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Predictive waves in the autism-schizophrenia continuum: a novel biobehavioral model

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Abstract

The brain is a predictive machine. Converging data suggests a diametric predictive strategy from autism spectrum disorders (ASD) to schizophrenic spectrum disorders (SSD). Whereas perceptual inference in ASD is rigidly shaped by incoming sensory information, the SSD population is prone to overestimate the precision of their priors' models. Growing evidence considers brain oscillations pivotal biomarkers to understand how top-down predictions integrate bottom-up input. Starting from the conceptualization of ASD and SSD as oscillopathies, we introduce an integrated perspective that ascribes the maladjustments of the predictive mechanism to dysregulation of neural synchronization. According to this proposal, disturbances in the oscillatory profile do not allow the appropriate trade-off between descending predictive signal, overweighted in SSD, and ascending prediction errors, overweighted in ASD. These opposing imbalances both result in an ill-adapted reaction to external challenges. This approach offers a neuro-computational model capable of linking predictive coding theories with electrophysiological findings, aiming to increase knowledge on the neuronal foundations of the two spectra features and stimulate hypothesis-driven rehabilitation/research perspectives.

Keywords: Autism Spectrum Disorder (ASD); Schizophrenic Spectrum Disorder (SSD); Autistic-Schizophrenic continuum; Decision-Making; Predictive Coding; Brain Oscillations; Brain Connectivity; Oscillopathies

Highlights

- ASD and SSD lay on two poles of the same predictive continuum.
- ASD is characterized by a bias towards prediction-error's overweighting.
- SSD tends to overestimate the precision of their predictive models.
- Brain oscillations are crucial in the transmission of prediction and prediction error.
- Different oscillatory profiles account for the predictive styles of ASD and SSD.

Introduction

Although more than a century has passed since the first descriptions of individuals belonging to the autism and schizophrenia spectrum, there is still a considerable knowledge gap about these conditions. The lack of theories capable of unraveling the mechanisms underlying symptomatology is partly responsible for the inability to identify appropriate treatments. This causes serious repercussions at the individual, family, and community level. Both spectra are characterized by an increased suicidal risk (Hawton et al., 2005; Kőlves et al., 2021; Teraishi et al., 2014) and with poor social adaptation resulting in high costs for the take care system (Jin and Mosweu, 2017; Rogge and Janssen, 2019).

For the afore-mentioned reasons, neurocomputational models have recently been introduced as a promising tool that can elucidate the neural mechanisms behind major neuropsychiatric conditions (Huys et al., 2021, 2016). For instance, predictive coding theory offers an explanatory model able to create a link between phenomenological symptoms and the computational process that accounts for them (Friston et al., 2014). This proposal states that perception is not strictly dependent on incoming sensory input but emerges from an inferential-like process in which stimuli are conditionally interpreted in light of aprioristic knowledge (Clark, 2013; Rao and Ballard, 1999). Following this framework, in ASD and SSD there would be an imbalance between stimulus and prediction-related information weightage resulting in maladaptive perceptual inference process (Sterzer et al., 2018; Van de Cruys et al., 2014). This imbalanced trade-off may stem from diametric reasons. Autistic spectrum would less exploit contextual and experience-based information to optimize perceptual inference, whereas schizophrenic spectrum overuses preconceived models (Corlett et al., 2019; Sinha et al., 2014). Although predictive coding can be considered an effective explanatory theory of some spectra features, there is a lack of neural evidence able to empirically reinforce the hypothesized mechanisms.

The proposed framework aims to link neuro-computational theories currently adopted to explain the peculiarities of ASD and SSD with lines of empirical research showing the involvement of brain rhythms in neural information exchange. Predictive coding assumes the presence of top-down messages descending the cortical hierarchy that try to fit bottom-up signals. Any discrepancy with the predicted state is conveyed via an ascending signal designed to update the current model. In this interplay, cortical oscillations may represent a neural solution to implement predictive processes (Arnal and Giraud, 2012; Bastos et al., 2020, 2012). Indeed, communication between brain regions is accomplished through mutual rhythmic co-ordination (Fries, 2015, 2005). A failure to fine-tune neural synchronization between predictive and prediction error units could lead to a predictive imbalance, which could be defined as an unbalanced trade-off between prediction and prediction error information. Crucially, converging evidence support the notion that oscillations are a pivotal biomarker underlying ASD and SSD features (Kessler et al., 2016; Reilly et al., 2018; Simon and Wallace, 2016; Uhlhaas and Singer, 2015). Indeed, both spectra are framed as oscillopathies given that abnormalities in the spectral profile and in the rhythmic communication between brain regions are consistently reported and correlated to behavioral dysfunctions (Grent et al., 2020; O'Reilly et al., 2017; Peiker et al., 2015b; Seymour et al., 2019; Wang et al., 2020). Core element of the proposed work is the assumption that disrupted oscillatory synchronization noted in ASD and SSD would subtend the maladjustments of the perceptual inferential process. The innovative aspect of the model we propose here consists of integrating multiple levels concerning the cognitive peculiarities of ASD and SSD and the related electrophysiological underpinning into a single theoretical framework that could inform personalized interventions for treatment of the disease and novel scientific investigation. Before discussing this integrative framework, we offer a brief introduction to the characteristics of these spectra and their interplay in the following sections.

1. Autism Spectrum Disorder (ASD) and Schizophrenic Spectrum Disorder (SSD)

Autism and Schizophrenia are two of the most prevalent mental disorders (Baio et al., 2018; Saha et al., 2005). Autism is characterized by restricted and stereotyped behavior (excessive adherence to routines, highly limited and fixed interests), communication problems, and social deficits (lack of socio-emotional reciprocity, deficiencies in developing and maintaining social relationships) (Volkmar and Reichow, 2013). Schizophrenia is characterized by a mixture of positive (such as delusions and hallucinations), negative (anhedonia, apathy, social withdrawal), and cognitive symptoms (disorganized thoughts, poor memory, altered cognitive control) (Tandon et al., 2013). In the early days of psychiatry, these two disorders were intertwined. In Bleuler's conceptualizations (1916), autism indicated a behavioral symptom of the schizophrenic manifestation characterized by alienation and social interaction avoidance. Moreover, in the first edition of the *Diagnostic and Statistical Manual of Mental Disorders* (DSM-I), children with autistic-type symptoms were diagnosed as having childhood-type schizophrenic reaction (American Psychiatric Association, 1952). The clinical difference between Schizophrenia and autism was officially confirmed only in DSM-III, creating a new category called *infantile autism*, placed in a different section with respect to schizophrenic disorders (American Psychiatric Association, 1980). The whole conceptualization of these two conditions has changed in recent years: a dimensional perspective (continuum) has replaced a dichotomous approach (present, absent) (Nelson et al., 2013). This change of perspective derives from the observation of a constellation of heterogeneous clinical manifestations that can be embedded in the diagnosis of autism or schizophrenia (Baker, 2013; van Os et al., 2009). This evidence has led to the introduction of Autism Spectrum Disorder (ASD) and Schizophrenic Spectrum Disorder (SSD) in recent diagnostic manuals (American Psychiatric Association, 2013). In line with the dimensional conceptualization of schizophrenia, schizotypal

personality disorder (SPD) has been included in the SSD given that the pervasive pattern of reduced capacity for close relationships and the cognitive and perceptual distortions observed in this disorder are qualitatively similar to those observed in schizophrenia (Lenzenweger, 2006). The Research Domain Criteria (RDoC) project is one of the leading promoters towards using a dimensional approach to comprehend mental health and mental illness fields (Insel, 2014). One of the key points of the project states that placing rigid barriers between normality and illness conceals essential information about how psychopathology gradually emerges throughout development. Crucially, it neglects the importance of risk and protective factors that can push an individual to a more or less extreme position along the spectrum (Cuthbert and Insel, 2013). Indeed, the spectrum conceptualization is corroborated by evidence indicating that there are no clear-cut boundaries separating autism and schizophrenia from the rest of the general population, as symptoms range from overt clinical manifestation to trait-like expressions of the two conditions (Baron-Cohen et al., 2001; Lenzenweger, 2018; Zavos et al., 2014). Moreover, consistent evidence points to an overlapped genetic etiology underlying ASD and autistic traits in the general population (Bralten et al., 2018; Massralli et al., 2019), as well as a higher rate of schizotypal traits being in genetic proximity to SSD (Torti et al., 2013; Walter et al., 2016).

2. Overlapping, opposite, or independent disorders?

The nature of the relationship between these conditions is complex (Chisholm et al., 2015). Although they have different features and classification criteria, there is a growing interest in studying the connections between these two entities due to some similarities in clinical presentation, genetic etiology, and neurobiological abnormalities (Crespi et al., 2010; Konstantareas and Hewitt, 2001; Pinkham et al., 2008).

A systematic review conducted by Zheng (2018) revealed that the prevalence of ASD in individuals with Schizophrenia ranged from 3.4 to 52%, and people with ASD had an odds ratio of 3.55 to manifest comorbidity with SSD compared to the typically-developed controls. A recent meta-analysis (Lugo Marín et al., 2018) ascertained that the pooled prevalence value of SSD in a sample with ASD diagnosis stands at 6.4%. An in-depth analysis of the two spectra' features can help to disambiguate this frequently highlighted co-occurrence. A recently advocated approach is based on a comparative analysis of diagnostic tests and questionnaire data utilized to assess the two conditions (Table 1). Using the Autistic Quotient (AQ) (Baron-Cohen et al., 2001) and the Schizotypal Personality Questionnaire-Brief Revised (SPQ-BR) (Cohen et al., 2010) scores taken from non-clinical populations, Dinsdale et al., (2013) demonstrated that a general factor related to socio-communicative impairments is common to both autistic and schizotypal traits. Conversely, there is a diametrically opposite relationship between autistic features and positive/cognitive-perceptual aspects of schizotypy. Zhou (2019) carried a psychometric analysis to investigate the relationships between self-reported autistic and schizotypal traits. The psychometric results showed a substantial overlap between negative schizotypal traits and the social-communicative impairment typically connected to autistic traits. After removing this common 'social difficult' element, the authors found a negative correlation between positive/cognitive schizotypal and autistic traits. A similar pattern of results can be evinced also in clinical populations. Trevisan (2020) recruited samples of adults with autism (n=53), Schizophrenia (n=39), and typical development (n=40) to whom the Autism Diagnostic Observation Schedule (ADOS-2) (Lord et al., 2012) and the Positive and Negative Syndrome Scale (PANSS) (Kay et al., 1987) were administered. The results showed that \simeq 44% of participants with Schizophrenia met ADOS-2 criteria for autism-spectrum despite not meeting DSM-5 criteria for autism diagnosis. Clustering ADOS-2 and PANSS items into positive and negative domains showed that the overlap between the two conditions relies

specifically on negative symptoms such as social-emotional lack of reciprocity, apathy, reduced nonverbal communication, reduced affect sharing, and social withdrawal. This is congruent with studies pointing to comparable deficits in mentalizing tasks (Chung et al., 2014) and communication ability (Levy et al., 2010; Tager-Flusberg et al., 2005), testifying the presence of a common deficit in social cognition (Ciaramidaro et al., 2018; Couture et al., 2010; Pinkham et al., 2020). In contrast, disorder-specific positive symptomology measured by the ADOS-2 and PANSS can accurately discriminate schizophrenic and autistic patients. Schizophrenic patients demonstrate a higher inclination to psychosis-like symptoms (such as delusions and hallucinations), whereas autistic people demonstrate a higher prevalence of ASD-related symptoms as strange mannerisms, fixed interests, and behavioral stereotypes. To summarize, it seems plausible that the comorbidity rate between the two disorders could be inflated by the common presence of the social/communication symptoms. For an accurate differential diagnosis, clinicians should refer to the positive/cognitive dimension that seems to have a higher capacity to disambiguate between the two conditions (Ford et al., 2017; Nenadić et al., 2021).

2.1. Cognitive profiles of ASD and SSD

Divergences between ASD and SSD are not only noticeable at the psychometric level. The cognitive constellation of the two spectra seems to point in opposite directions (Bölte et al., 2002). ASD shows less influence of contextual and global information connected to a bias towards local information processing (Happé, 1999). In visual search tasks where the target differs from distractors in small details, ASD individuals show above-average performance that depends on anomalously intensified perception of stimulus peculiarities (Joseph et al., 2009; O'Riordan et al., 2001). This enhanced reliance on details is also observable in neurotypical

individuals with an above-median number of autistic traits (Alink and Charest, 2020). ASD population shows abnormal perceptual experiences, characterized by hyposensitivity and/or hypersensitivity toward external stimulations, which can induce sensory overload (Baum et al., 2015; Green et al., 2016; Pellicano, 2013). In the social domain, the ASD population manifest a deficit in “mind-reading” connected to an inability to attribute mental states to self and others (Baron-Cohen and Wheelwright, 2004; Frith, 2001). In decision-making tasks, ASD individuals require to accumulate more evidence before making a decision than healthy controls, showing a circumspect reasoning bias (Brosnan et al., 2014), and the adoption of a more conservative criterion in perceptual decision-making tasks (Quinde-Zlibut et al., 2020).

Neurocognitive deficits are a hallmark of SSD (Calkins et al., 2010; Fatouros-Bergman et al., 2014; Kahn and Keefe, 2013; Mollon et al., 2018). A marked vulnerability has been observed in speed of processing, episodic memory, social cognition, and executive functions (Li and Spaulding, 2016; Louise et al., 2015). Working memory capacity is severely impaired in SSD (Barch and Smith, 2008; Lee and Park, 2005; Park et al., 1995) underpinned by abnormal activation pattern of the dorso-lateral prefrontal cortex (Potkin et al., 2009). The SSD population presents an advantage for global over local processing, manifesting a pattern opposite to autistic individuals (Russell-Smith et al., 2010). A similar dissonance with the ASD population regards the social cognition domain in which SSD exhibits a “hyper-mentalist” tendency reflected by a propensity to over-interpret the mental state of others (Ciaramidaro et al., 2015; Crespi and Badcock, 2008). Moreover, the SSD population tends to over-attribute events to their own agency (Garbarini et al., 2016; Haggard et al., 2003; Maeda et al., 2012), and manifest a tendency to “hyper-link” random events, exhibiting a conspiracy thinking style (van der Tempel and Alcock, 2015). In decision-making tasks, they exhibit an inclination to collect less information than controls before decision commitment (“*Jumping to conclusion bias*” (Garety and Freeman, 1999; Henquet et al., 2020)) and to underweight

evidence that goes against strong pre-established beliefs (“*Bias Against Disconfirmatory Evidence*” (Georgiou et al., 2021; Moritz and Woodward, 2006) accompanied by over-confidence to incorrect perceptual decisions (Moritz et al., 2014).

Study	Sample characteristic	Measures of SSD features	Measures of ASD features	Analysis	Summary of findings
Dinsdale et al. (2013)	605 undergraduate students (380 females and 225 males)	SPQ-BR	AQ	Principal component analysis	The first principal component reflected a general social alteration overlapping the two spectra. By contrast, the second principal component indicates that positive schizotypal features loaded in the opposite direction to autistic features.
Zhou et al. (2019)	2469 Chinese college students (27.7% males; mean age = 18.75, SD = 1.1)	SPQ	AQ	Principal component analysis & Network model	Great overlap between negative schizotypal traits and the social-communicative impairment of autistic traits. After extracting the shared ‘social difficulty’ component, a diametrical structure of positive schizotypal and autistic traits emerges.
Nenadiv et al. (2021)	640 young adult healthy subject (452 female and 188 males)	MSS, O LIFE, SPQ-B, CAPE-42	AQ	Principal component analyses	All sub-scales loaded positively on the first component while the second component showed a diametric pattern, with opposite loadings of scales measuring positive schizotypy and autistic traits.
Ford et al. (2014)	449 young adults (162 males and 287 female)	SPQ	AQ	Factor Analysis & Principal component analyses	The first factor reveals a great overlap between AQ and SPQ in social scales. The second and third factor discriminate a factor related to <i>Social Rigidity</i> and <i>Perceptual Oddities</i> that represented a specific phenotype in autistic and schizotypal tendency, respectively.
Ford et al. (2017)	1678 young adults (428 males, mean age = 25.96, SD = 6.47; 1250 females, mean age = 25.96, SD = 6.47)	SPQ, CATI	AQ	Exploratory factor analysis & Confirmatory factor analysis	The factor model supported shared and diametric subscales: four factors were specific to the common Social Disorganization phenotype, two factors were specific to paranoia and unusual perceptions of schizotypy, and one factor was specific to the autistic dimension of restricted interests.
Trevisan et al. (2020)	39 participants with schizophrenia diagnosis, 53 participants with ASD diagnosis and 40 healthy controls.	PANSS	ADOS-2	ROC curves analysis	Individuals with ASD and SSD showed an overlap in the negative symptom features. Disorder-specific positive symptomology discerns ASD and SZ individuals.
Wakabayashi et al., (2012)	662 students (328 males and 334 females)	SPQ	AQ	Regression analysis	Autistic spectrum and schizophrenia-spectrum traits showed common social-emotional difficulties. However, there was a negative correlation between the AQ score and the ‘Odd beliefs and magical thinking’ subscale of SPQ.

Table 1: Summary of principal studies investigating the relationship between ASD and SSD.

Notes: SPQ = Schizotypal Personality Questionnaire; O-LIFE = Oxford Liverpool Inventory of Feelings and Experiences; CAPE = Community Assessment of Psychic Experiences; MSS = Multidimensional schizotypy scale; CATI = Coolidge Axis II Inventory; PANSS = Positive and Negative Syndrome Scale; AQ = Autism-Spectrum Quotient; ADOS-2 = Autism Diagnostic Observation Schedule.

3. Bayesian inference along the ASD-SSD continuum

The Bayesian framework is a convincing approach to understand the perceptual decision-making deficits observed in ASD and SSD (Adams et al., 2013; Fletcher and Frith, 2009; Hemsley and Garety, 1986; Palmer et al., 2017; Sterzer et al., 2019). Within this approach, the brain is conceptualized as an inferential organ (von Helmholtz, 1867) that exploits the statistical regularities of the environment to optimize the perception of incoming stimuli (Garrido et al., 2013; Knill and Pouget, 2004). This hypothesis derives from pioneering theories (Ullman, 1980) that challenged bottom-up perceptual models (Gibson and Carmichael, 1966). On this latter view, sensory information processing is carried out in a unique direction, starting from low-level areas (i.e., primary sensory regions) to hierarchically higher-level areas implicated in information-integration (Britten et al., 1996; Shadlen et al., 1996). A bidirectional relationship is not contemplated in these models. However, both anatomical (Garrido et al., 2007) and functional (Romei et al., 2016b; Siegel et al., 2015) evidence has cast doubt on this framework. Predictive coding theory (Friston, 2005; Lee and Mumford, 2003; Rao and Ballard, 1999) makes a step further, integrating information flows originating from higher-hierarchical regions. According to this approach, the higher-order areas elaborate *priors beliefs* about the world's states, represented probabilistically, which will be conveyed to lower levels that compare these predictive signals with external input (Yon et al., 2019). The combination of prior belief distribution with the incoming sensory data (likelihood) is exploited to calculate the posterior probability, which will be used to infer which stimulus most likely elicited the sensation (Hohwy, 2012). Any discrepancy between model predictions and input generates a *prediction error* informing regions representing beliefs in order to update them (Bastos et al., 2012; Clark, 2013). The trade-off between maintaining and updating predictive models is determined by the precision associated with beliefs and prediction error: it would not be optimal to update well-established expectations (high prior precision) due to an ambiguous input signal (low sensory

precision); conversely, it is profitable to update predictions estimated to be unstable (low prior precision) in light of clear disconfirming evidence (high sensory precision) (Feldman and Friston, 2010; Hsu et al., 2019; Schröger et al., 2015). The perfect balance between the contribution provided by priors and predictive errors is crucial for a correct inference of the world's hidden states (Friston, 2010).

3.1. ASD and SSD: two opposite ways of making inferences about the external world.

The Bayesian approach to decision-making provides a valid model for understanding the different peculiarities in cognitive style observed in the two spectra. Indeed, each individual assigns a differential weight to priors and to the new information. People within the ASD and SSD spectra represent an extreme way of making this assignment (Dzafic et al., 2020; Fletcher and Frith, 2009; Sinha et al., 2014). Individuals within the autistic spectrum tend to rely on information carried out by external stimuli rather than prior or situational information to guide their behaviour, whereas the presence of ultra-precise abstract priors would play a crucial role in explaining the positive symptoms of SSD (Corlett et al., 2019; Van de Cruys et al., 2014). In the following paragraphs, we explore what mechanisms have been proposed to explain this differential balancing between external information and prior models.

3.1.1. Prediction in ASD

One of the popular models in the scientific panorama that links the symptoms observed in ASD to an imbalance in predictive functioning is the *Hypo-priors* hypothesis (Pellicano and Burr, 2012). This proposal argued that ASD symptoms derive from a lower weight placed on contextual information and predictions in perceptual inference. This theorization is in line with the Weak Central Coherence Theory (Frith, 2003). *Central coherence* designates the human's ability to determine the overall sense from a plurality of elements, and a weak central

coherence is related to an enhanced ability to process local details (Happé and Frith, 2006). This cognitive feature causes a more "realistic" experience of the world because perception is not shaped in the direction of priors and contextual information, relying primarily on incoming stimulus. This inclination confers a performance benefit in tasks where this capability is involved, such as in the block design test (Muth et al., 2014). In this task, participants have to arrange blocks with various colour patterns to recreate a given design. Individuals affected by autism and neurotypical participants with high autistic trait achieved better performance when the target design was presented as a 'whole', but they manifest similar performance to participants with low autistic trait when the given design was pre-segmented, revealing that people with ASD are able to visualize the design in terms of its constituent parts without the aid of pre-segmentation (Shah and Frith, 1993; Stewart et al., 2009). Jolliffe and Baron-Cohen (1997) conducted a study on adults with ASD and paired controls using the Embedded Figures Test that measures the ability to disassemble information from context or surrounding gestalt (Charman et al., 2013). ASD individuals were approximately twice as fast as neuro-typical controls matched on IQ. A similar pattern of results emerges when comparing people with high versus low autistic traits (Cribb et al., 2016).

However, underweighting priors and contextual information result in feeling a fragmented and unpreventable world. Events unpredictability is linked to a sensation of lack of control over the external environment that generates a continuous alertness state (Gallagher et al., 2014). To mitigate this emotional distress, ASD individuals would resort to repeated and stereotyped activities that, by definition, are more predictable (Goris et al., 2020; Grillon et al., 2017, 2008); this could, at least in part, explain the frequent association with anxiety disorders and insistence on sameness observed in ASD individuals (Black et al., 2017; Sinha et al., 2014). However, an alternative interpretation has been suggested proposing an overly precision given

to sensory prediction error in ASD (Karvelis et al., 2018; Van de Cruys et al., 2014). This tendency leads to an exaggerated sensitivity to small fluctuations in sensory input, which triggers a continuous updating of predictive models to accommodate these new cases. This continuous and inappropriate updating might cause the formation of priors having a negligible predictive value (Cannon et al., 2021). Regardless of the precise mechanism they all converge in the idea of a general tendency to privilege sensory information over prior expectations in ASD (Brock, 2012; Friston et al., 2013; Van de Cruys et al., 2013).

3.1.2. Prediction in SSD

Concerning SSD, both weaker and stronger predictive weight have been proposed to explain positive symptoms (Corlett et al., 2019; Sterzer et al., 2018).

The weaker prior hypothesis posits that SSD individuals are characterised by an inability to anticipate sensory events (Mishara and Sterzer, 2015), which entails that every stimulus is inherently surprising to them (Adams et al., 2013; Fletcher and Frith, 2009; Notredame et al., 2014; Sterzer et al., 2019). This pattern leads to an over-attribution of saliency toward sensory experiences promoting a delusional explication of reality (Heinz, 2002). This interpretation could explain the reduced mismatch negativity (MMN) signal observed in this population (Koshiyama et al., 2020; Näätänen et al., 2014), as frequent and infrequent stimuli are treated equivalently (Neuhaus et al., 2013; Randeniya et al., 2018). Furthermore, the weaker prior hypothesis offers an interpretation to the diminished susceptibility to some visual illusion, based on lifelong acquired expectations, observed in SSD (King et al., 2017). Dima and colleagues (Dima et al., 2010, 2009) examined schizophrenia patients' propensity to experience the hollow-face illusion that occurs when the presentation of a concave mask of a face is misperceived as a normal face. Results showed that schizophrenia patients are less prone to perceive this illusion. However, an entire branch of the scientific literature advocates for an alternative hypothesis,

pointing to overweighting of prior information as pivotal in the generation of SSD symptoms (Corlett et al., 2019; Horga and Abi-Dargham, 2019). According to this framework, positive symptoms, such as hallucinations, can be conceptualized as top-down effects on perceptual process, mediated by overly precise prior beliefs (Powers et al., 2016). At first glance, the strong prior hypothesis seems to be against a large body of evidence showing reduced top-down processing as the reason for hallucinations (Hugdahl, 2009). However, “top-down process” is a generic term used in the literature to describe several heterogeneous and dissociable processes (Rauss and Pourtois, 2013). For example, attentional impairment is considered a core symptom of the SSD as it has been associated with positive symptoms (Hugdahl et al., 2013; Gold et al., 2007) and with worse illness outcome (Milev et al., 2005). Nevertheless, numerous findings have highlighted that prior (e.g., expectations) and attentional information impact behaviour differently (Carrasco, 2011; Mulder et al., 2012), are mediated by dissociated mechanisms (Wyart et al., 2012), and are underpinned by different neural substrates (Kok et al., 2017, 2012). Thus, the attentional deficits highlighted in SSD individuals does not imply a concomitant reduction in the use of prior information. Indeed, numerous studies have demonstrated extreme susceptibility to probabilistic and expectation-related information in the SSD population (Barbalat et al., 2012; Gawęda and Moritz, 2021; Haarsma et al., 2020). For example, Powers et al., (2017) evaluated whether, in a visual-auditory conditioning task, the propensity to report tones when no sounds were presented could show increased intensity in patients with hallucinations and healthy control subjects who frequently report hearing voices. Results showed that the number of conditioned hallucinations and confidence correlates with hallucination severity. Computational model evidence (Mathys et al., 2011) shows that this propensity depends on the overweighting of priors' information. Kafadar (2020) confirmed the presence of a trend toward priors overweighting also in the high-risk psychosis population. In particular contexts, this over-reliance on prior information could be adaptive. Teufel (2015)

evaluated how the overweighting of prior information in SSD could lead to perceptual advantages in a task, such as the two-tone image perception, in which this information plays a critical role. At first glance, these black and white images seem indecipherable, but after gaining prior knowledge of image content, the perception of embedded images is facilitated. The study found that healthy individuals with a higher predisposition to delusion and hallucinations have a greater performance benefit from prior information of the image's content. However, this tendency to over-weight prior beliefs could also explain the predisposition toward observe meaningful patterns where there are none present (i.e., apophenia) typically observed in SSD population (Blain et al., 2020; Brugger and Graves, 1997; Mishara, 2010). These misperceptions often have a social dimension both at the auditory and the visual domains (Partos et al., 2016; Vercammen et al., 2008). Indeed, people at risk of psychosis tend to perceive human speech in noisy signals without being told whether speech is present (Kafadar et al., 2020) manifesting a prior towards perceiving auditory-verbal information (Alderson-Day et al., 2017). Furthermore, the prior for detecting faces in noise correlates with hallucination proneness as well as delusion proneness and the prior for detecting invisible direct gaze is significantly associated with hallucination proneness (Stuke et al., 2021). This points to the presence of an implicit high-level expectation pointing to the presence of socially relevant signals (e.g., faces, gaze, speech) in noisy and ambiguous stimuli.

Therefore, strong evidence is available for the presence of both weaker and stronger priors in SSD. A hierarchical interpretation has been suggested to reconcile this apparently conflicting evidence regarding the role of priors in SSD. This hypothesis proposes a different weight assigned to predictive information depending on the specific level that is considered.

Predictions generated at lower levels of the cortical hierarchy (i.e., sensory areas) would have reduced precision in the SSD population. This would lead to persistent signalling of prediction errors to high-level regions leading to an uncertain perceptual representation (Sterzer et al.,

2019, 2018). Since Kraepelin's pioneering studies (Dondé et al., 2019), low-level perceptual abnormalities and deficit in sensory integration have been consistently documented in SSD (Fenner et al., 2020; Ferri et al., 2018; Fotia et al., 2021; Javitt and Freedman, 2015; Martínez and Lopez-Calderon, 2018), both at the behavioural and physiological level (Javitt, 2009; Seymour et al., 2013). Interestingly, impaired sensory representations are related to the tendency to perceive hallucinations (Linszen et al., 2019; Marschall et al., 2020), and signal detection theory analysis (Powers et al., 2017) has found more liberal criteria and low perceptual sensitivity in hallucinations-proneness individuals. Faced with this sensory ambiguity, the perceptual inference would be shaped by ultra-precise higher-order predictions, encoded in upstream brain areas and aimed at shedding light on the pervading "sensory chaos" (Corlett et al., 2019); according to this view, the positive symptoms of schizophrenia would be a sort of compensatory response. Schmack and colleagues (Schmack et al., 2017, 2015, 2013) corroborated this hierarchical interpretation in a series of fascinating experiments using an intermittent presentation of a multi-stable stimulus. In this paradigm, participants are inclined to have the same percept between subsequent stimulus presentations due to an automatic generation of sensory predictions during the intermittent presentation. The percept survival probability from one presentation cycle to the following was found to be reduced both in schizophrenic and in high delusional traits individuals. Nevertheless, when a high-level abstract expectancy on the appearance of ambiguous stimuli was induced using a placebo-like manipulation (Sterzer et al., 2008), high-delusional participants showed greater exploitation of priors' information as shown by a higher probability of perceiving the belief-congruent stimulus. Critically, the two contrasting findings are strictly associated: the strength of the bias provoked by abstract-belief induction was strongest in participants characterized by weaker low-level predictions.

3.2. Predictions in a changing environment

The estimation of mutability of the external environment is central in driving model updating (Kalhan et al., 2021). An environment is considered volatile if the associations between cue-outcome within it are labile (Behrens et al., 2007). If the environment is stable, any errors incurred by the model should be attributed to probabilistic noise, whereas if the environment is changing, the errors should be attributed to a shift in the cue-outcome associations (Van de Cruys et al., 2017). Thus, environmental volatility acts as a modulator of the impact of prediction error on perceptual inference (Mathys et al., 2011). Both ASD and SSD populations have great difficulty in dealing with estimate environmental volatility (Goris et al., 2021; Hernaus et al., 2018; Powers et al., 2017). Recent evidence suggests that the ASD population manifests the tendency to over-attribute uncertainty to environmental volatility rather than probabilistic noise (Lawson et al., 2017). This peculiarity may imply that in ASD the outside world is burdened with an ineradicable amount of uncertainty that would suppress the development of robust context-driven expectations since the weight of the prediction error would be inflexibly inflated (De Martino et al., 2008; Goris et al., 2018; Palmer et al., 2015). It is conceivable that behavioral stereotypies and narrow activity are the result of their need to minimize as much as possible the environmental variability they cannot cope with.

People affected by psychosis manifest a diametric pattern with respect to ASD as they fail to note the volatility of cue-outcome associations, revealing a strong prior that external contingencies are fixed (Powers et al., 2017). Kafadar et al., (2020) demonstrate the presence of the same incapacity to prediction-update when task contingency evolves in clinical high risk for psychosis individuals. These results are in line with the tendency to maintain longer the initial hypothesis and the bias against disconfirmatory evidence (BADE), typically observed in the SSD population in which a previous model is maintained despite its unsuitability in the

current context (Eisenacher and Zink, 2017; Moritz and Woodward, 2006; Orenes et al., 2012).

3.3. Framing ASD and SSD along the predictive continuum

In the previous sections we have outlined the psychometric and behavioral evidence indicating the presence of a diametrical relationship between the autistic and schizophrenic spectrum. A key feature of our proposal is to consider this relationship as the result of contrasting predictive styles along the proposed continuum. We propose a mental health model based on the individual's ability to predict and maximally adapt to environmental demands accurately. Overall, a virtuous model of mental health poses a balanced capacity to statistically integrate sensory information (bottom-up processes) into its internal probabilistic representation (top-down process). Instead, an extreme approach characterizes ASD and SSD which leads to an ill-adapted reaction to external conditions. Individuals within the autism spectrum demonstrate a stimulus-driven approach to perceptual inference, as incoming sensory signals are over-weighted relative to prior information in posterior probability computation. A complementary process is observed in the schizophrenic spectrum where the inner world and preconceived abstract beliefs are pivotal for perceptual inference. In between, along the continuum, behavior results from an integration of sensory evidence and model-driven information resulting in balanced choice with more flexible adaptation to the environment. This evidence suggests the existence of a diametric approach in information processing along a continuum in which autism and schizophrenia lies at the two poles (Figure 1). In the next session we introduce the role that brain oscillations play in the predictive process and extend the proposed framework by linking their disruption to the symptomatology observed in the proposed ASD-SSD continuum.

Insert Figure 1 here.

4. Oscillations-based predictive coding and the interplay between feedforward and feedback connections

Various hypotheses exist about the neural implementation of predictive processes (Spratling, 2017). The key points common to the existing theories are concerned with I) the presence of distinct neural populations responsible for signaling predictions and prediction-error, and II) the need for communication between these two units (Friston, 2019). One of the more accredited implementations of predictive coding follows a hierarchical architecture proposing that predictions are fed back from higher to lower regions, while prediction errors are conveyed in a feed-forward manner following an opposite information flow (Bastos et al., 2012; Friston, 2010; Rao and Ballard, 1999). Since predictive coding theory posits the presence of propagation dynamics along the cortical hierarchy, brain rhythms are one of the neurophysiological mechanisms suitable for understanding the implementation mechanism of prediction and prediction-error transmission, due to their role in neural information-exchange (Arnal and Giraud, 2012; Bastos et al., 2020). The communication-through-Coherence (CTC) theory (Fries, 2015, 2005) claims that inter-areas communication is established when the oscillatory activity between two cerebral hubs occurs within the same frequency band and with a stable phase difference. By integrating this influential theory with predictive-coding, it is possible to conceive that prediction and prediction-error units exchange information through coupling at specific frequencies (Arnal and Giraud, 2012; Friston et al., 2015) and that any deficit in this “spectral connectome” may underlie the symptoms observed in autistic and schizophrenic spectra (Kessler et al., 2016; Uhlhaas and Singer, 2010).

Gamma and alpha rhythm seem to have a specific role in this process (Bastos et al., 2015; Fontolan et al., 2014; von Stein and Sarnthein, 2000). Alpha waves are oscillations in the frequency range of 8-13 Hz that are very prominent in occipito-parietal regions (Clayton et al.,

2018). According to the *Gating by Inhibition theory* (Jensen and Mazaheri, 2010; Klimesch et al., 2007), alpha rhythms have a fundamental role in maintaining an active and flexible mechanism of inhibition that reduces the processing capabilities of a given area irrelevant for the ongoing processing. One of the emerging functions involving this band is the conveyance of top-down predictions to sensory regions (Samaha et al., 2015; Sherman et al., 2016). De Lange et al. (2013) observed a pre-stimulus alpha modulation in posterior areas in trials in which participants had a prior expectation about the upcoming net direction of stimulus motion. Temporal expectations have been associated with alpha desynchronization (Rohenkohl and Nobre, 2011), which tracks the cumulative probability of target appearance (Bauer et al., 2014). It is conceivable that the underlying mechanism of these findings depends on a release from inhibition by alpha desynchronization in task-specific regions as the probability of the target appearance increases (Foxe and Snyder, 2011).

Likewise, modulation of gamma-band activity has been observed in several neuronal processes (Jia and Kohn, 2011). Attended stimuli cause stronger gamma oscillations than non-attended stimuli (Jensen et al., 2007) and gamma-band activity in prefrontal cortex correlates with the number of items held in working memory (Roux et al., 2012). In the predictive coding framework, mounting evidence suggests that gamma-band activity is crucial to prediction-error spread (Arnal and Giraud, 2012; Chao et al., 2018; Sedley et al., 2016). Violations of priors derived from lifelong learning generate increased gamma activity in task-specific areas (Brodski et al., 2015). Gamma response correlates to the mismatch between expectations and concretely presented stimulus: there is more activity when the stimulus is unpredicted (Bauer et al., 2014). This effect is evident even without external stimulus presentation as unexpected omission intensifies gamma activity in sensory regions (Todorovic et al., 2011).

At the circuit level, van Kerkoerle et al. (2014) have shown that gamma and alpha waves propagate in the feedforward and feedback pathways, respectively. Micro-stimulation of the primary visual area (V1) area leads to enhanced gamma power in extra-striate area (V4); instead, V4 stimulation leads to V1 alpha power increase. Using the granger-causality index, Michalareas et al. (2016) showed that "*causal influences along feed-forward projections were predominant in the gamma band, while causal interactions along feedback projections were predominant in the alpha-beta band*". Therefore, it can be hypothesized that predictive information travels along the feedback connections by exploiting alfa/beta synchronization, whereas information related to discrepant signals is conveyed in the opposite stream via gamma synchronization. Strong confirmation of this formulation comes from a multi-unit recording study conducted by Bastos and colleagues (2020). Manipulating the predictability of objects during a working memory task, they showed that feedback functional connections from high to low-level areas are enhanced during predictable blocks with a peak at alpha/beta frequencies. The enhanced functional connectivity during predictable blocks is most robust between deep layers of the prefrontal cortex and the rest of the brain areas. In the feedforward direction, the modulation of functional connectivity is greater in the unpredictable relative to the predictable samples, with a peak in the gamma-frequency range. This evidence is in accordance with rhythms-based models in which (gamma-based) prediction errors ascend the cortical hierarchy and (alpha/beta-based) predictions descend the cortical hierarchy. A proper trade-off between the contribution provided by these two streams of information supports adaptive predictive inference (Figure 2A).

5. Predictive waves in SSD and ASD and the imbalance between feedforward and feedback connections

Accumulating evidence considers structural and functional connectivity indices as reliable diagnostic biomarkers suitable for detecting ASD and SSD (Friston et al., 2016; Jeste et al., 2015; Karlsgodt, 2020). White matter anomalies are detectable years before diagnosis, associated with a higher long-term dysfunctionality, and present throughout the spectra (Blanken et al., 2017; Carletti et al., 2012; Dickinson et al., 2021; Wolff et al., 2012; Zhou et al., 2014). These structural impairments pave the way for the disruption of oscillatory synchronisation. Both ASD and SSD are increasingly conceived as oscillopathies as pathological changes in the normal profile of brain rhythmicity have been extensively related to behavioural deficits (Kessler et al., 2016; Murphy and Benítez-Burraco, 2017, 2016; Simon and Wallace, 2016; Uhlhaas and Singer, 2015). In the following sections we introduce a perspective advocating the relationship between asynchronies in the oscillatory profile and failures in perceptual inference process along the proposed ASD-SSD continuum.

5.1. Predictive waves in SSD

Schizophrenia is conceived as a disconnection disorder (Friston et al., 2016; Friston, 1998; Schmitt et al., 2011). A large analysis conducted on 1963 schizophrenic patients from the ENIGMA Schizophrenia DTI Working Group proves a widespread reduction of fractional anisotropy (a very widely used measures that may be relates to white matter fiber integrity) in schizophrenia patients (Kelly et al., 2018). White matters disturbances have been related to cognitive impairment and symptoms of schizophrenia, such as memory deficits and auditory hallucinations (Hubl et al., 2004; Kubicki et al., 2007). Furthermore, these abnormalities are already present in young individuals at risk of psychosis and in individuals with high schizotypal traits proving the presence of analogous neurobiological bases (Karlsgodt et al., 2009; Nelson et al., 2011). These structural deficits are coupled with deficits in rhythmic communication

between distinct brain areas as shown by hypo- or hyper-synchronisation between brain regions in SSD (Olejarczyk and Jernajczyk, 2017; Rolls et al., 2020). These abnormalities in the rhythmic transmission of information could underlie the predictive imbalances observed in SSD (Fogelson et al., 2014).

Anomalies in alpha synchronization tuning could be a key driver of these deficits (table 2). In task-related regions, there is a modulation of alpha power when participants can predict the identity of the incoming stimulus (Mayer et al., 2016), which prepares the brain for upcoming perception (Romei et al., 2010; Samaha et al., 2018). Alpha power modulation in sensory areas reflects a state of biased perception in which the number of hit rates increases, regardless of the stimulus presence (Iemi et al., 2017; Samaha et al., 2017). Higher alpha power in parieto-occipital cortical sites is evident in participants with a higher propensity to induce meaning in coincident events (Rominger et al., 2019) and an abnormal modulation of alpha activity in frontal and temporoparietal regions has been connected to maladjustment of expectation regarding the behavior of their partners in the Ultimatum Game in schizophrenic patients (Billeke et al., 2015). Abnormal alpha activity is present also in neurotypical individuals with high schizotypal traits in frontal, central and occipital areas (Fuggetta et al., 2014). The origin of alpha modulation in early sensorial regions derives from top-down signals from the executive control areas (e.g., frontal region) (Capotosto et al., 2017; Popov et al., 2017). Given the crucial role of alpha in conveying predictive information and in biasing perception (Clayton et al., 2018), the proposed framework states that the tendency to overweight aprioristic knowledge observed in the SSD population could rely on inflexible synchronization from high to low-level regions in the alpha band which shapes the excitability of sensory areas as a function of prior knowledge. (Table 6, hypothesis 1; Figure 2B). At first glance, this hypothesis seems to be incompatible with the definition of schizophrenia as a disorder of brain connectivity (Friston and Frith, 1995). Nevertheless, the nature of the disorders in cerebral mapping in the SSD

population is elusive and uncertain. Despite a stream of evidence points to the presence of reduced connectivity in schizophrenia (Lawrie et al., 2002; Papousek et al., 2014; Trajkovic et al., 2021; Vercammen et al., 2010), there are also fMRI and EEG/MEG findings testifying the presence of excessive connectivity (Anticevic et al., 2015; Cao et al., 2019; Krishnadas et al., 2014; Siebenhühner et al., 2013; Xie et al., 2019). For example, Liu et al., (2019) observed enhanced alpha band functional connectivity in superior parietal, right temporal, and left occipital brain regions in first-episode schizophrenia and ultra-high risk for psychosis population. Kam et al., (2013) identify the presence of increased coherence in the lower alpha frequency spectrum (8–10 Hz) in centro-temporal and in upper alpha frequency (10–12 Hz) in centro-parietal and parietal-temporal regions in schizophrenia patients and higher schizophrenia polygenetic risk score is associated with elevated resting-state theta (3–7 Hz) and alpha (7–12 Hz) coherence (Meyers et al., 2021). Similarly, Rutter et al., (2013) highlighted a trend towards enhanced coherence between the frontal gyrus and the rest of the brain in theta (4–8 Hz) and alpha (8–14 Hz) frequency bands in schizophrenic patients and higher fronto-parietal within-network connectivity is associated with poor illness outcome (Collin et al., 2020). Furthermore, a large number of studies pointing to the presence of reduced functional connectivity in SSD population does not indicate the directionality of connectivity anomalies (Mechelli et al., 2007). Rolls et al., (2020) demonstrated that, on average, the forward effective connectivities were smaller in the SSD population relative to controls, but the backward connectivities tended to be larger. Since forward connections are stronger than feedback connections, functional connectivity (which does not discriminate between the two) could be lower in SSD due to the reduction in the (stronger) forward connectivity (Rolls, 2021). Scientific research using effective connectivity indices points in this direction. In a resting-state study, Gao et al., (2020) observed an increased Granger causality from Broca's area and Broca's homologue to the bilateral Superior Temporal Gyrus (STG) in

patients with schizophrenia with auditory hallucinations, which was also associated with the severity of hallucinations. Furthermore, correlation analysis showed that Granger causality from the STG to the right homologue of Broca's area was negatively correlated with the severity of hallucinations, confirming the presence of reduced forward information flow in patients with positive symptoms. These connectivity pattern peculiarities show also functional correlates. In an explicit gaze discrimination task, schizophrenic patients show increased top-down inhibition from frontal areas to the visual cortex that contribute to poorer social cognition (Tso et al., 2021). Stronger influence of high-level areas on visual regions during gaze discrimination could reflect increased reliance on higher-level prior to determine the decision about the nature of gaze. This could represent the neural underpinning of the tendency to report the presence of socially significant signals in noisy and ambiguous stimuli highlighted in the previous section (Stuke et al., 2021). In corroboration of this hypothesis, functional evidence (Schmack et al., 2013) has revealed that, in a perceptual decision-making task, the neural underpinning of priors overweighting in high delusion-proneness individuals relies on increased functional connectivity between frontal and occipital regions. Related findings come from an auditory odd-ball study conducted recently by Dzafic et al., (2021). Analyzing brain activity through EEG recording, the researchers found that brain responses to unexpected sounds were smaller in participants with schizophrenia than in those without the disorder testifying to a reduced prediction errors signaling. Crucially, participants who experienced more psychotic-like symptoms showed stronger top-down connectivity from the left inferior frontal gyrus (IFG) to the superior temporal gyrus (STG). These connectivity abnormalities could be behind the maladaptive inferential process observed in SSD. Moreover, participants who experienced more hallucinations showed weaker bottom-up connectivity from the STG to IFG. This suggests that strong maladaptive predictions may lead to reduced transmission of ascending prediction errors. Indeed, much neural and computational evidence suggests that,

already at the lower levels of the sensory hierarchy, neural activity reflects a mixture of stimulus-related signals and top-down information deriving from high-level areas (Haefner et al., 2016; Nienborg and Cumming, 2009; Nienborg and Roelfsema, 2015). Critically, if too much weight is given to reentrant signals coming from these regions, the activity of the sensory areas may conform rigidly according to top-down-information, leading to a self-confirmation loop (Talluri et al., 2018; Wimmer et al., 2015). Furthermore, an inability to modulate these (alpha-based) signals in response to repeated external invalidation could be the neural underpinning of impairments in the processing of disconfirmatory evidence in SSD (Eisenacher and Zink, 2017; Hemsley and Garety, 1986). Thus, future studies based on the proposed bio-behavioural model will need to explore whether prior's overweight depend on alpha hyper-synchronization that induces a bias at the level of the sensory cortices.

However, the mechanism that causes an over-use of prior knowledge might not depend on an excessive influence on the activity of sensory areas exerted by higher level areas, but rather on an impoverishment in the encoding of sensory data. The predictive coding theory assumes that the weight given to incoming sensory signals in belief updating is discounted according to their precision, in order to avoid updating established models due to noisy inputs (Tassinari et al., 2006). In the previous paragraph we have showed that low-level perceptual abnormalities and deficit in sensory integration have been consistently documented in SSD (Butler et al., 2008). Thus, another hypothesis arising from the proposed framework states that the presence of reduced precision in sensory evidence encoding in the SSD population would lead to a fixed prediction errors' underweighting in perceptual inference. A neural marker associated with efficient sensory coding is the alpha velocity. Alpha oscillations act as an internal clock whose rapidity determines the temporal resolution of the perceptual process (Samaha and Postle, 2015) and the integration vs. segregation across sensory modalities (Bastiaansen et al., 2020; Cecere et al., 2015; Cooke et al., 2019; Migliorati et al., 2020). The reduction and acceleration

of alpha speed using tACS widens and shrinks the sensory integration window, increasing and reducing the illusion susceptibility (Cecere et al., 2015). Similar findings have been reported by Minami and Amano (2017) and Zhang et al., (2019). Furthermore, individuals with faster alpha oscillations sample the stimuli at a higher rate leading to a finer visual temporal resolution, and alpha speed increases when participants perform demanding visual tasks in which enhanced visual information processing is required (Haegens et al., 2014). Critically, some studies demonstrated that alpha peak frequency in posterior areas as well as the propagation of alpha waves in the cortical hierarchy is significantly lower in the SSD population (Fuggetta et al., 2014; Murphy and Öngür, 2019; Karson et al., 1988; Trajkovic et al., 2021; Yeum and Kang, 2018). Ramsay et al., (2021) demonstrated that schizophrenic individual showed reduced alpha speed compared to the control group over every electrode site at rest. Crucially, reduced individual alpha speed was predictive of lower sensitivity in a visual task and related to impaired global cognition. Moreover, sensitivity measures fully mediated the relationship between alpha speed and global cognition index suggesting that deficits in stimulus discrimination fully account for the relationship between lower alpha speed and weakness in global cognition. Thus, it is possible that a primary sensory deficiency triggers cascade mechanisms that lead to the generation of the neurocognitive deficits observed in schizophrenia. As illustrated in the previous sections, an additional neural feature involved in the routing of stimulus-related information are gamma oscillations (Bastos et al., 2015). In the study of Bastos et al. (2020), switching from a predictable to an unpredictable block led to large prediction-error in the first post-switching trials. Analyzing spectral correlates, the study showed a strong gamma increase that peaks in these trials. It would be stimulating to analyze how the gamma response in SSD is modulated by predictions' invalidation. Literature evidence indicates a decrease of this frequency band in a multitude of cognitive processes in the SSD population (table 3; Reilly et al., 2018; Senkowski and Gallinat, 2015; Uhlhaas and Singer,

2013), regardless of current medication (Minzenberg et al., 2010) and gamma power was found to be negatively correlated to schizotypal personality traits in first-degree relatives of schizophrenia patients (Chen et al., 2019). Several studies have shown that connectivity in the gamma frequency is reduced in SSD during visual and auditory processing (Mulert et al., 2011; Uhlhaas and Singer, 2015, 2010) and that there is a negative correlation between gamma-based connectivity from occipital to anterior prefrontal cortex and the PANSS scores (Fujimoto et al., 2013). Recent studies proved a reduced granger causality index in gamma-based feedforward connections in visual cortices in SSD coupled with a diminished oscillatory gamma response to novel presented (i.e., unpredictable) stimuli (Grent et al., 2020; Sauer et al., 2020). These results point to a reduced ability of the visual system to tune gamma oscillations optimally. According to our model, this may lead to a deficit in the forward propagation of stimulus-based information leading to its underweighting in perceptual inference.

Crucially, the abnormalities of alpha and gamma oscillations hypothesized to be the underlying reasons of the reduced weight given to sensory information in the SSD population could be intertwined due to their strong synergy: gamma amplitude is phase-locked to occipital alpha oscillations (Canolty and Knight, 2010; Osipova et al., 2008; Spaak et al., 2012), and this coupling is enhanced during visual tasks (Voytek, 2010). White et al. (2010) provide evidence of weakened alpha-gamma interactions in schizophrenia during sensory information processing. Using a joint independent component analysis, the authors observed a significant correlation between the alpha-dominated component and the evoked gamma power in the healthy group, whereas in schizophrenic patients this relationship was abolished. Our model hypothesizes that the altered alpha-gamma relationship in SSD population would lead to poorer perceptual sampling. Alpha activity provides a clock mechanism through periods of inhibition repeated every ~100 ms generating cycles of cortical excitability (*duty-cycle*) within the two pulses (Bonnefond et al., 2017; Jensen et al., 2012). Gamma oscillations are nested in

the excitability phases of the alpha rhythm in order to represent the information of each *perceptual snapshot* (Bonnefond and Jensen, 2015; VanRullen and Koch, 2003). It can be conceived that individuals with faster alpha have an increased number of windows of excitability in which the gamma-rhythm can be embedded, ensuring a finer representation of the stimulus. Thus, the reduced speed of alpha oscillations in SSD would result in an imprecise prediction error spread due to the reduced number of duty-cycles in which the gamma rhythm can be nested. Crucially, an inaccurate prediction error is less able to counter-act pre-existing priors that, thus, rigidly orient perceptual inference (table 6, hypothesis 2; Figure 2B).

However, we emphasize that the strong prior hypothesis and the imprecise prediction-error forwarding hypothesis are not mutually exclusive. Indeed, the presence of poor and chaotic sensory processing could generate a cascade mechanism imposing more precise priors in the higher level of the cortical hierarchy. Evidence suggests that overwhelming people with ambiguous information generates a feeling of lack of control that leads individuals to embrace conspiracy theories or superstitious thoughts to cope with them (Whitson and Galinsky, 2008). Therefore, it is possible to speculate that such an effect may trigger, in SSD people, the impulse to seek an explanation and, thus, finally forge delusional beliefs (Berkovitch, 2017).

Table 2. A summary of EEG/MEG task-based studies showing alteration in alpha oscillations in SSD

Study	Sample characteristic	Paradigm	Summary of findings
Fuggetta et al., (2014)	16 high schizotypy participants (Mean age = 19.80 ± 1.19) 16 low schizotypy participants (Mean age = 20.46 ± 1.93)	Resting State	High schizotypal individuals show increased low-alpha power in frontal, central and occipital areas.
Goldstein et al., (2015)	13 ScZ patients (mean age = 33.2 ± 10.7) 10 control patients (mean age = 36.5 ± 8.8) 13 control participants (mean age = 38.2 ± 11.2)	Resting State	Individuals with ScZ demonstrated decreased alpha EEG power in frontal and occipital areas relative to healthy controls
Hu et al. (2020)	23 high positive schizotypy participants (mean age = 19.17 ± 1.40) 19 high negative schizotypy participants (mean age = 19.68 ± 1.73) 18 control participants (mean age = 21.00 ± 3.88)	Resting State	Negative schizotypy connected to greater alpha connectivity in posterior regions. Positive schizotypy connected to decreased alpha band occipital connectivity.
Kam et al., (2013)	76 bipolar patients (mean age = 41) 132 ScZ patients (mean age = 40) 136 controls participants (mean age = 39)	Resting State	ScZ patients exhibited greater Alpha1 coherence at the central-temporal region and Alpha2 coherence in both central-parietal and parietal-temporal regions relative to controls
Kim et al., (2015)	90 ScZ participants (mean age 33.39 ± 9.94) 90 control participants (mean age = 37.44 ± 10.25)	Resting State	ScZ patients showed decreased alpha-2 activity.
Kustermann et al., (2016)	14 ScZ patients (Mean age = 37.1 ± 11.9). 25 control participants (Mean age = 33.1 ± 11.4).	Cued delayed response task	ScZ patients failed to show hemifield-specific alpha modulation in posterior hemisphere.
Liu et al., (2019)	28 FEP patients (mean age = 25.86 ± 7.33) 28 CHR participants (mean age = 24.1 ± 6.56) 28 controls participants (mean age = 24.14 ± 3.71)	Resting State	The FES and CHR groups displayed increased resting-state alpha connectivity compared with the healthy controls
Murphy et al., (2019)	22 FEP patients (Mean age = 22.0 ± 2.7) 22 control participants (Mean age = 23.1 ± 2.7)	Steady-state visual evoked potentials	Patients had attenuated responses to SSVEP stimulation at alpha frequencies.
Ramsay et al., (2021)	95 ScZ patients. 86 control participants.	Visual attention task	Schizophrenia group showed slower alpha speed associated with poorer performance in a visual task
Trajkovic et al., (2021)	24 high Schizotypy participants (mean age = 23 ± 0.5)	Resting State	High Schizotypal participants shows a significant slowing down of posterior alpha frequency along with reduced connectivity in the alpha range

Summary

Although the evidence in alpha is mixed, it can be observed a reduction in its speed combined with synchronization anomalies in the SSD population.

Notes: ScZ = schizophrenic patients; CHR = clinical high-risk criteria for psychosis; FEP = first-episode psychosis.

Table 3. A summary of EEG/MEG task-based studies showing alteration in gamma oscillations in SSD

Study	Sample characteristic	Paradigm	Summary of findings
Fujimoto et al., (2013)	10 male ScZ patients (mean age = 30.9 ± 5.0) 10 control participants (mean age = 28.5 ± 4.6)	Oddball task	Occipito - frontal connectivity in the gamma band correlate negatively with PANSS score.
Grent et al., (2020)	119 CHR participants (mean age = 22 ± 4.4) 26 FEP patients (mean age = 24 ± 4.2) 38 participants with affective disorders (mean age = 23 ± 4.7) 49 control participants (mean age = 23 ± 3.6)	Visual grating task	Reduced occipital gamma-band power across all visual cortex ROIs and altered visual cortex forward connectivity in gamma band in FEP. Differences in γ -band phase-clustering were found for both CHR-P and FEP participants compared with HC
Grützner et al., (2013)	16 patients with chronic schizophrenia (mean age = 38.2 ± 9.3) 16 control participants (mean age = 34.2 ± 10.6)	Mooney faces	Reduction in spectral power in the higher gamma band in ScZ patients which was correlated with schizophrenic symptoms.
Hamm et al., (2011)	17 ScZ patients (mean age = 40.7). 17 control participants (mean age = 39.7).	Steady-state auditory tones	ScZ patients had reduced gamma response to 40-Hz stimuli in right auditory area.
Mulert et al., (2011)	18 patients with chronic schizophrenia (mean age = 39.8 ± 10.5) 16 control participants (mean age 44.4 ± 6.8).	Passive listening of click trains presented at 40 Hz	Decreased gamma - phase synchronization between left and right Heschl's gyri in patients with ScZ
Murphy et al., (2019)	22 FEP patients (Mean age = 22.0 ± 2.7) 22 control participants (Mean age = 23.1 ± 2.7)	Steady-state visual evoked potentials	Patients had attenuated responses to SSVEP stimulation at gamma frequencies.
Popov and Popova (2015)	46 ScZ patients (mean age = 37 ± 9) 58 control participants (mean age = 34.4 ± 11.6)	Resting State	ScZ patients showed lower gamma power. Gamma power correlated with performance on a working memory task in healthy control, but this relationship was abolished in ScZ.

Summary

Overall, the table shows the presence of a reduced gamma amplitude associated with a lack of synchronization along this frequency band in the SSD population.

Notes: ScZ = schizophrenic patients; CHR = clinical high-risk criteria for psychosis; FEP = first-episode psychosis.

Table 4. A summary of EEG/MEG task-based studies showing alteration in alpha oscillations in ASD

Study	Sample characteristic	Paradigm	Summary of findings
Cornew et al., (2012)	27 children with ASD (mean = 9.8 ± 2.3) 23 TD controls (mean = 10.8 ± 2.5).	Resting State	Higher alpha band power at posterior temporal and occipital regions in ASD.
Keehn et al., (2017)	19 children with ASD (Mean age 14.4 ± 1.6) 21 TD children (Mean Age = 14.3 ± 1.4).	Resting state + Rapid serial visual presentation paradigm (RSVP)	Children with ASD had significantly decreased resting alpha power in posterior and central electrodes. Children with ASD did not show posterior alpha desynchronization to behaviourally relevant targets.
Mathewson et al., (2012)	15 ASD adults (mean age = 35.5 ± 10.6). Control group of 16 adults (mean = 35.7 ± 7.6).	Resting State	Coherence in posterior brain regions in the alpha band was inversely correlated with attention to details scale score.
Murias et al., (2007)	18 male adults with ASD (mean age = 22.66 ± 4.4) 18 control male adults (mean age = 24.93 ± 6.82)	Resting State	Reduced low alpha power in ASD. Reduced Fronto-parietal and Fronto-occipital alpha coherence in ASD.
Murphy et al., (2014)	16 ASD participants (mean age = 12.22 ± 1.71) 17 TD participants (Mean Age = 12.20 ± 1.93).	Attentional task	No modulation of preparatory alpha - band activity according to task demands in posterior regions in ASD.
Pierce et al., (2021)	31 ASD participants (mean age = 11.3 ± 1.6) 31 control participants (mean age = 10.6 ± 1.9)	Resting State	Children with ASD showed significantly decreased resting alpha power compared to their TD peers.
Seymour et al., (2019)	18 participants with ASD (mean age = 16.67 ± 3.2) 18 TD control (mean age = 16.89 ± 2.8).	Basic visual perception task	Reduced alpha - based V4-V1 feedback connectivity in ASD. Reduced alpha-gamma coupling in primary visual area.
Ye et al., (2014)	16 adolescents with ASD (mean age 14.4 ± 1.1 years) 15 TD controls (mean age 14.9 ± 0.9 years).	Resting State	Occipito-parietal regions showed disconnection from widespread brain areas in the alpha band in ASD.
Zeng et al., (2017)	21 children with ASD (mean age = 9.9 ± 1.5). 21 TD children (mean age = 10.1 ± 1.3).	Resting State	Global functional connectivity in ASD was significantly lower in the alpha band.

Summary

The table shows the presence of a reduced alpha amplitude associated with a lack of synchronisation along this frequency band in the ASD population.

Notes: ASD = autism spectrum disorder; TD = typical development

Table 5. A summary of EEG/MEG task-based studies showing alteration in gamma oscillations in ASD

Study	Sample characteristic	Paradigm	Summary of findings
Cornew et al., (2012)	27 children with ASD (mean = 9.8 ± 2.3) 23 TD controls (mean = 10.8 ± 2.5).	Resting State	Higher gamma band power in posterior brain regions in ASD.
Khan et al., (2015)	15 children with ASD (mean age = 11.4 ± 3.7) 20 TD children (mean age = 11.9 ± 2.8).	Passive vibrotactile stimulation	Feedforward functional connectivity at 25 Hz between S1 and S2 was increased in ASD.
Kitzbichler et al., (2015)	15 children with ASD (mean age = 12.5 ± 4.45). 15 TD children (mean age = 13 ± 4.8).	Resting State	Enhanced gamma-mediated feedforward processing in ASD.
Orekova et al., (2007)	40 ASD boys 40 TD boys	Passive video viewing	Higher gamma power in Centro-parietal areas in ASD.
Peiker et al., (2015)	20 ASD participants (mean age = 31.2). 20 control participants (mean age = 31.5).	Slit-viewing paradigm	Decreased gamma-band coherence between bilateral superior temporal sulci
Takesaki et al., (2016)	18 children with ASD (mean age = 6.9). 18 TD children (mean age = 7.16).	Visual reasoning task	Stronger occipito-frontal connectivity in the gamma band was associated with higher performance in ASD.
Van Diessen et al., (2015)	19 ASD individuals (mean age 10.6 ± 4.1) 19 matched controls (mean age 10.1 ± 3.8).	Resting State	Higher gamma power in frontal, parietal, and temporal channels in ASD.
Ye et al., (2014)	16 adolescents with ASD (mean age 14.4 ± 1.1 years) 15 TD controls (mean age 14.9 ± 0.9 years).	Resting State	Hyperconnectivity in gamma range in frontal and temporal regions.

Summary

Overall, the results show the presence of an enhanced gamma amplitude associated with a hyper-synchronisation along this frequency band in the ASD population.

Notes: ASD = autism spectrum disorder; TD = typical development

5.2. Predictive waves in ASD

Although there is strong evidence of multiple alterations in oscillatory synchronization in ASD, few studies have directly assessed their relationship to predictive process impairments.

Anatomical evidence demonstrated a widespread impairment in white matter projections,

particularly in the corpus callosum (CC), bilateral frontal-occipital fasciculus, right arcuate fasciculus, and right uncinate fasciculus (Dimond et al., 2019; Galvez-Contreras et al., 2020), and autistic symptom severity are connected to prominent overconnectivity in posterior brain regions (Keown et al., 2013). A study using a large cohort of children (430 ASD and 554 controls) showed that EEG coherence analysis between brain areas can identify children with ASD with a classification success of 86% (Duffy and Als, 2012). An EEG study (Goris et al., 2018) found that autistic patients exhibit a lower susceptibility to contextual information in an odd-ball paradigm reflected by a reduced modulation of the mismatch negativity wave as a function of the probability of occurrence of the deviant stimulus. These results provide electrophysiological evidence of the inability to adjust the magnitude of prediction error in accordance with the external context, resulting in a bias towards model over-correction. In the spectral domain, alpha oscillations are particularly affected in ASD (table 4; Simon and Wallace, 2016). Individuals with ASD show reduced power in alpha band (Canton et al., 1986; Chan et al., 2007) across many brain regions, including the frontal (Murias et al., 2007; Dawson et al., 1995), temporal (Dawson et al., 1995), occipital and parietal (Keehn et al., 2017; Murias et al., 2007) lobe. A review conducted by Wang et al. (2013) suggests the presence of a U-shaped pattern of power abnormalities: alpha is reduced, whereas lower and higher frequencies are hyper-represented. Deficits in alpha wave amplitude are coupled with issues in synchronization between different cortical areas along this band. Decreased alpha phase coherence across frontofrontal, frontotemporal, and frontoparietal connections at 3 months of age predicted higher level of ASD symptoms at 18 months (Dickinson et al., 2021). In a resting-state paradigm, Mathewson et al. (2012) found a negative association between preferential attention to detail scores and alpha coherence in posterior brain areas. During task conditions adults with ASD do not modulate posterior alpha synchronization when facing behaviourally relevant targets (Keehn et al., 2017) and showed a reduced connectivity

compared to neurotypical individuals in the alpha band in a network with a main hub in the right inferior frontal gyrus in a Go/No-go task (Yuk et al., 2020). Mixed results emerge when considering gamma frequency bands (table 5; Kessler et al., 2016; Simon and Wallace, 2016). Some evidence shows a reduction in both power and coherence indices in the gamma band in ASD participants, underlying poorer behavioural performance (Peiker et al., 2015a; Sun et al., 2012). However, there is also evidence pointing in the opposite direction showing an increase in gamma responsiveness in ASD. In a resting-state study, connectivity strength in gamma band positively correlates with ADOS score (Kitzbichler et al., 2015). Takesaki et al. (2016) prove that stronger functional connectivity from occipital to higher-order regions within gamma band (but not in the alpha and beta) is related to higher sensitivity in visuo-spatial task in the ASD participants. Using a dot motion discrimination task, Peiker et al. (2015b) demonstrated greater gamma power modulation in the ASD population as the motion intensity increases.

In sum, it is possible to conceive that in the ASD population there is a general tendency towards alpha under-coordination associated with a counterbalanced over-expression of higher frequencies (Brown et al., 2005; Keehn et al., 2017; O'Reilly et al., 2017; van Diessen et al., 2015). These spectral features could underpin the tendency to overestimate stimulus-related information in ASD (Figure 2C).

Given the prominent role of alpha-band oscillations in prior signaling (Bastos et al., 2020), a first hypothesis of the proposed model on ASD population states that the dysfunction in fine-tuning of frequency bands involved in conveying priors could be the core feature underlying of decreased susceptibility given to prediction-based information in this population, as theorized by Pellicano and Burr (2012) (table 7, hypothesis 1, Figure 2C). The lack of top-down signaling would cause a weak regulation of downstream areas activity, which becomes susceptible to even slight input fluctuations, resulting in frequent occurrence of prediction errors (Kessler et

al., 2016). Nevertheless, an opposite hypothesis taking into account the prominent role of gamma-band oscillations in prediction-error signaling (Todorovic et al., 2011) states that the excessive gamma-band synchronization observed in ASD population would induce a sustained forward propagation of prediction-error signals that provokes the build-up of loose predictions that have almost no impact when flow back through the hierarchy (Table 7, hypothesis 2, Figure 2C). A study conducted by Khan (2015) demonstrates that during a vibrotactile stimulation, feedforward functional connectivity between S1 (primary somatosensory cortex) and S2 (secondary somatosensory cortex) was significantly greater in the autistic participants than in healthy participants, testifying to an increase in bottom-up processing in ASD. This reliance on bottom-up processing relative to top-down prior information may lead to an increased veridical representation of the external world (Aru et al., 2018; Karvelis, 2018). Although in a bidirectional model it is not trivial to infer which is the source of the problem and which is a secondary consequence, a recent research conducted by Seymour et al. (2019) suggests the validity of the *hypo-priors* hypothesis. In this study, ASD and healthy control performed a visual sensory task while their brain activity was recorded through magnetoencephalography (MEG). Results show that both healthy and ASD participants exhibited a strong increase from V1 to V4 connectivity in post-stimulus time that peaks in the gamma range, indicating a comparable level of feedforward information flow. However, in the healthy group there was a concurrent prominent increase in alpha-based feed-back connectivity from V4-to-V1 that was reduced in ASD. Crucially, there was an association between the Autistic Quotient score and the Granger causality values in the alpha band indicating that increased V4-to-V1 feedback connectivity is related to lower autistic traits. Future studies embracing the proposed bio-behavioral model need to elucidate whether this failure in alpha-based top-down signaling noted by Seymour et al, (2019) in a passive viewing task could be the neural basis of the reduced use of prior information observed in ASD at the

behavioral level. Furthermore, similar to the possibility that predictive deficits in SSD may be due to a dual mechanism of over-signaling of prior models and under-weighting of stimulus-based information, it cannot be excluded that in ASD reduced (alpha-based) predictions signaling and increased (gamma-based) external information weighting are concomitant causes of the imbalance between prediction and prediction-error weightage. Indeed, Seymour et al., (2019) also highlights that inefficiency in long-range top-down connections is correlated with un-coupling between gamma power and alpha phase at the level of primary visual cortex. This evidence suggests the presence of a weakness in top-down signalling in ASD that leads to a lack of orchestration of downstream activity which becomes less constrained from feedback information flows (Kessler et al., 2016; Mamashli et al., 2021; Seymour et al., 2017; Varela et al., 2001).

Insert Figure 2 here

5.3. Predictive waves in a changing environment

As we pointed out in the previous sections, there is converging evidence of an opposite approach along the ASD-SSD continuum in external volatility estimate. The oscillatory correspondences of these peculiarities are still poorly understood. It would be relevant to determine how ASD modulate alpha and gamma synchronization in paradigms in which prediction and prediction-error must be weighted according to external volatility estimation. Moving from a stationary context to a new one having different associations, prior expectations have to be ignored compared to the incoming input to facilitate the acquisition of new models (Lawson et al., 2017). At the neural level, this should connect to decreasing alpha signalling (due to reduced precision of prior model) as the external volatility increased. We propose that

this contextual shift would have less influence on alpha responses in ASD individuals, since they tend to discount external predictive information regardless of context (Crawley et al., 2020; Palmer et al., 2017) as they assume that an ineradicable great amount of uncertainty is intrinsically linked to external world such that prior models have always associated a low precision (Lawson et al., 2017) (Table 7, hypothesis 3). Moreover, Bayesian inference models argue that prediction errors should be underweighted when the current environment is estimated to be stable and increased when it is changing. According to the proposed bio-behavioural model, it is conceivable that in neurotypical subjects the gamma-based prediction error response tracks this volatility-based modulation, whereas in ASD individuals this relationship would be altered as volatility is rigidly overestimated by them (Palmer et al., 2017) (Table 7, hypothesis 4).

An opposite behavioural pattern has been outlined in SSD. Indeed, SSD individuals have a strong prior that environmental contingencies are fixed due to low volatility associated to the external world (Diaconescu et al., 2020; Kafadar et al., 2020; Powers et al., 2017). Therefore, they may not be able to update a structured belief whenever it is no longer appropriate resulting in rigidly exploiting the overly precise expectations previously created. We state that, following the contextual change, the SSD individuals will not rescale the precision associated with the established model, leading to unchanged alpha signalling (due to un-reduced precision of prior model) underpinning belief-update abnormalities (Table 6, hypothesis 3). Moreover, this issue could be exacerbated by the poor precision of sensory encoding. The reduction of alpha speed paired with low gamma synchronization observed in SSD could be related to the inability to effectively sample and convey incoming stimulus information that aid belief-update in a mutable environment. Following this line, the belief-update problem could have a low-level root due to intrinsic inability of the perceptual system to organise a sufficiently structured percept which prevents SSD individuals from reversing pre-existing expectations (Table 6, hypothesis 4).

Table 6. A list of testable hypotheses associated with our novel framework in the SSD pole	
1. Priors hyper-signalling in SSD	
Background: Alpha rhythm is central in conveying predictive information and conditioning perception. Higher top-down synchronization underpins greater use of prior knowledge in SSD (Schmack et al., 2013).	Hypothesis: Higher top-down connectivity in alpha frequency would underpin the overweight of prior knowledge that bias sensory cortex activity in SSD.
2. Imprecise prediction-error forwarding in SSD	
Background: Alpha speed correlates with sensory sampling efficiency and gamma band activity is related to prediction error signalling. Both parameters appear to be altered in SSD (Ramsay et al., 2021; Uhlhaas & Singer, 2015).	Hypothesis: Lower alpha speed combined with lower gamma synchronization would lead to imprecise prediction errors spread in SSD.
3. Rigid (over)-signaling of prediction in SSD	
Background: SSD individuals do not update a pre-structured belief when passing to the new context (Powers et al., 2017). This is due to the tendency not to decrease the precision associated with the pre-established model in function of external volatility (which is rigidly underestimated).	Hypothesis: The (alpha-based) signaling of pre-established expectations would remain stably high regardless of the contextual change in SSD.
4. Rigid (under)-signaling of prediction error in SSD	
Background: As the environment changes, external information must be weighted more heavily to update past models. The ability to precisely encode and transmit incoming information is crucial for belief-update.	Hypothesis: Lower alpha speed and lower gamma synchronization would lead to inefficient conveyance of contrasting information in SSD pivotal to belief-update in a changing environment.

Table 7. A list of testable hypotheses associated with our novel framework in the ASD pole	
1. Priors hypo-signalling in ASD	
Background: Predictive information travels along feedback connections via alpha synchronisation. Feedback connectivities are affected in ASD, particularly in the alpha band (Seymour et al., 2019).	Hypothesis: Deficient top-down connectivity in alpha frequency would underpin the underweight of prior knowledge in ASD.
2. Overweighted prediction errors forwarding in ASD	
Background: Gamma-band oscillations have a prominent role in prediction-error signaling via feed-forward connectivity. Bottom-up connectivity is increased in the ASD individuals and underlies sensory abnormalities (Khan et al., 2015).	Hypothesis: Higher bottom-up gamma synchronization in ASD would induce sustained forward propagation of prediction error signals that continually invalidate prior models.
3. Rigid (under)-signaling of prediction in ASD	

<p>Background:</p> <p>Moving from a stationary environment to a new one, previous expectations must be ignored with respect to the incoming input (Palmer et al., 2017). This contextual shift lead to reduced (alpha-based) prior signaling as long as the new expectations are acquired (Bastos et al., 2020).</p>	<p>Hypothesis:</p> <p>The alpha-based predictive signaling would be fixedly low regardless of the contextual volatility in ASD</p>
<p>4. Rigid (over)-signaling of prediction error in ASD</p>	
<p>Background:</p> <p>The prediction error must be discounted according to the degree of volatility that the environment exhibits. ASD individuals do not shape prediction error signals according to context as they tend to overestimate the volatility of the external environment (Lawson et al., 2017).</p>	<p>Hypothesis:</p> <p>The gamma-based prediction error response would fixedly high regardless of the contextual volatility in ASD.</p>

6. Concluding remarks and future perspective

From psychometric, behavioral, and physiological evidence, an emerging framework can be delineated which suggests that the predictive disorders present in the two spectra could be considered antithetical to each other due to underlying oscillatory mechanisms pointing in different directions. Although maladjustments in the oscillatory profile are extensively demonstrated in ASD and SSD, there are limited attempts to systematically integrate these findings within the predictive coding framework. One of the aims of this work is to stimulate more investigation linking these two topics by offering an overview of the state of the art. Within the proposed continuum model, (mal-)adaptive behavior is linked to its neurobiological roots, which are more amenable to scientific questioning than the rigid symptom-based clinical diagnoses classically used, which have proved to be unreliable guides to understanding mental health and what causes mental illness (Insel et al., 2014). Indeed, the model draws some crucial assumptions about the mechanisms leading to these diametric approaches to the interaction with the environment (see Table 6 and 7). By investigating the proposed hypotheses, it would be possible to go beyond symptom-based clinical and behavioral phenomenology by determining which electrophysiological markers underpin the altered

predictive mechanisms that lead to ill-adaptation. An important aspect to be underlined is that several assumptions of the present work are suitable to be tested in future studies using neuro-computational models. Indeed, the predictive coding theory finds a natural mathematical counterpart in the Bayesian approach. According to the Bayesian rule for optimal estimation, the maximum likelihood of the external events, which is generated by the present sensory information, should be shaped by a prior probability to generate a prediction which minimizes the overall error probability. Neurocomputational models can implement these ideas in rigorous quantitative terms, via reentrant models which include bidirectional synapses, and where prior expectations can be encoded using learning algorithms (e.g., Hebbian rules or error backpropagation rules). Moreover, the notions of predictive coding and neural oscillations can be joined together to account for on-line dynamic sensory processing in a more physiological way (Alamia and VanRullen, 2019). This can be simulated using models able to mimic oscillations in populations of neurons (e.g., neural mass models), where brain rhythms emerge from the feedback arrangement of excitatory and inhibitory populations (Cona et al., 2011; Ursino et al., 2010). In this regard, different rhythms can play different roles within this theoretical framework, coding separately for sensory (i.e., likelihood) information and for prior expectation in a flexible and easily modifiable way. Hence, we claim that the fundamental aspects, summarized in the present work in qualitative terms, can represent a natural background for future more quantitative neurocomputational investigations.

Synthesizing the evidence collected, it is possible to state that in ASD there would be a bias towards stimulus-related information due to a pattern comprising ineffective alpha-mediated feedback signaling and/or over-expression of high-frequency bands related to prediction error. Instead, in SSD can be delineated an overly precise prediction related to hyper-signaling of prior information from high-level regions to sensory areas that would shape perception as a function of prior knowledge and/or poorly accurate low-level processing that does not have the

capacity to update established predictions. Differences in the processes underlying perceptual inference imbalance in the two spectra imply the need for different interventions to rebalance the dysfunctional dynamics. Although cognitive-perceptual peculiarities have a greater ability to differentiate the two disorders (Zhou et al., 2019) and are associated with a significant capacity to predict the long-term impacts of the disorders, such as the level of functional, social, and occupational capacity, these deficits do not receive the proper attention from the clinician (Barch and Ceaser, 2012; Nyrenius and Billstedt, 2020; Wallace et al., 2016). Moreover, there are currently no effective treatments to address these issues (Minzenberg and Carter, 2012). The Bayesian perspective may be valuable for defining new and innovative clinical guidelines to deal with imbalances in predictive abilities (Haker et al., 2016). Recently, approaches pointing in this direction have been proposed. Strategic Modification of Priors (SMOP) (Krupnik, 2019; Krupnik and Cherkasova, 2019) is an approach that aims to re-frame the acquired aprioristic models by promoting the integration of prediction-error signals coming from external sources. SMOP perspective can be extremely promising to downscale the ultra-confidence associated with abstract prediction observed in SSD. On the contrary, starting from the assumption that the ASD population tends to struggle with prediction, the '*predictive parenting*' intervention (Hallett et al., 2021) focuses on the relevance of assisting this population to construct a model of the external environment by setting up predictable and controlled spaces that can help them to cope with sensory overwhelm, combined with the acquisition of management techniques to deal with the unpredictable.

These clinical perspectives can be integrated with new-generation techniques to ensure longer-lasting and more successful impact. Converging evidence points to the benefits of using virtual reality (VR) interventions combined with consolidated therapy. The most significant advantage, especially for the ASD population, is that the patient can move in a controlled and more predictable environment which can be set according to the personal functional level,

offering an individually tailored treatment option (Mesa-Gresa et al., 2018). A VR-based training significantly improved cognitive measures related to attention processes and visuospatial cognition in ASD participants (De Luca, 2021), and these progresses were paired with modulation of fronto-parietal connectivity in the alpha and theta frequency range. Acting on oscillatory indices through non-invasive brain stimulation approaches is another promising novel approach. As the reported evidence suggests that the emerging predictive imbalance may be related to alterations in cortical oscillations of feed-forward and feed-back long-range connections (Kessler et al., 2016), novel neurostimulation paradigms, such as oscillatory entrainment paradigms via frequency-tuned rhythmic transcranial magnetic stimulation (rTMS) (Romei et al., 2016a; Thut et al., 2011), and transcranial alternating current stimulation (tACS) (Cecere et al., 2015) could be exploited to entrain oscillatory activity in a given frequency band and thus shaping, by mimicking, functional (vs. dysfunctional) oscillatory activity imposed by the externally imposed oscillator (Romei et al., 2016a; Wolinski et al., 2018). Other recent neurostimulation developments are specifically targeting long-lasting plastic changes of neural networks via a novel paradigm called cortico-cortical Paired Associative Stimulation (Chiappini et al., 2020, 2018; Pitcher et al., 2021; Romei et al., 2016b). These protocols may represent ideal candidates for prospective restorative protocols, because capable of modulating neural connectivity of the targeted networks in the feedback and feedforward direction as well as enhancing or suppressing oscillations patterns depending on the individual's position within the continuum, offering a highly specific, information-based tailored approach (Beynel et al., 2019; Romei et al., 2011; Thut et al., 2011; Veniero et al., 2013). This is an attractive characteristic for non-invasive, non-pharmacological, and long-lasting interventions in oscillopathies such as ASD and SSD (Romei et al., 2016c).

Figure Captions

Figure 1:

On the x axis are depicted **different ways** of interacting with the external world in the autistic and schizophrenic spectrum. Individuals within the **autism spectrum** tend to guide their behaviour by information gathered from the external environment, relying less on predictive models (sensory-driven choice). In the **schizophrenic spectrum**, an opposite process is observed in which the internal model and preconceived beliefs seem to be the node on which perceptual inference is pivoted (model-driven choice). Both of these extreme approaches lead to an **ill-adapted** reaction to external conditions (y axis).

In between, behaviour results from an integration of sensory evidence and model-driven information resulting in balanced choice with more flexible adaptation to the environment.

Figure 2:

- A. In the general population there is a harmonised integration (posterior, red gaussian distribution) between stimulus information (sensory evidence, yellow distribution) conveyed through feed-forward connections (yellow arrow) and belief information (prior, blue distribution) conveyed through feed-back connections (blue arrow).
- B. In the SSD population, perceptual inference is shaped primarily on internal beliefs.

According to the priors hyper-signalling hypothesis, the exaggerated precision associated with priors is the pivot of SSD symptoms. The neural underpinning may lie in a rigid synchronisation from high-to-low level areas in the cortical hierarchy (table 6, hypothesis 1).

An alternative mechanism consists of an impoverishment in the coding of the prediction error that provokes its underweighting in perceptual inference. At the neural scale, this hypothesis points to a forward routing of corrupted prediction error caused by an inability to optimise gamma synchronization and alpha speed at the sensory level (table 6, hypothesis 2).

- C.** In the ASD population, perceptual inference is shaped primarily on incoming sensory information.

According to the priors hypo-signalling hypothesis, attenuated priors are responsible for the perceptual experience of autistic people. The neural underpinning may depend on a weakness in (alpha-based) feed-back connectivity (table 7, hypothesis 1).

A different interpretation suggests the presence of an overly precision given to sensory prediction error in ASD that may stem from increased (gamma-based) feed-forward connectivity (table 7, hypothesis 2).

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