence interval based on 5000 bootstrap iterations (bias-corrected).

Results

Expectations modulate decision-making strategies

We computed the SDT indices *d′* and *c* to investigate the effect that prior information has on perceptual decision-making (figure 1). The conducted analysis replicates the previous study [4] showing that priors affected the criterion ($F_{2,158}$ = 88.73; $P < .01$; $\eta_p^2 = 0.53$) but not the sensitivity ($F_{2,158}$ = 1.22; $P > .30$; $\eta_p^2 = 0.015$). Specifically, the participants adopted a more liberal criterion in trials preceded by high-probability cue ($c_{high} = -0.02 \pm 0.05$) relative to trials preceded by medium- probability cue ($c_{mid} = 0.37 \pm 0.05$; $t_{79} = -9.76$, $P < 0.01$; $d = -1.10$) and low-probability cue (c_{low} = 0.63 ± 0.05; $t_{79} = -9.87$, $P < .01$; $d = -1.10$), in which the criterion were located in more conservative position relative to the neutral condition ($t_{79} = 7.15$, $P < .01$; $d = 0.80$). DDM parameters (Supplementary figure S3) confirm these patterns of results: individuals increased the starting point in the high-probability trials relative to both medium-probability trials ($q < 0.01$) and low-probability trials ($q < 0.01$) and lowered the starting point in the low- relative to medium-probability trials ($q < 0.01$). We found no difference in the others DDM parameters.

Alpha oscillations track human decision-making strategies

We corroborated that the low- vs high-probability condition were associated to a different suppression of alpha amplitude in posterior regions (Supplementary figure S3). Moreover, we assessed how individual differences over the tendency to shape alpha oscillations modulated the effect that prior exerted in decision-making. To this end, we partitioned the sample, through a median split approach (Figure 2A), between those who exhibited a strong reduction in alpha amplitude in the high- compared with the low-probability condition (ie, the *believers*) vs those who showed a more nuanced modulation (ie, the *empiricists*). The two groups showed different decision-making profiles: the prior-dependent modulation of the decision criterion (Δ criterion$_{believers} = 0.88 \pm 0.10$, Δ criterion$_{empiricists} = 0.42 \pm 0.07$; $t_{78} = 3.78$, $P < .01$; $d = 0.85$) were greater in individuals prone to shifting alpha amplitude (Figure 2B), while the sensitivity ($d'_{believers} = 1.41 \pm 0.10$; $d'_{empiricists} = 1.35 \pm 0.09$; $t_{78} = 0.40$, $P > 0.70$; $d = 0.09$) were not distinguishable between the two groups. This result was also supported by Pearson's correlation, which demonstrated that the degree of alpha modulation correlates positively with the level of Δ criterion (Supplementary figure S5). Furthermore, we verified that the alpha effect in tracking predictive styles is spatially localized to electrodes contralateral to stimulus presentation (Figure 2C). These findings proved the reliability of alpha fluctuations in detecting the different weights that prior knowledge plays in establishing decision-making biases in the general population.

The individuals' position along the ASD–SSD axis drives the predictive strategy adopted

To test whether individual position along the ASD–SSD axis could intercept the predictive style employed, we used principal component analysis to extract the component (ie, PC2) showing opposite loading between the AQ and SPQ subscales (Supplementary Table S2, Supplementary figure S6). Then, we evaluated whether the PC2 individuals scores were significantly different between believers and empiricists. The independent sample *t*-test conducted showed the presence of a significant difference in the PC2 scores ($PC2_{believers} = 0.26 \pm 0.17$, $PC2_{empiricists} = -0.26 \pm 0.13$; $t_{78} = 2.39$, $P = 0.02$; $d = 0.54$), proving that the believers were closer to the positive schizotypal end of the continuum, whereas the empiricists were more shifted toward the autistic pole of the continuum (figure 3; Supplementary figure S3).

A very similar pattern of results emerged when comparing the AQ and SPQ subscale scores in the believers' group vs the empiricists' group (see supplementary materials): autistic and negative schizotypal traits exhibited a similar pattern of decision-making tendencies, being more prominent in the empiricist group (figure

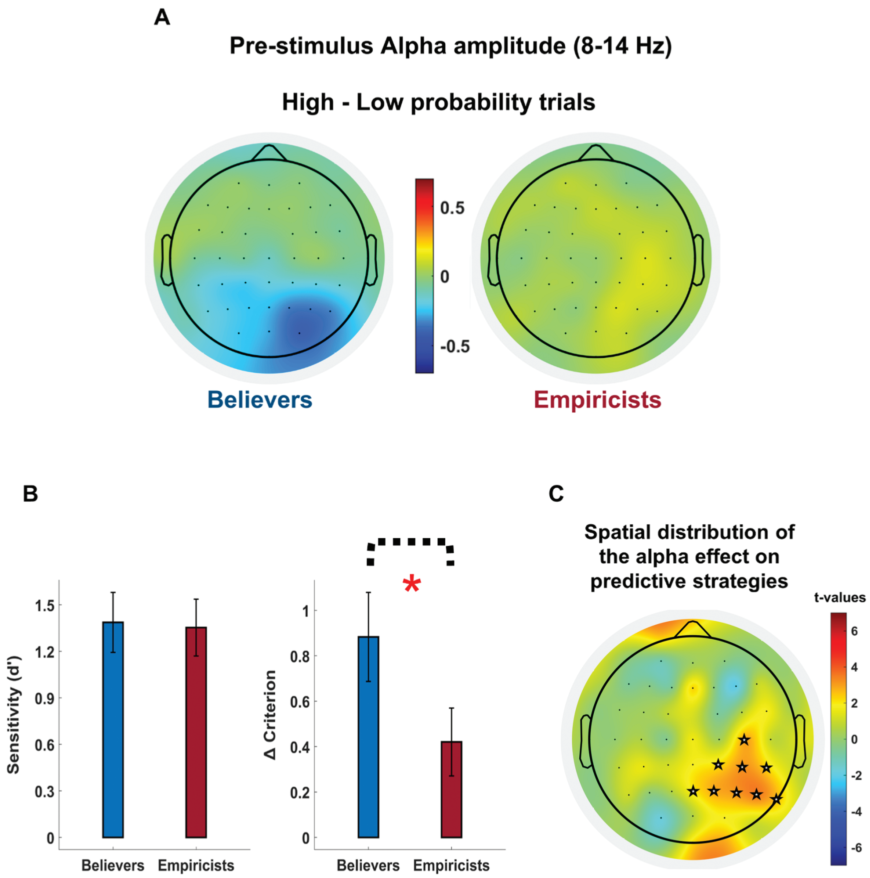

Figure 2. Electrophysiological correlates of prior processing. (A) Topography of differential activations between the high- and low-probability conditions in the alpha band in the pre-stimulus window in the above- (believers) and below- (empiricists) median alpha modulators groups. (B) The two groups exhibited undifferentiated sensitivity in the task. However, the decision-making strategy adopted was significantly different: while believers highly moderate the criterion according to the prior, empiricists are less constrained by it. (C) Statistical analysis of the spatial specificity of the alpha effect in tracking individual predictive strategies. Stars mark the electrodes where prestimulus alpha oscillations significantly discriminate between the believer's and empiricist's styles (see supplementary materials). This data-driven approach confirms a spatially localized effect mainly involving posterior cortical regions contralateral to stimulus presentation.

4A); conversely, positive schizotypal traits (eg, magical thinking) were more present in the believers' group (figure 4B).

Correlation analysis

To corroborate the results obtained from the median-split analysis, we also showed that the PC2 score is significantly correlated with Δ alpha amplitude (Supplementary figure S8; $r = 0.24$, $P = .03$), proving that the closer the individuals are to the schizotypal (vs autistic) pole of the continuum, the more (vs less) biases their alpha amplitude in a prior-dependent fashion. Similarly, we demonstrated the presence of a positive relationship between proximity to the schizotypal pole and the magnitude of criterion modulation in the high- vs low-probability condition (Supplementary figure S8; $r = 0.28$, $P = .01$). Then, we performed a multiple linear regression analysis to better understand the relation between these variables by placing the ASD–SSD continuum factor, the Δ Alpha Amplitude and the interaction between these two variables as predictors of Δ criterion. The analysis showed that the regression was significant ($F_{3,76} = 4.94$, $P < .01$), with both Δ alpha amplitude (β = 0.26, $P = .02$) and the ASD-SSD continuum factor (β = 0.33, $P = .02$) [but not their interaction (β = −0.18, $P = .17$)] emerged as significant predictors of the prior-based modulation of the decisional criterion (Δ criterion).

Mediation analysis

To further understand the inter-relation between ASD–SSD continuum factor, Δ criterion and Δ Alpha Amplitude, we conducted a mediation analysis to examine whether Δ Alpha Amplitude mediated any effect that the ASD–SSD continuum factor exerted on the Δ criterion (figure 5). We found a significant mediation effect (c = 0.04, 95% CI: 0.001–0.083), whereby relatively greater Δ Alpha Amplitude mediated the positive association between ASD–SSD continuum factor and Δ

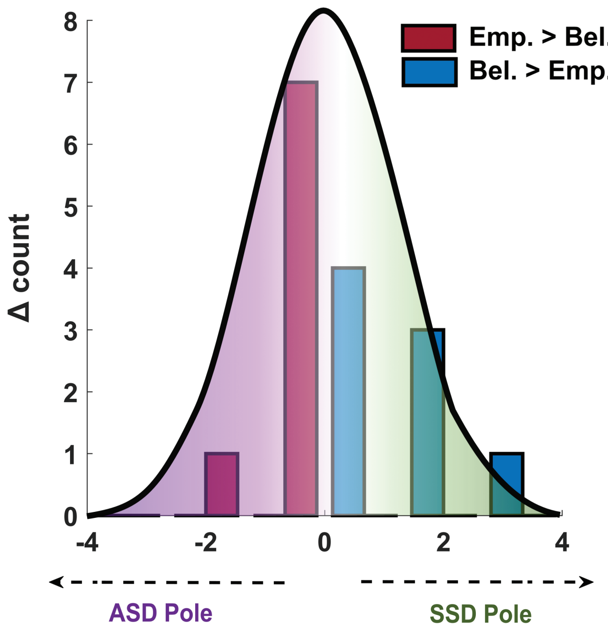

Figure 3. The position along the ASD–SSD continuum directs the adoption of the predictive strategy. Individual scores concerning the ASD–SSD continuum factor are significantly different among the two groups. On the *x*-axis is represented the ASD–SSD continuum factor extracted through PCA, whereas on the *y*-axis is represented the difference between the number of believers and empirical participants. Believers were overrepresented in the schizotypal branch of the continuum ($PC2_{believers} = 0.26 \pm 0.17$), while empiricists ($PC2_{empiricists} = -0.26 \pm 0.13$) were placed more closely to the autistic pole of the continuum.

criterion (ie, lower Δ criterion in individuals closer to the ASD pole). Moreover, the analysis showed that there was significant residual direct effect of ASD–SSD continuum factor on Δ criterion (c = 0.13, 95% CI: 0.003–0.256) suggesting that the impact of ASD-SSD continuum factor on Δ criterion are partially mediated by the Δ Alpha Amplitude.

Discussion

Humans develop a constellation of different representations of the external world, even in the face of the same sensory experience.[6,30] According to the Bayesian framework, these differentiations could be grounded on a different integration of prior knowledge with new information coming from the external world: some people are more prone to base their inferences on accumulated models and experiences, while others tend to rely more on input presented in the here and now. In this research, we explored whether these different predictive styles could be also routed by dispositional factors related to autistic and schizotypal traits. In accordance with the autism-schizophrenia continuum model,[11] ASD and SSD are associated with a diametrical behavioral/cognitive pattern resulting from a distinct weight given to priors and new sensory information.[31–33] Positive SSD symptoms tend to be associated with priors-driven perception[17,34,35] and opposition toward evidence that contradicts preconceived beliefs,[36]

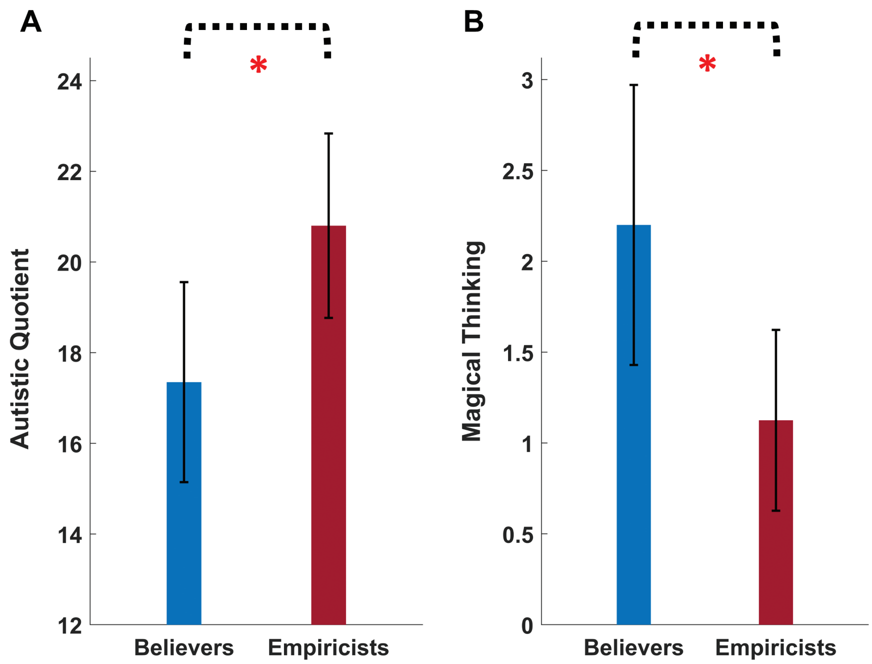

Figure 4. Positive autistic and schizotypal traits discriminate believers from empiricists. (A) The number of autistic traits is higher in the cluster of individuals adopting the empiricist strategy ($AQ_{empiricists} = 20.80 \pm 1.00$) than in those adopting the believer strategy ($AQ_{believer} = 17.35 \pm 1.09$). (B) Magical thinking is overrepresented in the cluster of individuals adopting the believer's strategy ($\text{Magical thinking}_{believer} = 2.20 \pm 0.38$) than the ones embracing the empiricist's approach ($\text{Magical thinking}_{empiricists} = 1.13 \pm 0.25$).

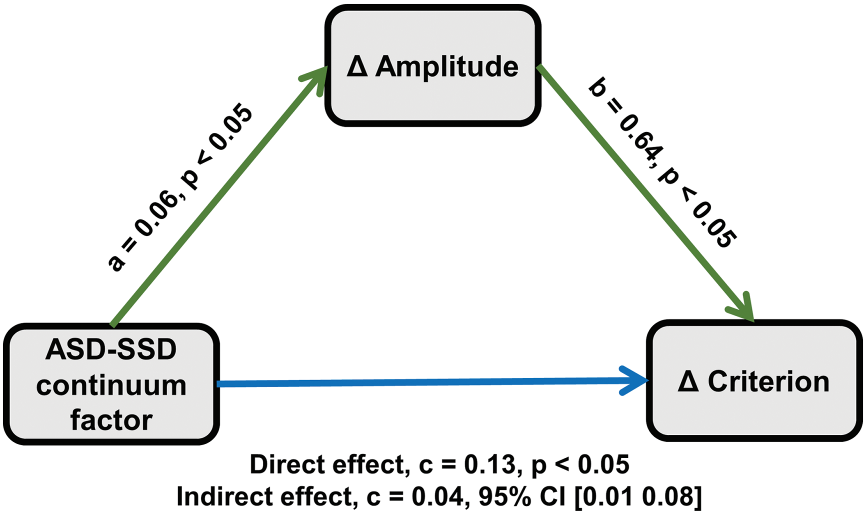

Figure 5. Mediation Analysis. Alpha amplitude modulation mediates the positive relationship between the ASD–SSD continuum factor and Δ criterion (ie, higher Δ criterion in individuals closer to the SSD pole). Therefore, the relationship between the position along the continuum and the criterion is explained by the concurrent modulation that the ASD–SSD factor exert on alpha amplitude.

whereas ASD is characterized by overweighting of external evidence[13,37] compared to prior knowledge.[38,39] Therefore, we expected that adopting a predictive style that overweights vs underweights prior models may be prompted by a predominance of schizotypal vs autistic traits, respectively.

To investigate these hypotheses, we used data from humans performing a probabilistic detection task, while noninvasively recording their neural activity using EEG. We have shown that providing prior knowledge about the target probability created a strong response bias in human observer, without affecting their visual sensitivity. However, the degree of bias-shifting was highly different among participants. Using the electrophysiological data collected, we were able to identify a neural signature that distinguish individuals that overweight (*believers*) vs underweight (*empiricists*) expectation-like information in perceptual inference: *believers* showed extensive shaping of alpha oscillations in perceptual regions, while *empiricists* showed a reduced modulation. This finding proves that alpha rhythms are a reliable electrophysiological index able to discriminate participants' predictive behavior, confirming the role this frequency band plays in shaping perceptual outcomes.[8,40–44] According to the SDT framework, observers evaluate the presence vs the absence of the stimulus by assessing whether the strength of the internal responses exceeds the decisional criterion. Following this framework, a voluntary regulation of prestimulus alpha oscillations could impact the criterion through a modulation of the excitability of the cerebral cortex.[45] The reduction of alpha amplitude in high- vs low-probability trials would increase the cortical excitability that, in turn, would magnify the strength of the internal responses making it easier to exceed the decisional criterion.[4,42,46,47]

Importantly, we analyzed whether individuals adopting the believer vs empiricist strategies showed differences in schizotypal vs autistic traits. First, we performed a PCA to extract the dimension showing opposite loading between the AQ and SPQ subscales. The conducted analysis showed that the second component (PC2) showed diametrical saturations with the positive schizotypal and autistic scales, confirming the opposite nature between these two dimensions.[26–29] Crucially, we identified that PC2 scores were statistically different in the two groups: the empiricists showed negative mean values (ie, they were more shifted toward the ASD pole), while the believers showed more positive values (ie, they were more shifted toward the SSD pole).

It is important to emphasize that these findings contrast with some evidence pointing toward an opposite effect linked to reduced prior processing in SSD,[48] as reflected by the reduced susceptibility to expectancy-driven illusions (eg, the hollow-mask illusion[49]). This conflicting evidence could be interpreted through a hierarchical model of predictive coding.[11,50–52] According to this proposal, the weight assigned to predictive information in SSD could be subordinate to the hierarchical level from which it is generated: whereas predictions generated at lower levels of the cortical hierarchy (eg, sensory areas) would have reduced precision, higher-order beliefs and explicit prior information (like the one employed in the current study) would be hyper-processed in the SSD population.[17,53]

Furthermore, we corroborated the results highlighted by the PCA analysis by investigating the contribution of AQ and SPQ subscales in orienting the adoption of predictive styles. First, we demonstrated that participants within the believers group manifested less autistic and negative schizotypal traits compared to the empiricists.

The finding that negative schizotypal traits share similarities in cognitive style with autistic traits is in line with empirical research showing the presence of comparable cognitive and perceptual phenomena that tie these two dimensions together. For example, both negative schizotypy and autistic traits predicted weaker rubber hand illusion effects.[54,55] Subsequently, we showed that believers manifested higher rate of positive schizotypal traits relative to the empiricists. In particular, magical thinking was the subscale of the SPQ that was most strongly expressed in the believers' group. Magical thinking is connected with increased susceptibility to psychosis,[56] antiscientific attitudes,[57] illusory perception,[58–60] and it is genetically connected to schizophrenia.[61] Crucially, participants with higher magical ideation tend to rely on a limited amount of objective evidence to construct meaningful models, which are also overestimated,[62] and showed decreased activity in the cognitive evaluation network during the processing of evidence that contradicts a belief.[63] Following these lines, a higher number of magical thinking would favor the adoption of the believer's style due to the propensity to promote the overestimation of the precision of prior knowledge, such as the expectation-like information provided in the task, at the expense of incoming information.

Finally, to better understand the relation between ASD–SSD continuum factor, Δ criterion and Δ Alpha Amplitude, we conducted a mediation analysis which proved that the influence exerted by the position along the ASD–SSD continuum on behavior was mediated by the degree of alpha amplitude modulation. This finding suggests that ASD and SSD traits could shape the use of probabilistic priors through opposite modulation on alpha wave amplitude.[64]

The described results fit into the growing literature aimed at identifying the behavioral and electrophysiological signatures underlying Bayesian processing[65–69] and inter-individual differences in the predictive machinery.[11,31,52,70] For the first time, we have demonstrated that the position along the ASD–SSD continuum directs the predictive strategies adopted by individuals. This is particularly important because it shows that, even within the general population, it is possible to trace signs of the presence of different approaches toward predictive inference that depends on subclinical personality traits. Future studies should investigate whether the directionality of the effect played by position along the ASD–SSD continuum is maintained even when interoceptive priors are introduced, given their role in modulating decision-making outcomes.[71,72] It should be noted that, in the task employed, both strategies led to the same result in terms of accuracy. For this reason, we conceive these styles as two different, but equally valid, strategies within the proposed experimental set-up. Follow-up studies should investigate whether different contexts can elicit performance gains/losses as a function of the predictive style promoted by the ASD and SSD traits. For example, the tendency to favor the believer predictive style would explain why positive schizotypal traits were correlated with a performance advantage when the prior knowledge aid to interpret a highly ambiguous bottom-up signal,[73] whereas the tendency to favor the empiricists predictive style would explain why AQ traits favor the perception of specific details when they are contained in global patterns.[74–76] Moreover, since these peculiarities in information processing and in neural regulation are already evident in the sub-clinical population, they could be important factors both in identifying markers that signal early risk toward the development of mental disorders, and in understanding the mechanisms contributing to the onset of manifest clinical forms along the ASD–SSD continuum. In this regard, it would be crucial for future studies to evaluate the behavioral and neural indices outlined involving patients with positive SSD symptoms and ASD patients. This would allow to evaluate the developmental trajectory of predictive strategies, assessing whether they become more rigid, inflexible, and context-independent as one approaches the ends of the continuum.

Supplementary Material

Supplementary material is available at https://academic.oup.com/schizophreniabulletin/.

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