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THE NEURAL BASES OF PREDICTIVE STYLES ALONG THE AUTISM- SCHIZOPHRENIA CONTINUUM

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Summary

Abstract

The present thesis aimed to push the boundaries of understanding on the pivotal role played by neural oscillations in modulating Bayesian inference and decision-making processes. Additionally, it explored how inter-individual differences in Autistic and Schizotypal traits shape the neuro-behavioral mechanisms underpinning perceptual inference. A primary contribution of this work is the development of a novel bio-behavioral model of the Autism Spectrum Disorder (ASD) - Schizophrenia Spectrum Disorder (SSD) continuum. This model conceptualizes both conditions as disorders of predictive abilities, stemming from disruptions in brain oscillatory patterns. Building on foundational insights, the thesis employs advanced computational models and state-of-art EEG methodologies to elucidate the distinct oscillatory signatures of predictive processing and understand the rhythmic underpinnings of maladaptive predictive inference in ASD and SSD. Specifically, the research investigated 1) the brain connectivity patterns related to ASD-SSD continuum, 2) the behavioral and electrophysiological mechanisms of prior knowledge integration in decision-making, and 3) how dispositional factors associated with ASD and SSD traits direct individual predictive strategies in both laboratory settings and real-world scenarios. These studies provided a comprehensive understanding of cognitive styles and brain oscillatory codes governing perception, decision-making, and health-related attitudes, contributing significantly to our knowledge of how these mechanisms underlie manifestations observable in the ASD-SSD continuum.

General Introduction

Perceptual decision-making stands as the fundamental pivot shaping our daily existence, guiding us through the spectrum of ordinary alternative choices to the profound moments that define our life. At its core, decision-making is the process by which we select a particular course of action or a preferred alternative among multiple options. This complex cognitive process involves assessing information, weighing potential outcomes, and ultimately arriving at a conclusion. Examining perceptual decision-making through computational perspectives such as Signal Detection Theory and Sequential Sampling Models allows a deep dive into the complex process of distinguishing signals from noise, unravelling the dynamics behind decision-making mechanisms. Within these frameworks, sensitivity and bias parameters play crucial roles—sensitivity reflects the accuracy in perceiving stimuli, while bias pertains to the inclination to report (vs. not report) perceiving a stimulus regardless of its actual presence (vs. absence).

The Bayesian brain hypothesis enriches the framework by proposing that the brain uses not just sensory cues but also prior probabilities to contextualize perceptions and influence choices based on past experiences and present circumstances. This inferential-like process enables the cognitive system not only to react to stimuli but also to anticipate and prepare for them in advance. The first pivotal question driving this thesis revolves around whether prior information enhance the capacity to discern the signal from noise, thereby boosting sensitivity, or if it predisposes to respond in specific ways, thus shaping decisional bias.

Furthermore, recent literature underscores the pivotal role of neural oscillations in shaping perceptual decision-making processes. Specifically, alpha oscillations (8-14 Hz) emerge as significant predictors of decision outcomes. Yet, an intriguing question arises about alpha rhythms: do they modulate perceptual sensitivity or criterion, or do they fulfill both roles? Unraveling the precise decisional role played by alpha oscillations stands as another primary aim within the scope of this work.

Furthermore, delving into the rhythmic application of Bayesian inference sheds light on the pivotal role played by the interplay among oscillatory synchronization across various cortical regions. This framework postulates that alpha/beta rhythms synchronization facilitates the top-down transmission of predictive information, while gamma synchronization in the feedforward pathway is crucial for transmitting prediction errors.

The exploration of these computational frameworks and neural oscillations will become even more compelling when viewed within the landscapes of Autism Spectrum Disorder (ASD) and Schizophrenia Spectrum Disorder (SSD). ASD encompasses various conditions marked by difficulties in social communication, interaction, and sensory experiences. In contrast, SSD is characterized by a spectrum of symptoms including positive manifestations (e.g., hallucinations), negative aspects (e.g., social withdrawal), and cognitive impairments (e.g., working memory deficits).

How these two conditions could be framed in the Bayesian brain framework? A novel hypothesis will be explored that conceptualize ASD and SSD as the two extremes of the same predictive continuum. Specifically, while ASD would lean towards underweighting contextual and prior information, prioritizing sensory data, SSD would hyper-emphasise prior information, leading to distinct perceptual distortions and decision-making biases. Additionally, this exploration will delve into how adopting a decision-making approach rooted in prior beliefs (as observed in SSD) or sensory evidence (as observed in ASD) correlates with the formation of (mal)-adaptive attitudes, such as perspectives on vaccination. This investigation holds substantial relevance in our current context, where these choices have broader ramifications beyond the individual, impacting society as a whole. Furthermore, this work introduces a novel framework suggesting that disruptions in neural oscillations observed in ASD and SSD could potentially serve as neural markers underlying altered perceptual processing and decision-making biases. With this framework as a guiding principle, the thesis aims to delve into the operational role of alpha oscillations within the context of decision-making in both ASD and SSD. Investigating whether specific patterns in alpha oscillations signify altered sensory processing or cognitive biases in these conditions, and exploring whether there exists a distinct prevalence of feedback versus feedforward connectivity patterns characterizing these conditions, stands as the central aim of this stream of investigation. These questions aim to reveal intricate connections between computational frameworks, neural oscillations, and the distinct perceptual and decision-making characteristics exhibited in these neurodevelopmental conditions.

Perceptual Decision-making

Introduction

Each day, our cognitive system navigates through a substantial volume of information conveyed by our senses. The ability to use such information to choose the most suitable action among various possible plans is a crucial aspect of human as well as animal cognition (Gold and Shadlen, 2007). Across millennia of evolution, our powerful "brain hardware" has evolved to swiftly process and make nearly instantaneous decisions in response to these stimuli. Simple examples from common experience include standing at a pedestrian crossing and determining the optimal moment to cross. In the blink of an eye, our brain performs complex operations that would require tons lines of code to program a machine to achieve similar results: estimating the speed of oncoming cars, calculating the time needed to cross the pedestrian stripes, evaluating whether it's less than the time needed for approaching vehicles to reach the critical point, continuously monitoring all phases of the process to adjust the behavioral plan online, and so on. The surprising aspect is that, while performing calculations of such complexity, our brain also has sufficient resources to engage in other cognitive tasks, such as talk with a friend. This underscores the remarkable capacity of our brain and its heuristics to quickly and efficiently make decisions. Yet, despite this incredible processing ability, human decisions deviate from optimality in numerous cases (Tversky and Kahneman, 1992). In fact, it is impossible for the brain to encode all external information precisely and in real-time, resulting in the loss or coarse encoding of many pieces of information. It is precisely in the recognition of this limitation that there has been a shift from conceptualizing human perception as a purely bottom-up and stimulus-driven process (Gibson and Carmichael, 1966) to a constructive process in which the brain plays an active role in interpreting the informational streams coming from the external environment (Gregory, 1970). Subsequently, this viewpoint found its way into various theories, shaping the conceptualization of this process as Bayesian inference. This led to the characterization of perception as a type of statistical inference (Yuille and Kersten, 2006), reliant on implicit and probabilistic decision-making processes to construct the most probable representation of the stimulus within a given context. From this perspective, the cognitive system engages in inferring the external event that prompted the sensory evidence registered by our perceptual systems. In this process, the brain relies on past experiences to assess different a priori hypotheses, seeking the one that best corresponds to the factual sensory evidence. Consider the earlier scenario involving determining the presence or absence of a car (h1 or h2) before making a decision. The brain assesses the probabilities that incoming evidence supports specific hypotheses, resembling a judge weighing evidence for exoneration (h1) or conviction (h2). Alongside sensory evidence, prior probabilities of hypotheses, influence this process (Gold and Stocker, 2017). These Priors represent the probabilities of a hypothesis being true before receiving sensory evidence. For instance, in a bustling city like Rome during rush hour, the baseline probability of a vehicle being present when we are about to cross will be much higher, the exact opposite if we were in a remote village late at night. In a laboratory setting, the prior probability can be easily manipulated, for example, by increasing the likelihood of presenting a certain stimulus or preferentially rewarding certain decisional outcomes.

In the decision-making process, all prior probabilities and accumulated evidence are synthesized into a 'Decision Variable' (DV). When determining the moment to act, this DV is weighed against a 'decision rule' (Gold and Shadlen, 2007). A feasible decision rule might involve setting a specific criterion value for the DV. If this threshold is surpassed, it lends support to a particular hypothesis and the ensuing actions, while falling below it shifts attention to an alternative interpretation of reality. Subsequent to making a choice, specific actions are executed, and their consequences play a pivotal role in assessing the entire decision-making process. This evaluation is critical and adaptive, shaping future decision-making through modulation based on the outcomes. External feedback, like when someone warns us about crossing the road too hastily, or implicit feedback, like realizing an incorrect assessment of an approaching car's speed influenced our decision not to cross, can initiate this evaluative process.

After delineating the components in decision-making (Figure 1) and their interplay, the following sections will focus on presenting three pivotal theoretical frameworks that model the perceptual decision-making process: Signal Detection Theory (SDT) (Green and Swets, 1966), Sequential Sampling Models (SSM) (Ratcliff and McKoon, 2008), and Predictive Coding (Rao and Ballard, 1999).

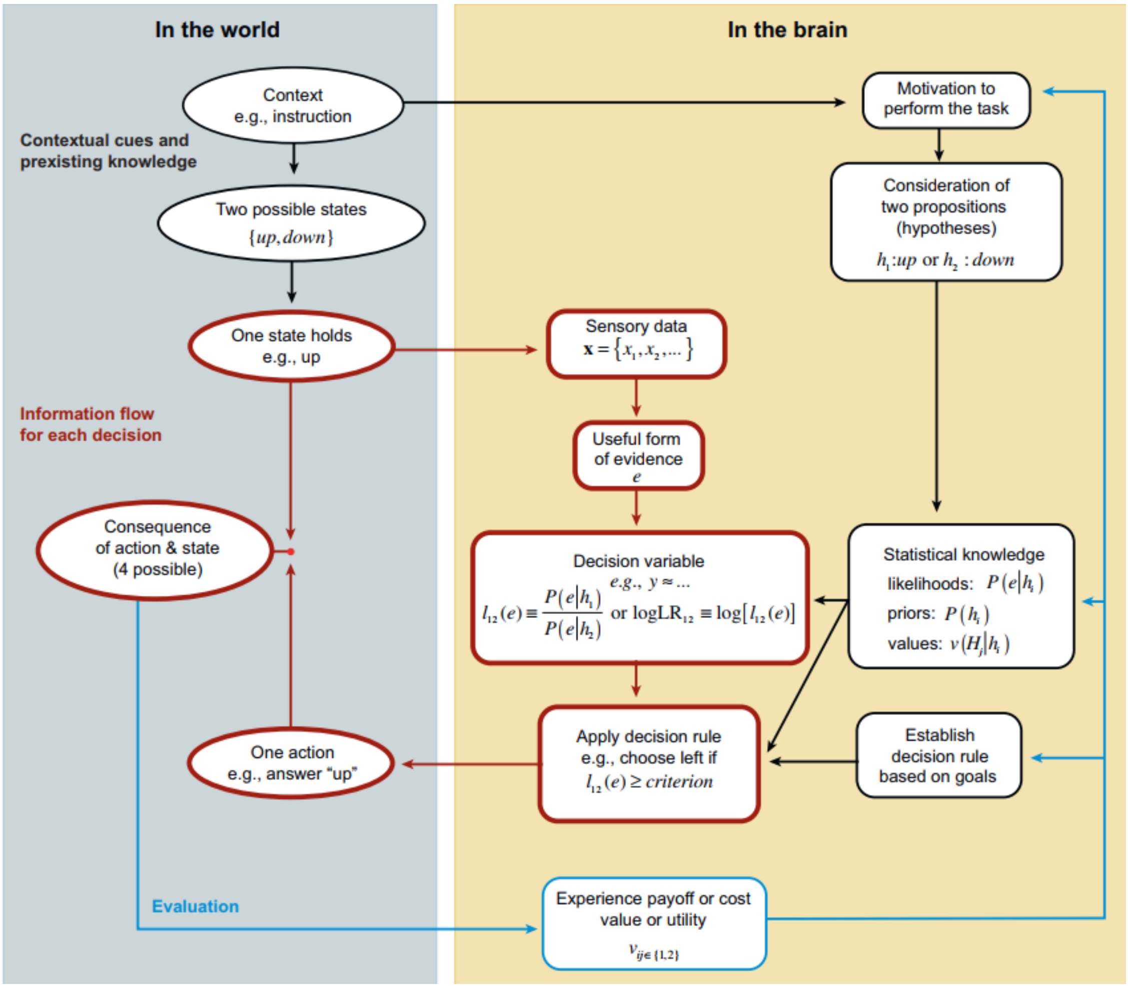

Figure 1 illustrates the components involved in a simple decision between two alternatives. On the left side, there are elements pertaining to the external world, while the right side represents components within the decision-making process in the brain. The black elements establish the context, the red elements constitute the decision-making, and the blue elements assess and potentially modify the decision process.

From Gold and Shadlen, 2007 *https://doi.org/10.1146/annurev.neuro.29.051605.113038*

Computational Perspectives on Perceptual Decision-Making

Decision modelling is a robust and systematic approach used to analyse decision-making processes across diverse domains. It involves representing underlying decision parameters through formalized structures, improving clarity in understanding factors that influence outcomes, revealing their implications and addressing uncertainties linked to different choices.

One of the most widely used computational model to unravel the intricate mechanisms at play in decision-making is Signal Detection Theory (SDT). Introduced initially by Green & Swets (1966), this framework demonstrates remarkable versatility across various domains such as psychology, medical diagnosis, and statistical judgment (Macmillan and Creelman, 2004). Stanislaw & Todorov (1999) highlighted three critical tasks where the application of SDT proves essential: Yes/No Tasks, Rating Tasks, and Forced-Choice Tasks. SDT operates on three key assumptions:

1. The perceptual system extracts a value called evidence (e) from the incoming sensory signal.
2. The evidence extracted by the perceptual system is subject to a certain amount of variability (noise).
3. The specific decision is linked to the setting of a criterion that will be applied to the collected evidence.

To grasp these three concepts, consider a simple visual detection task. Here, a stimulus presentation generates an "internal response" based on the neurophysiological responses of neurons sensitive to that stimulus. For instance, in tasks involving motion discrimination, the internal response is proposed to result from the firing rates of neurons sensitive to different directions of motion (Britten et al., 1996; Shadlen et al., 1996). This internal response is subjected to noise that derive from both internal (e.g., fatigue) or external (i.e., ambiguous stimulus) sources, leading to varied responses even with the same stimulus presentation. SDT posits that observers must discern whether the internal response is due to the signal or attributable to noise. Internal responses to target stimuli and noise can be modeled as probability curves, where the width of these curves represents the variability of the internal response to the same visual stimulation. Crucially, these curves may exhibit some overlap, emphasizing the challenge in ambiguous decisions to discern whether an internal response is due to the target or noise. In order to commit to a decision, observers apply a criterion to the internal response. When the internal response surpasses the chosen criterion, an observer assumes the stimulus is present, while the absence of the stimulus is reported in the opposite case. Given these premises, SDT assumes there are four possible decision-making outcomes: *hit* (signal present and observer says "*yes, I have seen the target*"), *miss* (signal present and observer says "*no, I have not seen the target*"), *false alarm* (signal absent and observer says "*yes, I have seen the target*"), and *correct rejection* (signal absent and observer says "*no, I have not seen the target*").

The placement of the criterion significantly influences the proportions of hits and false alarms, underscoring its pivotal role in the decision-making process. Specifically, setting a liberal criterion would lead to both an increase in the number of hit rate and false alarm rate. This occurs because in the majority of the signal-present trials, the internal response exceeds this lax criterion. However, even in noise-only trials, there's a higher likelihood that the internal response crosses this more permissive threshold, contributing to increased false alarms. Conversely, adopting a conservative criterion would lead to fewer false alarms that are, however, paired by a reduction in the hit rate.

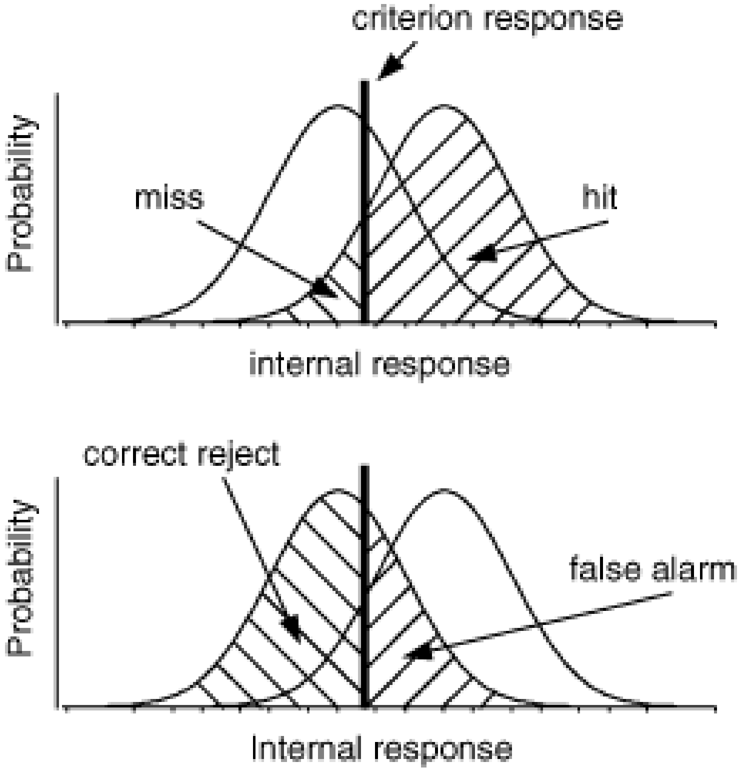

Figure 2 illustrates how Signal Detection Theory (SDT) frames the decision-making process between two stimulus classes. The internal response probability of occurrence curves for noise-alone and signal-plus-noise trials is depicted. Due to the overlapping curves, the internal response for a noise-alone trial may exceed that for a signal-plus-noise trial. The dissimilarity of the curves, measured by the distance between the mean values *of Gaussian probability distributions, reflects the efficiency of discriminative ability (d' index). The placement of the criterion, marked by vertical lines, plays a pivotal role in determining decision outcomes. If the internal response surpasses the chosen criterion, the observer concludes the presence of the stimulus; conversely, the absence of the stimulus is reported if the response falls below the criterion.*

From: https://www.cns.nyu.edu/~david/courses/perception/lecturenotes/sdt/sdt.html

The figure 2 elucidates how SDT frame the decision-making process between two stimulus classes. In this representation, the two Gaussian probability distributions depict the internal response generated by the presence or absence of the target stimulus. To make a decision, the placement of the criterion is crucial: when the internal response exceeds it, a decision is made; otherwise, the opposite decision is reached. Measuring the distance between the mean values of these distributions provides an index of the dissimilarity of the curves, shedding light on the efficiency of discriminative ability (Stanislaw and Todorov, 1999). This index, denoted as d', is influenced by both internal factors (e.g., a more efficient perceptual system enhances discrimination) and external factors (e.g., paying attention to the stimulus increases the distance between the curves). Additionally, the choice of where setting the criterion can be shaped by contextual factors (for instance, in unfamiliar environments, a more cautious approach might be wise due to unknown risks associated with false alarms) or inherent traits/conditions (e.g., children with Autism tend to adopt a more conservative criterion in their perceptual decision-making process, Quinde-Zlibut et al., 2020).

Signal Detection Theory (SDT) effectively explains the factors influencing decision outcomes but faces limitations when it comes to include Reaction Times (RT). This is particularly disadvantageous because the same decisional parameters (i.e., perceptual sensitivity, d') could be achieved using different decision times. Sequential Sampling Models (SA models) step in to fill this gap (Ratcliff and McKoon, 2008). SA models can be considered an evolution of the SDT model as they also account for the temporal factor (Ratcliff et al., 2016). These models propose that decisions result from the accumulation of evidence regarding two alternatives (h1, h2), ceasing upon reaching a certain criterion (Figure 3). This family of computational models posits that evidence accumulation occurs through sequential integration over time, incorporating information (momentary evidence) signalled by sensory processor (Heekeren et al., 2008). The accumulation process theoretically begins at a midpoint between two threshold values (starting point). Over time, the computed decision variable (DV) updates until it reaches a threshold value, signifying the concrete decision. The starting point parameter influences where the process initiates, introducing a crucial element that sets the stage for subsequent decision dynamics. In presence of a bias toward one alternative, the starting point of the accumulation process could be located closer to the boundary that signal that choice (Mulder et al., 2012). Other key parameters involve the drift rate and threshold value settings. Drift rate refers to a fundamental parameter that characterizes the average rate of information accumulation during a decision-making process. Specifically, it quantifies how quickly evidence is gathered in favor of one of the available choices over time. Within the Sequential Accumulation context, the drift rate mirrors the strength and quality of sensory evidence extracted from a stimulus, influencing the direction and pace at which the decision variable accumulates toward a decision threshold. A higher drift rate signifies quicker and more decisive decision-making, while a lower drift rate suggests slower and less certain evidence accumulation. Threshold values represent the points where accumulated evidence hits a critical level, leading to a decision. They define the boundaries between choices, significantly impacting the speed-accuracy trade-off inherent in decision-making (Lerche and Voss, 2018). Furthermore, sequential sampling models incorporates a parameter known as non-decision time, encompassing the time needed for processes unrelated to the decision itself—such as sensory processing and motor response execution. Numerous SA models, all with the mentioned elements, have emerged over time. The two most widely used include the Drift Diffusion Model (DDM) and the Race Model (RA) (Ratcliff et al., 2016). In the DDM, the difference in momentary evidence for two options is integrated into a single accumulator, while in race models (Boucher et al., 2007), different evidence accumulators exist for each response alternative, competing to reach the threshold value.

In conclusion, SA models, unlike SDT models, exhibit a higher level of complexity by incorporating the temporal aspect into theorization. These models have effectively elucidated behavioral and neurophysiological data across diverse paradigms, ranging from perceptual and economic decision-making to reinforcement learning. Their capacity to analyse various facets of the decision-making process—including choices, reaction times, confidence levels, and the balance between speed and accuracy—contributes significantly to their extensive utilization in research contexts.

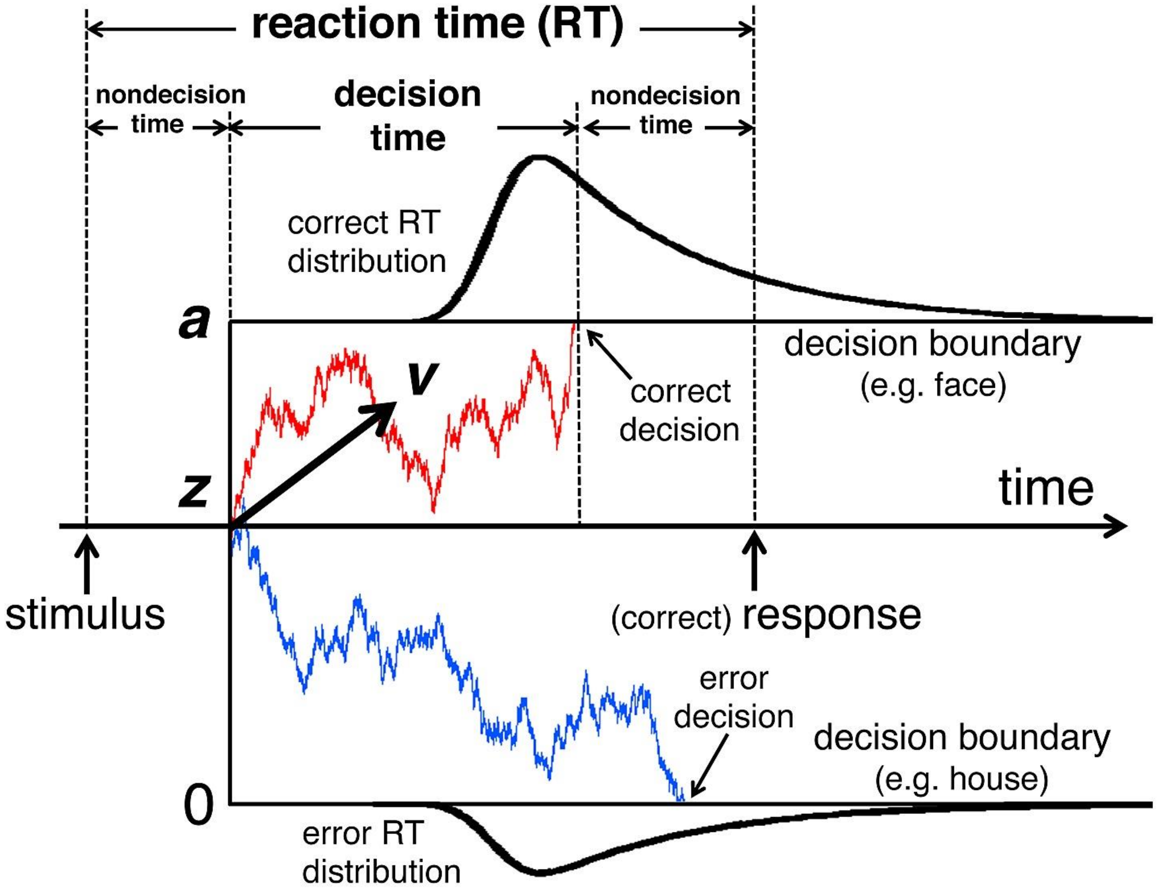

Figure 3. Drift-Diffusion Model (DDM) is a mathematical framework representing decision-making processes. Key components include the drift rate (v, speed of evidence accumulation), decision threshold (a), starting point (z) and non-decision time. Widely applied in psychology and neuroscience, DDM offers insights into how individuals make decisions, providing a quantitative analysis of cognitive processes.

From https://plos.figshare.com/articles/figure/_The_drift_diffusion_model_DDM_/1279706

The Bayesian brain hypothesis

Predictive coding represents a significant leap forward compared to traditional models such as SDT and DDM (Rao and Ballard, 1999). While SDT and DDM have been instrumental in parameterizing decision-making processes, predictive coding introduces a paradigm shift by delving into the intricacies of the brain's predictive nature. Indeed, within the predictive coding framework, the emphasis transitions from mere information accumulation to an active and dynamic prediction-oriented process. According to this framework, brain continually generates predictions about incoming sensory information (Knill and Pouget, 2004). These predictions are then compared with the actual sensory input, and any disparities (i.e., prediction errors) drive further adjustments and updates to the internal model. This predictive nature allows the brain to not only respond to stimuli but also anticipate and prepare for them in advance.

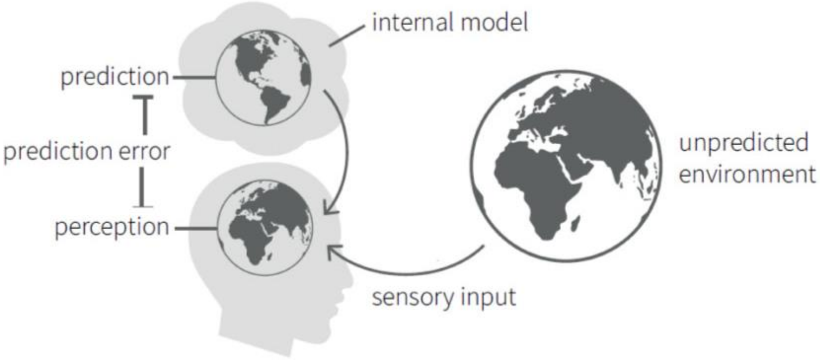

Figure 4. Illustrative representation of the "Bayesian brain" concept proposing the existence of an internal model within the brain containing beliefs about environmental states. These beliefs generate predictions regarding sensory inputs. The difference between the real and predicted sensory inputs, known as prediction error, is instrumental in refining the internal model. Adapted from https://doi.org/10.3389/fpsyt.2016.00107

The historical roots of the model can be traced back to Helmholtz's theorizations (1867), one of the first authors to liken the perceptual process to an inferential process. This process involves computing "beliefs" about the states of the world, which will later be tested through comparison with actual signals from the external environment (Figure 4). At the neural-organization level, it has been proposed that predictions are computed by hierarchically higher stages. These stages send a copy, via feedback connections, to lower-order regions responsible for comparing these predictions with the incoming signal. In case a discrepancy is detected, a prediction error signal is generated, which is then conveyed to higher stages via feedforward connections, aiming to update/optimize predictions (Figure 5, Friston and Kiebel, 2009). Numerous models draw on the hypothesis that the brain plays an active role in perception. Many of them have developed rather different hypotheses about the nature of the signal encoded by low-level neurons, whose discharge is not solely seen as an indicator of a potential prediction error but is rather considered a fusion between a bottom-up signal derived from the external word and a top-down signal indicating beliefs, priors, and biases processed by the rest of the brain (Haefner et al., 2016; Hanks et al., 2011; Urai et al., 2019; Wimmer et al., 2015). Understanding the brain's predictive mode of operation sheds light on its usefulness in decision-making, as it improves efficiency by diminishing the requirement for extensive real-time information processing. Embracing this interpretative line, the accumulation process theorized by SA models would be better explained by not referring to a process of diffusion of accumulated evidence towards two threshold values but as an evolving probability distribution over time on possible causes of sensation (Hesselmann et al., 2010). The process, like in SA models, is considered to be time-dependent, as it continues until the most probable cause of the inputs is identified, a process that requires gradual "adjustments" in prediction using generated prediction errors (Friston and Stephan, 2007).

Furthermore, embracing this theoretical proposal provides insights into various physiological mechanisms observed at neural levels. For instance, in the r*epetition suppression effect*—a phenomenon identified in neuroimaging studies—the neural activity elicited by events fully predicted by the system is reduced (Auksztulewicz and Friston, 2016). This reduction can be attributed to the decrease in neural activity when events are fully expected by the system and no prediction-errors are then generated. Moreover, predictive coding framework is able to explain the *end-stopping effect* observed in neurons of the primary visual cortex when these neurons exhibit heightened activation in response to an oriented line terminating within their receptive field. Conversely, their response weakens when the same stimulus surpasses its spatial boundaries (Hubel and Wiesel, 1965). This intriguing neural activity has been subsequently interpreted as a signal of prediction error, challenging the notion that it solely results from the perceptual analysis of information within the receptive field. The explanation lies in the predictability of extended lines, influenced by contextual information from the surrounding region, leading to diminished error-signaling responses (Rao and Ballard, 1999).

In conclusion, predictive coding takes a step further by not only considering the accumulation of evidence over time, as seen in DDM, but by fundamentally acknowledging the brain's proactive role in shaping predictions and refining them in real-time. This nuanced approach provides a richer and more comprehensive understanding of decision-making processes, bridging the gap between cognitive models and the intricate workings of the neural machinery.

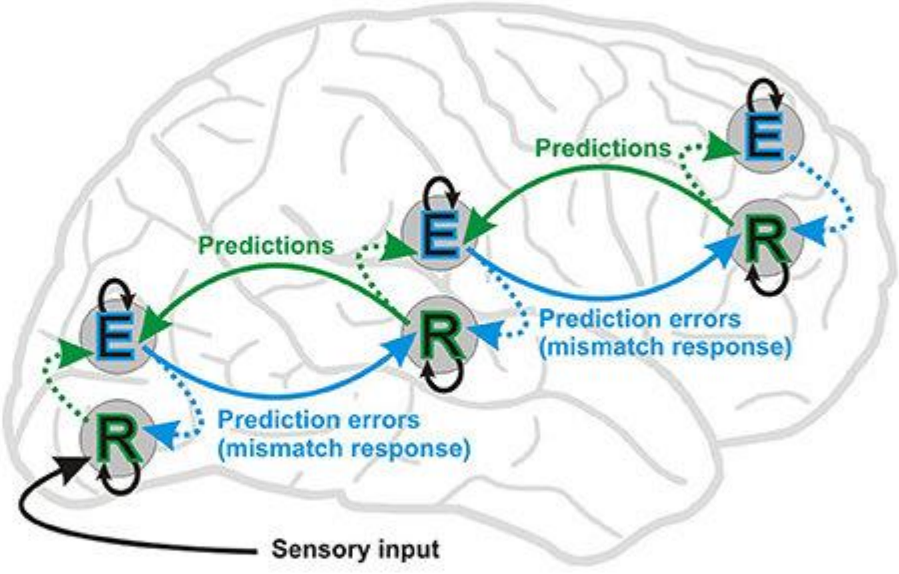

Figure 5. The figure illustrates communication between two neuronal populations: error units (E) and Predictive/Representation units (R). In this framework, bottom-up connections convey prediction errors, while top-down connections carry predictions to diminish these errors. Representation units encode sensory input causes, receiving input from error units. The level of complexity of internal representations increases as one moves to hierarchically superior nodes in the predictive chain.

From https://www.frontiersin.org/articles/10.3389/fnhum.2014.00666/full

Unraveling the Oscillatory Code of Bayesian Inference

Introduction

Across a wide array of systems, oscillatory patterns emerge as a common feature. From biological processes such as the beating of the heart and breathing to physical phenomena like the oscillations of pendulums and celestial bodies, rhythmicity is prevalent and observable. This pervasive rhythmicity extends its presence into the intricate landscape of our brain. In this context, these cyclic patterns take shape as neural rhythms—regular, cyclical electrical activity generated by synchronized groups of neurons (Klimesch, 2018). These oscillations manifest as fluctuations in the membrane potential of neurons, creating distinct frequency bands that can be observed through various neuroimaging techniques, such as electroencephalography (EEG), magnetoencephalography (MEG), and local field potential (LFP) recordings. The intricate genesis and governance of these neural oscillations involve complex interplays among excitatory and inhibitory neurons, synaptic connections, and neuromodulatory systems. This nuanced interplay fosters synchronized neural activity, facilitating effective communication between cerebral regions and the seamless integration of information across neural networks.

The following chapter initiates with a historical perspective, tracing the evolution of brain activity registration from Richard Caton's groundbreaking work in 1875 to Hans Berger's revolutionary contributions in 1929, culminating in the birth of Electroencephalography (EEG). This historical foundation establishes a framework for appreciating EEG's significance in capturing the dynamic nature of cognitive, perceptual, linguistic, emotional, and motor processes, providing a unique lens into neural dynamics. Delving further, we explore a fundamental EEG data analysis methodology: Frequency Analysis. This method unveils the fascinating world of neural oscillations, highlighting their profound association with various cognitive processes. This comprehensive understanding sets the stage for a more focused examination of the pivotal role played by brain oscillations, particularly the alpha rhythms (8-14 Hz), in shaping the outcomes of perceptual decision-making. Subsequently, we delve into uncovering how these brain oscillations play a crucial role into Bayesian inference processes.

How can we measure brain oscillations?

In exploring the realm of neural oscillations, the choice of investigative tools plays a pivotal role, and high-temporal-resolution techniques, such as EEG, emerge as exceptional instruments for unravelling the intricacies of neurocognitive processes (Cohen, 2014). Richard Caton made the pioneering endeavor to record brain activity in 1875. This marked the inception of investigating neural activity through electrical recordings. However, the contemporary Electroencephalography owes its conceptualization to the contributions of Hans Berger in 1929. Berger introduced a non-invasive technique that revolutionized the study of electrical brain activity. This technique involved the application of multiple electrodes to the subject's scalp, paving the way for a more comprehensive understanding of neural dynamics. The significance of EEG lies in its ability to capture the dynamic nature of cognitive, perceptual, linguistic, emotional, and motor processes, which unfold within milliseconds. Unlike the hemodynamic response, which operates at a considerably slower pace, EEG provides a finely tuned lens to observe fast, dynamic, and temporally sequenced cognitive events (Purves et al., 2017). Beyond the temporal aspect, the advantages of EEG extend to its direct measurement of neural activity. Studies have demonstrated that the signals recorded through EEG represent postsynaptic potentials of neocortex neurons (Cohen, 2017), offering direct insights into neural activity occurring in the cortex. This direct link to neural dynamics sets EEG apart from MRI-based measures which lack the same precision in capturing neural events. Typically, the application of the EEG methodology is considered non-invasive, utilizing electrodes strategically placed on the scalp, commonly referred to as "scalp EEG." In contrast, an invasive counterpart known as Electrocorticography (ECOG) or "intracranial EEG" requires surgical intervention, placing electrodes on the cortical surface (Keene et al., 2000). The International 10-20 system stands as a globally acknowledged framework for delineating and executing the placement of scalp electrodes (Figure 6, Klem et al., 1999). Its genesis aimed at instituting standardized testing methodologies, ensuring the comparison of study outcomes through the scientific method. This method operates on the assumption that a consistent relationship exists between the electrode's location and the underlying cerebral structures. Conventionally, the 10-20 system relies on the identification of anatomical landmarks such as the nasion, inion, and preauricular points. Subsequently, electrodes are systematically positioned at fixed distances from these points, following increments of 10% or 20%, thereby accommodating variations in head size. To achieve finer spatial resolution in EEG recordings, the 10-10 configuration was introduced. This setup includes additional intermediate sites between those defined in the 10–20 system, resulting in a total of 64 electrodes. As illustrated in the figure xxx, each assigned electrode placement site is identified by a letter corresponding to the specific lobe or brain area it monitors. This includes frontal (F), temporal (T), parietal (P), occipital (O), and central (C). Further distinguishing these electrodes, a numerical identifier is used: even numbers indicate placement on the right side of the head, while odd numbers indicate positions on the left. In addition, "Z" electrodes are strategically positioned on the sagittal plane of the skull, primarily serving as reference and measurement points. This systematic approach establishes a standardized labeling and positioning system for precise electrode placement during EEG recordings.

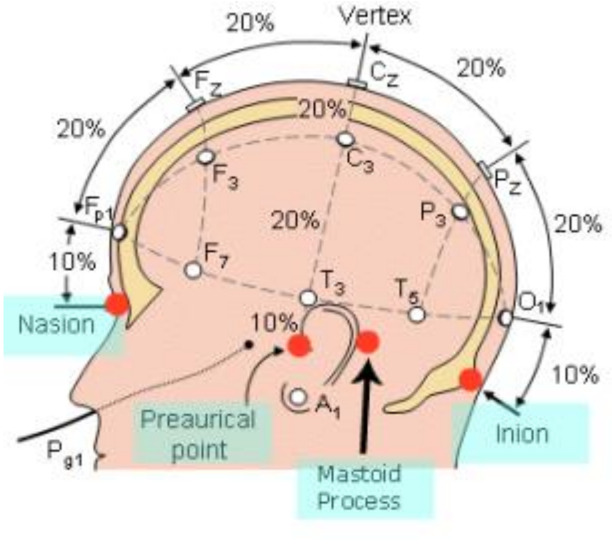

Figure 6. The 10-20 system for electrode placement in electroencephalography (EEG). Electrodes are positioned on the scalp at standardized distances, with labels indicating the brain region (e.g., F for frontal, C for central) and hemisphere (odd number for left, even number for right). This system ensures consistent electrode positioning for reliable comparisons across studies.

From https://sleeptechstudy.wordpress.com/2013/05/13/the-international-1020-system-of-electrode-placement/

As previously discussed, the signals captured by EEG serve as a representation of the postsynaptic potentials of neurons situated in the neocortex. But what precisely do these signals convey? They signify the measurement of voltage fluctuations stemming from ionic current flows within the neurons of the brain. Neurons communicate through electrical impulses, and this activity results in subtle voltage changes that manifest on the scalp (Gazzaniga, 2004). Each electrode records these changes as a continuous trace, reflecting the collective electrical activity of numerous neurons in the underlying brain region. In a living brain, EEG patterns are not flat or random. Instead, they exhibit dominant rhythms categorized into specific frequencies. These rhythms reflect fluctuations in the excitability of neuron populations, displaying complex spatiotemporal patterns with variations in amplitude, timing, and frequency. Understanding these fluctuations forms the core of modern cognitive electrophysiology, a field dedicated to unravelling the connections between these neural patterns and various cognitive and perceptual processes (Cohen, 2017).

Within the realm of EEG data analysis, two prominent methodologies take precedence—Event-Related Potentials (ERPs) and Frequency Analysis. ERPs refer to the electrical brain activity changes that occur in response to specific stimuli or events (Luck, 2014). These changes are measured as deviations from the ongoing EEG activity and represent the brain's neural processing associated with the presentation of stimuli, such as visual or auditory inputs. ERPs are extracted by aligning EEG recordings to the onset of a specific event or stimulus, averaging multiple trials to enhance the signal-to-noise ratio. ERPs are characterized by their millisecond-level timing accuracy, offering insight into the brain's real-time information processing. They consist of distinct components, each reflecting different stages of cognitive or perceptual processing. These components are named based on their polarity, latency, and functional significance. For instance, the P300 component is associated with attention and memory processes and often peaks around 300 milliseconds after a stimulus (Huang et al., 2015). Another example is the N170 component, linked to face perception, typically occurring around 170 milliseconds after viewing a face (Rossion et al., 2003). Frequency Analysis is another crucial dimension in EEG data-analysis, involving the examination of specific frequency components within brain recordings. This analytical method is fundamental in investigating the role of neural oscillations (Siegel et al., 2012). Five primary frequency bands can be identified in EEG research (Figure 7, Klimesch, 2018). These include *Delta* (δ; 0.5-4 Hz), *Theta* (θ; 4-8 Hz), *Alpha* (α; 8-14 Hz), *Beta* (β; 14-30 Hz), and *Gamma* (γ; above 30 Hz). Among these oscillations, low-frequency neural activity, notably in the alpha-band, has repeatedly been associated with neuronal excitability, perception and decision-making (Ippolito et al., 2022). These prominent rhythms reach their maximum amplitude over parieto-occipital brain regions and fall within a frequency range of approximately 8–14 Hz (Clayton et al., 2018; Klimesch, 1999). Traditionally, alpha oscillations have been associated with thalamic activity, a connection reinforced by studies demonstrating a significant decrease in alpha oscillations following thalamic lesions (Lukashevich and Sazonova, 1996). Electrophysiological recordings have revealed synchronization between alpha oscillations in the visual cortex and the thalamus, notably in thalamocortical neurons (Chatila et al., 1993). These neurons, responsible for transmitting visual information to the cortex, align their spike patterns with the peaks and troughs of alpha oscillations, modulated by inhibitory signals from interneurons in the lateral geniculate nucleus (Chatila et al., 1993; Hughes et al., 2004). Moreover, alpha oscillations are influenced by cortical activities. Coherence analysis indicates stronger connectivity of alpha oscillations within cortical domains compared to connections between the cortex and the thalamus (Lopes da Silva et al., 1973). This suggests a dual contribution to alpha generation: while the thalamus plays a significant role, the cortex independently contributes to modulating alpha oscillations. At the functional level, alpha oscillations have been theorized to actively participate in inhibiting neural processing (Jensen and Mazaheri, 2010). For example, an increase in alpha power during memory retention indicates reduced processing of irrelevant stimuli, correlating with enhanced memory performance (Bonnefond and Jensen, 2013, 2012). Substantial evidence supporting this notion stems from a Transcranial Magnetic Stimulation (TMS) study (Romei et al., 2010) showing that stimulating the brain with an alpha frequency pattern (10 Hz) redirects attention away from the visually stimulated area.

The subsequent paragraph delves into the role of oscillatory patterns as the blueprint for perceptual decision-making processes.

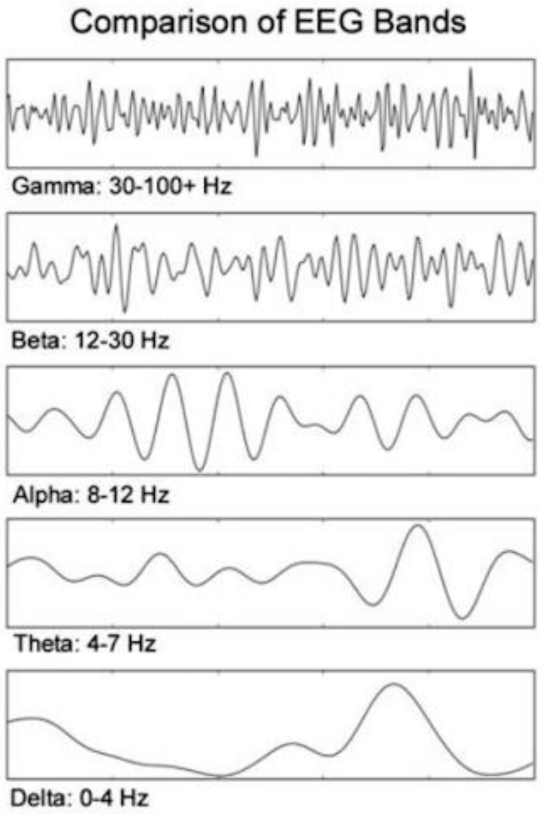

Figure 7. Representation of human brain waves including delta (0-4 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz), and gamma (30-40 Hz) frequencies. Each wave corresponds to distinct neural activities and is crucial for understanding brain function and cognitive processes.

From https://mclean.basisindependent.com/2021/03/26/week-3-the-abcs-of-neural-oscillations/

The role of neural oscillations in perceptual decision-making

Recent advancements in understanding the neural underpinning of perceptual decision-making have been driven by the convergence of psychophysical experiments, brain activity measurements, and computational modeling. Central to our current understanding is the concept that sensory mechanisms provide varying levels of evidence regarding the presence of a specific perceptual feature, often referred to as sensory evidence (Gold and Shadlen, 2007). For instance, in macaques, the firing rate of neurons within the motion-direction-sensitive area MT signifies the degree of sensory evidence supporting a particular direction at a given location (Britten et al., 1996;

Shadlen et al., 1996). The critical moment in decision-making occurs when this sensory evidence is assessed against a criterion (in the Signal Detection Theory domain) or a decision threshold (in the Drift Diffusion Model domain), necessitating a specific level of evidence for a decision to be made. However, an agent's decision-making is susceptible to moment-to-moment fluctuations in the physiological states governing sensory and decision processes (Iemi and Busch, 2018). Recent evidence from physiological and computational studies has established a consistent link between spontaneously occurring brain states before sensory input and subsequent variability in perceptual decisions. Notably, spontaneous neural oscillations in the alpha-band have emerged as pivotal predictors of trial-to-trial variability in decision outcomes for identical sensory inputs (Figure 8, Samaha et al., 2020). In tasks where participants have to detect the presence of stimuli near their perceptual threshold, a consistent discovery emerges: there is a heightened rate of correctly identifying the stimuli when there is a decrease in alpha power around the time of stimulus presentation (Ergenoglu et al., 2004; van Dijk et al., 2008). Moreover, this decline in alpha power also correlates with an increased reporting of TMS-induced phosphenes (Romei et al., 2008b). The classic interpretation of these findings proposed that lower prestimulus alpha power enhances precise stimulus perception, hence leading to higher hit rates.

However, this interpretation might oversimplify the intricate mechanisms underpinning these observations. In fact, the experimental designs employed in previous studies investigating the relationship between prestimulus alpha power and perception often lacked the capacity to distinguish between changes in sensitivity and alterations in decision criteria. Sensitivity refers to the ability to discriminate between signal and noise (i.e., the ability to perceive the stimulus accurately), while decision criteria refer to the participant's willingness to report perceiving a stimulus, regardless of its actual presence. In the context of Signal Detection Theory (SDT), an increase in hit rates or in phosphenes report could stem from two potential sources: heightened sensitivity or a more liberal decision criterion. Lower prestimulus alpha power might indeed enhance sensory processing, improving the brain's ability to detect and process incoming stimuli more accurately. This heightened sensitivity could enable participants to better differentiate between the presence and absence of the stimulus, consequently elevating hit rates. Alternatively, reduced alpha power could affect criterion placement rather than perceptual sensitivity, potentially prompting individuals to adopt a more liberal criterion. This adjustment might elevate hit rates without necessarily improving sensitivity.

Crucially, investigations into false alarm rates across multiple tasks revealed a compelling correlation: reduced prestimulus alpha power correlated with a heightened inclination among participants to report the presence of the stimulus, even in its absence (Limbach and Corballis, 2016), and to report perceiving illusory visual stimuli (Lange et al., 2014). This pattern, coupled with increased hit rates, indicates liberalization of the decisional criterion when prestimulus power is desynchronized. Further investigations delving into prestimulus power's impact on perceptual decisions in yes/no detection tasks highlighted its influence on both hit rates and false alarm rates (Iemi et al., 2017). These findings suggest that weaker prestimulus alpha oscillations induce a more liberal detection criterion, prompting observers to report perceiving a stimulus even in its absence. Conversely, increased prestimulus oscillation leads to a more conservative criterion, resulting in more misses but fewer false alarms (Iemi et al., 2017). Additional support comes from Kloosterman et al. (2019) study, where intentionally inducing a more liberal criterion reduced prestimulus alpha amplitude over posterior electrodes. Moreover, lower prestimulus alpha levels corresponded to observers displaying higher decision confidence (Samaha et al., 2017) and reporting increased subjective visibility of stimuli (Benwell et al., 2017). On the contrary, alpha power consistently showed no noticeable influence on response accuracy across various studies (Benwell et al., 2022; Nelli et al., 2017). In summary, reduced alpha power prompts a more liberal criterion and heightened confidence without altering sensitivity (d'). This implies that alpha oscillations might be regarded as an electrophysiological marker influencing another crucial factor in signal detection theory: the decisional criteria that establish the level of sensory activity necessary for a response (Samaha et al., 2020). These findings underscore the impact on decision criteria without fully disclosing their underlying nature, leaving room for various potential explanations. However, subsequent studies have suggested that this bias is not due to a top-down, strategic inclination to respond in a specific manner (i.e., decision bias), but rather because the observer's perception of the world is authentically transformed (Iemi et al., 2017).

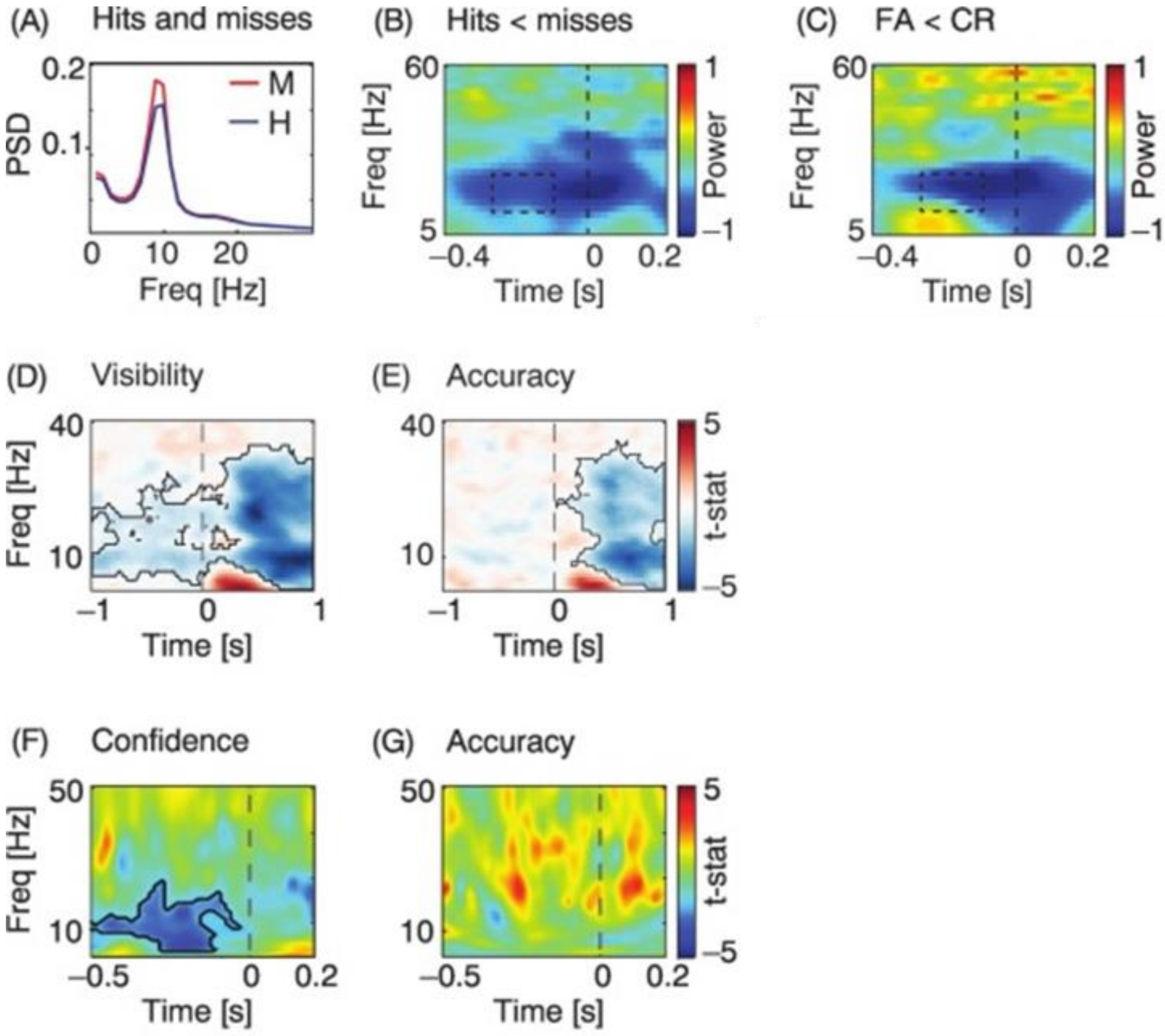

Figure 8. Association between pre-stimulus power and visual responses.

Power spectrum extracted from spontaneous brain activity recorded using MEG sensors positioned over occipital regions before detected stimuli ('hits') and undetected stimuli ('misses') (A). Consistently replicated findings reveal heightened alpha amplitude before missed stimuli. (B) Illustrates the time-frequency representation of peristimulus EEG power, contrasting hits with misses. (C) Similarly contrasts false alarms with correct rejections in a detection task. Recent analyses on trials lacking stimuli indicate that low prestimulus alpha power not only result in more hits but also more false alarms. (D) Displays the single-trial regression analysis predicting peristimulus EEG power across time and frequency based on subjective visibility ratings. (E) Additionally predicts accuracy in a luminance discrimination task. Significant relationships are denoted in black, with prestimulus power negatively correlating with visibility but exhibiting no relation to accuracy. (F) Highlights single-trial multiple regression, predicting EEG power from confidence. (G) Also predicts accuracy in an orientation discrimination task. Once again, prestimulus alpha power displays a negative association with subsequent decision confidence but not accuracy. From https://doi.org/10.1016/j.tics.2020.05.004

Until now, our exploration has primarily revolved around the amplitude of alpha waves, yet the crucial query remains: which oscillatory parameters are responsible for precise perception? One candidate hypothesis is the individual alpha peak (IAF). IAF is a stable and heritable neurophysiological marker (Angelakis et al., 2004; van Beijsterveldt and van Baal, 2002) able to predict individual differences in several cognitive domains such as memory performance (Klimesch, 1997), the g factor of intelligence (Grandy et al., 2013) and attentional performance (Zhang et al., 2021). Recently, IAF has emerged as a prominent neurobiological candidate implicated in governing the temporal parsing of sensory processing into distinct temporal units. This hypothesis is based on the concept that the human perceptual machinery functions as a discrete system (Pöppel, 1997) that samples the continuous stream of incoming sensory information into distinct temporal integration windows (VanRullen, 2016)**.** Similar to other sampling-based processes, the acquisition rate plays a fundamental role in determining the accuracy and fidelity of the resultant representation. In this context, alpha rhythms may play an active role in the segmentation of visual inputs and in regulating the pace of sensory processing with faster alpha oscillations resulting in higher temporal resolution and more accurate perceptual experience. Indeed, individuals with higher IAF exhibit more accurate flash discrimination (Samaha and Postle, 2015) and the reduction vs. acceleration of alpha speed by means of tACS widens vs shrinks the sensory integration window, increasing vs. reducing the proneness to experience the double-flash illusion (Cecere et al., 2015; Venskus et al., 2021). Similarly, Minami and Amano (2017) demonstrated that peak alpha frequency (and not peak alpha power) can be shaped by tACS modulating the illusory jitter perception; in the same vein, Zhang et al. (2019) showed that applying tACS at different frequencies along the alpha band alters subjects' perceptual switching rate in bistable colour-motion binding stimulus: higher alpha frequency led to a faster perceptual switch through shortening perceptual epochs of the active binding. Moreover, it has been shown that IAF tends to speed-up vs. slow-down when the task requires sensory segregation vs. integration, respectively (Ronconi et al., 2023; Sharp et al., 2022; Wutz et al., 2018). Moreover, Tarasi and Romei (2023) demonstrated that the variability in trait alpha speed in a large sample of individuals within the general population intercepts inter-individual differences in perceptual performance in a contrast detection task (Figure 9). Specifically, individuals who showed lower threshold for contrast detection exhibited a relatively higher peak alpha frequency than participants requiring stronger contrast. This result corroborates the growing literature on the topic suggesting that higher alpha frequencies would promote higher perceptual resolution by creating more sampling frames that would increase the amount of accumulated sensory evidence per unit time (Cecere et al., 2015; Samaha and Postle, 2015). The possibility of sampling the signal more frequently would translate into a more faithful representation of the external input, resulting in a higher discriminative capacity. Moreover, this result suggests the validity of this relationship even when controlling for the number of false alarms, helping to eliminate any interpretation related to bias. Moreover, the nature of the experimental paradigm used gave additional insights for linking alpha velocity to a fundamental sampling mechanism as the use of such a simple contrast measure was useful to explore the role of IAF in a basic visual process.

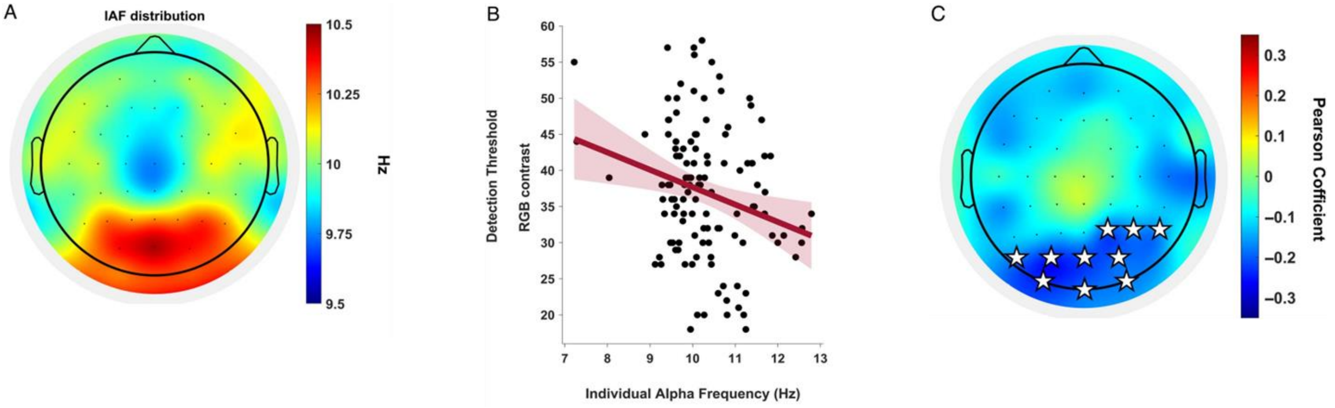

Figure 9. Individual alpha frequency predicted the absolute value for contrast detection.

(A) Distribution of Individual Alpha Frequency (IAF). IAF exhibits higher values in posterior regions but lower values when derived from central electrodes. (B) Pearson correlation analysis revealed a significant negative correlation between trait IAF and visual threshold (r = −0.24, p = 0.007). This correlation suggests that a lower IAF is associated with a higher contrast level required for signal detection. This observed relationship remained robust to outliers (r_skipped = −0.24, CI [−0.38, −0.09]) and was confirmed using Bayesian correlation (Bayes Factor = 4.04). Shaded areas depict confidence bounds. (C) IAF in the posterior electrode cluster (Oz, O2, O1, PO4, POz, PO3, PO7, P6, P4, P2) successfully predicted individual threshold levels. Specifically, a higher IAF was linked to increased perceptual acuity, indicating a lower contrast level needed for accurate perception.

From https://doi.org/10.1162/jocn_a_02026

Compelling evidence in this domain arises from a recent study conducted by Di Gregorio and Trajkovic et al. (2022), which causally established a functional differentiation between the frequency and amplitude of alpha rhythm in influencing objective perceptual awareness and subjective perceptual awareness, respectively. This was achieved by applying rhythmic transcranial magnetic stimulation (rTMS) with three aims: 1) decreasing individual alpha frequency (IAF) by 1Hz, increasing IAF by 1Hz, or entraining alpha amplitude by precisely targeting the IAF. Notably, the reduction in IAF led to decreased d', whereas the acceleration of IAF resulted in heightened sensitivity in the task. Crucially, while augmenting alpha amplitude through stimulation at the IAF did not exhibit any discernible effect on task accuracy, it crucially impacted subjective perceptual awareness.

Rhythmic implementation of the Bayesian brain

Understanding how alpha rhythms influence decisional outcome sets the stage for exploring the rhythmic implementation of Bayesian inference. Considering the various hypotheses concerning the neural substrates of predictive processes (Spratling, 2017), a convergence emerges on two critical aspects: the presence of distinct neural populations responsible for signaling predictions and prediction errors and the necessity for their intercommunication (Friston, 2019). A prevailing model, rooted in a hierarchical architecture (Bastos et al., 2012; Friston, 2010; Rao and Ballard, 1999), proposes a top-down conveyance of predictions and a bottom-up transmission of prediction errors across cortical regions. As this implementation posits a dynamic flow of information within the cortical hierarchy, it is wise to assume that brain rhythms could be a conduit for understanding prediction and prediction-error mechanisms (Arnal and Giraud, 2012; Bastos et al., 2020), as they have a fundamental role in neural networks communication (Fries et al., 2015). Notably, the interplay between gamma and alpha rhythms stands out as pivotal in orchestrating prediction-related neural mechanisms (Bastos et al., 2015; Fontolan et al., 2014; von Stein and Sarnthein, 2000). Alpha oscillations appear to facilitate top-down predictions into sensory regions (Samaha et al., 2015; Sherman et al., 2016). For example, alpha amplitude is shaped as a function of expectations about stimulus directions (De Lange et al., 2013) or by temporal expectations (Rohenkohl and Nobre, 2011; Bauer et al., 2014). Interestingly, studies have shown an increase in alpha power within the sensory cortex during self-generated stimuli (Cao et al., 2017; Stenner et al., 2014) and the phase of alpha oscillations in the pre-stimulus period predicts the impact of stimulus and temporal expectations on perceptual decisions (Samaha et al., 2015; Sherman et al., 2016).

Concurrently, gamma-band activities exhibit a distinct involvement in encoding prediction errors within the predictive coding framework (Arnal and Giraud, 2012; Chao et al., 2018; Sedley et al., 2016). Studies highlight gamma's responsiveness to violations of priors (Brodski et al., 2015) and intensified activity in response to unpredicted stimuli or omissions (Todorovic et al., 2011; Bauer et al., 2014). Moreover, circuit-level dynamics reveal a segregation of gamma and alpha oscillations in feedforward and feedback pathways, respectively (van Kerkoerle et al., 2014). Such segregation aligns with the concept that prediction-related information travels through these pathways: bottom-up gamma synchronizations for conveying prediction errors and top-down alpha synchronization for descending predictions (Michalareas et al., 2016; Bastos et al., 2020).

While gamma oscillations could be crucial for prediction-error signaling, IAF could be crucial for dictating the precision of sampled sensory information. According to this line, faster alpha oscillations would significantly impact the construction and adaptation of predictive models. The premise lies in the notion that faster alpha oscillations enable more efficient sampling of sensory information, leading to the creation of more accurate and adaptive predictive models or priors. As described in the previous paragraph, individuals with higher IAF tend to exhibit enhanced abilities in discriminating sensory stimuli, indicating a more faithful representation of the external world (Cecere et al., 2015; Samaha & Postle, 2015). This enhanced sampling capability would translate into the construction of more precise and nuanced prior models, improving the accuracy of predictive models. Moreover, the advantage conferred by a higher IAF would extend beyond initial model building. Faster alpha oscillations would enable better recognition of changes in prior precision. Individuals with higher IAF exhibit heightened sensitivity to alterations in sensory inputs (Tarasi and Romei, 2013), facilitating more efficient updating of priors in response to changing environmental cues. This adaptability in recognizing shifts in prior precision, rooted in the ability to sample sensory information more effectively, would contribute to a more flexible and adaptive predictive system. The hypothesized relationship between IAF and gamma oscillations suggests a dynamic interplay in predictive coding. Faster alpha frequencies are thought to regulate the precision of how sensory information is sampled, aiding in the construction of more accurate predictive models. Meanwhile, gamma oscillations are responsible for conveying prediction errors throughout the cortical hierarchy. A faster IAF might enable heightened precision in sensory sampling, potentially enhancing the conveyance of prediction errors via gamma oscillations. This interplay would contribute to a more refined and adaptable predictive system, allowing the brain to adeptly respond to environmental cues and deviations.

Moreover, it is plausible to hypothesize a control mechanism that directs prior learning and regulates the implementation of priors. Absent this control mechanism, previously acquired models could operate unchecked, lacking an evaluation process that assesses their appropriateness in relation to the context and incoming stimuli. Therefore, contemplating the hypothesis of a control mechanism directing learning and overseeing prior implementation, the integration of theta oscillations becomes pivotal within the predictive coding framework. Theta oscillations have long been associated with a comprehensive mechanism governing cognitive control implementation (Cavanagh and Frank, 2014). This proposition stems from its observed engagement in goal-directed behaviours where cognitive control processes optimize performance for future challenges, indicating its relevance across diverse cognitive contexts (Cavanagh et al., 2012). Moreover, theta rhythms manifest in response to novelty, conflict, errors, and negative feedback, underscoring their connection with situations requiring cognitive control (Cavanagh et al., 2012). Studies on working memory note heightened theta activity during high load and increased task difficulty, serving as a predictive factor for subsequent long-term memory retrieval (Sauseng et al., 2010). Similarly, in interference resolution tasks, theta power indicates cognitive control recruitment (Hanslmayr et al., 2008), and its activity decreases with the successful suppression of competing associations, highlighting its role in resolving interference (Ferreira et al., 2014). Theta activity peaks in brain regions such as the anterior cingulate cortex (ACC) and coordinates with executive regions to regulate the level of cognitive control as needed (Cavanagh et al., 2012). Specifically, during conflict scenarios, there is an increase in theta phase synchronization between the mid-frontal and lateral prefrontal cortex (lPFC), aiding in adaptive adjustments to task objectives. Moreover, post-error theta phase synchronization between mid-frontal and occipital sensory regions indicates top-down control over stimulus processing to prevent future response errors (Figure 10, Cohen et al., 2009; Nurislamova et al., 2019). Integrating theta oscillations into the predictive coding framework and neural oscillations paradigm prompts an intriguing hypothesis. Given its association with cognitive control, theta rhythms might serve as a monitoring system regulating prior expectations and their utilization during predictive processing. Its potential role could involve evaluating the consistency between incoming sensory information and prior expectations, adjusting predictive models when discrepancies arise. This aligns with the concept that theta acts as a versatile control mechanism adaptable to various cognitive demands, implicating it in monitoring and optimizing predictive processes in the brain.

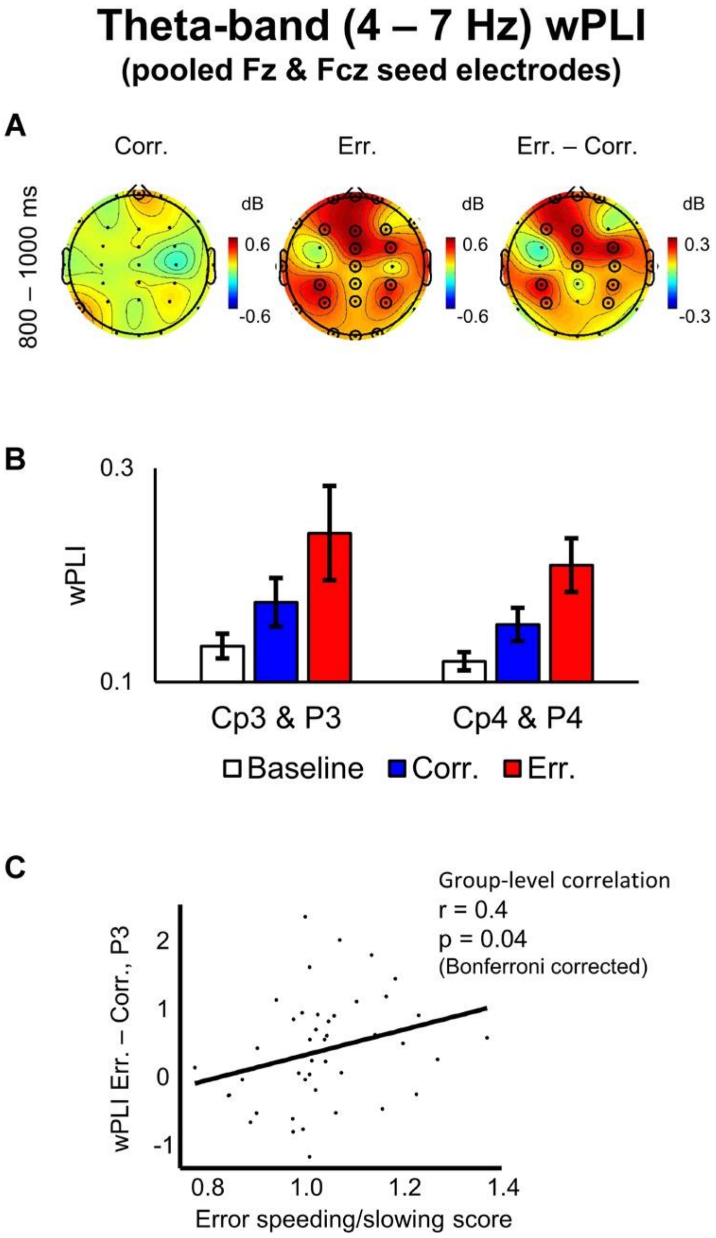

Figure 10. Theta-band wPLI values from aggregated Fz and Fcz seed electrodes were examined for their correlation with error speeding/slowing scores(that measure how quickly or slowly errors are made relative to the speed of correct responses). (A) Topographical maps showcase baseline-corrected theta-band wPLI values during the post-response window, with the left map representing accurate responses, the middle map depicting errors, and the right map illustrating the difference between errors and correct responses. Significant electrodes are denoted by black circles. (B) Bar plots visualize wPLI data for left posterior parietal electrodes (combined Cp3 and P3) and right posterior parietal electrodes (combined Cp4 and P4) within the 800–1000 ms post-response timeframe. (C) The discrepancy in theta-band wPLI values at the P3 electrode between error and correct responses correlates with the error speeding/slowing score.

From: https://doi.org/10.3389/fnint.2019.00014

In summary, the exploration of predictive processes within neural networks converges on key elements: the existence of distinct neural populations for predicting and processing prediction errors, and the crucial intercommunication between them through feedforward and feedback channels. This hierarchical model suggests a top-down transmission of predictions and a bottom-up conveyance of prediction errors across cortical regions. Brain rhythms, especially alpha and gamma oscillations, play vital roles in these predictive mechanisms (Figure 11). Alpha oscillations are associated with top-down predictions, aiding in sensory region modulation, while gamma oscillations encode prediction errors, particularly when expectations are violated or unpredicted stimuli occur. Moreover, individual alpha peak frequency (IAF) could determine the precision of sampled sensory information, impacting the creation and adaptation of predictive models. A faster IAF allows more efficient sampling, potentially enhancing the conveyance of prediction errors by gamma oscillations, refining the brain's adaptive predictive system. Finally, integrating theta oscillations into this framework appears pivotal, given their association with cognitive control and conflict monitoring processes. Indeed, the absence of a mechanism to evaluate the appropriateness of prior models poses a risk of these models operating without any form of validation. Theta oscillations could potentially serve as regulators of prior expectations, adapting predictive models by evaluating incoming sensory information against established models, thereby optimizing predictive processes in the brain.

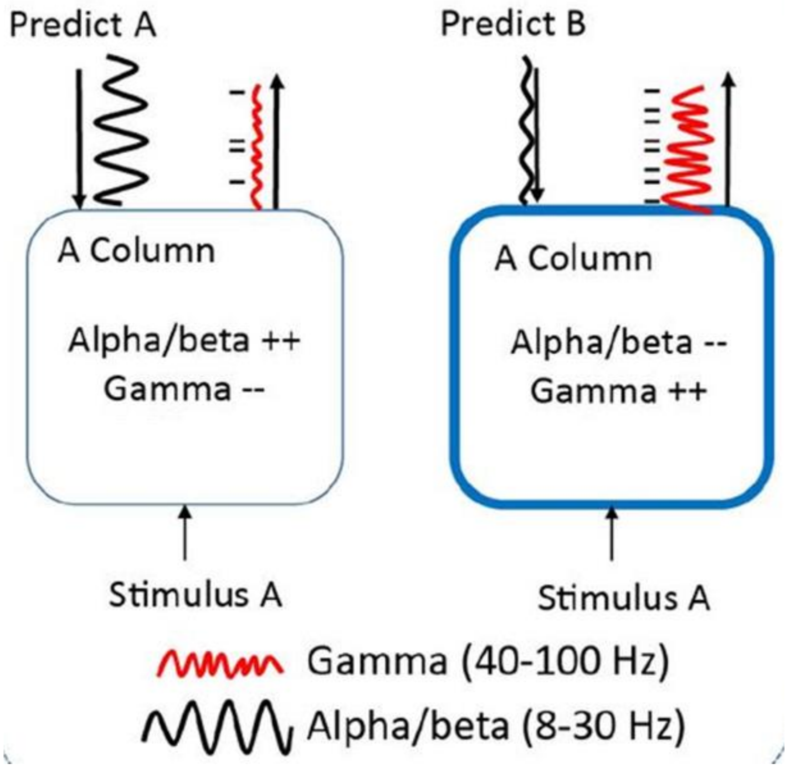

Figure 11. The sensory cortex actively prepares to process its preferred stimulus, referred to as stimulus A, through feedback alpha/beta activity. This heightened alpha/beta activity effectively inhibits the processing of stimulus A by reducing neural spiking and gamma activity, thereby minimizing the feedforward outputs. In situations where there is no anticipation or prediction for stimulus A, there is a reduction in feedback alpha/beta activity directed towards the A column. As a result, the A column becomes more responsive or excitable, responding to stimulus A with increased gamma activity, heightened neural spiking, and an intensified feedforward response. From [*https://www.biorxiv.org/content/10.1101/2020.01.27.921783v1.full*](https://www.biorxiv.org/content/10.1101/2020.01.27.921783v1.full)

Bayesian Perspectives on Autism and Schizophrenia Spectra

Introduction

This chapters on Autism Spectrum Disorder (ASD) and Schizophrenia Spectrum Disorder (SSD) delve into the multifaceted landscapes of two distinct yet interconnected spectrums of neurodevelopmental conditions. ASD is characterized by intricate challenges in social communication and interaction (Tanguay, 2011). Moreover, peculiarities in sensory processing have taken center stage, adding a significant layer to our comprehension of ASD beyond its social behavior aspects (Kessler et al., 2016). On the other hand, SSD encompasses disruptions in perceptual, emotional, and behavioral processes and it is marked by positive, negative, and cognitive symptoms (Tandon et al., 2013).

Both spectrums exhibit a diverse array of traits and behaviors, urging us to comprehend these conditions beyond their clinical confines. Within the ASD spectrum, the concept of the broad autistic phenotype (BAP) (Losh et al., 2009) and autistic traits (Simon Baron-Cohen et al., 2001a) broadens our understanding, unveiling a continuum of traits present not only in diagnosed individuals but also within the general population. Similar to ASD, SSD is viewed on a continuum, expanding to include schizotypal personality disorder (SPD) and schizotypy (Raine, 1991), manifesting as milder SSD traits observable in individuals without meeting the diagnostic criteria.

Both spectrums converge under the lens of Bayesian inference. This chapter will systematically delve into predictive coding frameworks, serving as a structured blueprint to illuminate and comprehend their distinctive perceptual and decision-making styles. Despite their different presentations, both conditions deviate from typical predictive coding processes (Corlett et al., 2019; Sinha et al., 2014), indicating a profound relationship between their atypical cognitive processes and the interplay between prior expectations and sensory information along these spectra. ASD leans towards a tendency to prioritize sensory information over contextual cues, whereas SSD showcases an overemphasis on pre-existing beliefs, influencing perceptions and interpretations of reality.

This exploration seeks to unveil the intricate nuances within these spectra, offering a deeper understanding of their underlying mechanisms and paving the way for more refined interventions and support strategies.

Autistic Spectrum Disorder (ASD)

Autism Spectrum Disorder (ASD) encompasses a wide array of neurodevelopmental conditions that significantly impact social communication, behavior, and sensory experiences. Defined by the Diagnostic and Statistical Manual of Mental Disorders (DSM-5), ASD is characterized by two primary domains: difficulties in social communication and interaction, alongside restricted and repetitive behavioral patterns. Social communication and interaction impairments present as challenges in verbal and nonverbal communication, intricately entwined with difficulties in forming and sustaining meaningful connections. Moreover, ASD individuals manifest deficits in "mind-reading," struggling to attribute mental states to themselves and others (Baron-Cohen and Wheelwright, 2004; Frith, 2001). At the same time, the presence of restricted and repetitive patterns of behavior, interests, or activities portrays a multifaceted picture, including stereotyped behaviors, intense absorption in fixed activities, and a reluctance to embrace change. The onset of ASD typically occurs during the developmental period, but the spectrum allows for diverse developmental trajectories, with symptoms potentially emerging later in life. This variability underscores the individuality inherent within ASD and highlights the varying support needs of those across the spectrum.

Beyond the clinical criteria, in the recent years a full spectrum conceptualization has been proposed for describing the ASD phenotype (Tanguay, 2011). For example, the concept of the broad autistic phenotype (BAP) has been proposed. It refers to a constellation of personality tendencies, cognitive patterns, and behaviors that are similar to, but milder than, those typically observed in individuals diagnosed with Autism Spectrum Disorder. These characteristics are often seen in relatives of individuals with ASD and extend across a spectrum, encompassing a range of social, communicative, and behavioral features. BAP traits include subtle impairments in social interactions, such as difficulties in interpreting social cues, feeling uncomfortable in social settings, or displaying rigid and repetitive behaviors (Hurley et al., 2007). Moreover, individuals within the BAP might exhibit intense interests in specific topics or activities, akin to those observed in ASD individuals, but to a lesser degree. Similarly, the concept of autistic traits refers to a broader continuum of behaviours and tendencies present in the general population. These traits align with features commonly associated with ASD, such as attention to detail, adherence to routines, and heightened sensory sensitivities, albeit to a degree that does not significantly impair daily functioning (Lewton et al., 2019; Ruzich et al., 2015; Stewart et al., 2009). Indeed, individuals in the general population might possess varying degrees of these characteristics without meeting the diagnostic criteria for ASD. Understanding the BAP and autistic traits offers insight into the diversity of human cognition and behavior, emphasizing that features associated with ASD exist on a continuum, with varying degrees of impact on an individual's daily life.

While atypical social behavior has long been synonymous with ASD spectrum, recent focus has shifted towards understanding the significance of sensory abnormalities within this condition (Kessler et al., 2016). Reports indicate that over 90% of individuals diagnosed with ASD encounter sensory irregularities (Hazen et al., 2014; Leekam et al., 2007). For example, individuals with ASD frequently describe severe hyper-sensitivity to stimulating inputs, although a subset also experiences hypo-sensitivity (Ben-Sasson et al., 2009). Furthermore, individuals with ASD tend to exhibit a bias toward local information processing over global or contextual information, as seen in their enhanced performance in visual search tasks that hinge on focusing on small details (Joseph et al., 2009; O'Riordan et al., 2001). This reliance on details extends to neurotypical individuals with high autistic traits (Alink and Charest, 2020). However, the emphasis on local details is linked with challenges in perceiving the broader picture. For instance, individuals with ASD demonstrate reduced susceptibility to perceiving illusory figures such as Kanisza triangles (Bölte et al., 2007; Walter et al., 2009) and they exhibit slower performance on tasks involving hierarchical figures, where the coordination between local and global levels of processing is required (Scherf et al., 2008). Moreover, ASD individuals experience abnormal perceptual experiences potentially leading to sensory overload (Baum et al., 2015; Green et al., 2016; Pellicano, 2013) and they are characterized by a "circumspect reasoning bias", needing more evidence before making decisions and adopting a conservative criterion in perceptual decision-making tasks (Brosnan et al., 2014; Quinde-Zlibut et al., 2020). This broad spectrum of sensory experiences adds a significant layer to our understanding of ASD beyond its traditionally emphasized social behaviour aspects.

Schizophrenia Spectrum Disorder (SSD)

Schizophrenia Spectrum Disorder (SSD) encompasses a diverse array of mental health conditions characterized by disruptions in cognitive, perceptual, emotional, and behavioral processes. According to DSM-5, SSD is characterized by diverse set of symptoms, often categorized into positive, negative, and cognitive domains. Positive symptoms entail alterations in perception and thought, such as hallucinations and delusions, where individuals may experience sensory perceptions without external stimuli or hold beliefs inconsistent with reality. Negative symptoms involve deficits in emotional expression, motivation, and social engagement, leading to a reduced ability to experience pleasure or engage in routine activities. Cognitive symptoms encompass impairments in attention, memory, and executive function, affecting an individual's ability to properly process information and make decisions effectively. The onset of SSD typically emerges in late adolescence or early adulthood, presenting with a range of symptom severity and variability in the course of the disorder. This variability highlights the diverse nature of SSD, shedding light on the unique needs of individuals across the spectrum.

Beyond clinical boundaries, current discussions have broadened to include a wider understanding of SSD, similar to the expanded conceptualization seen in ASD (Tandon et al., 2013). For example, the schizotypal personality disorder (SPD) has been proposed to be part of this spectrum as it shows a milder constellation of traits and behaviors akin to, but less severe than, those observed in individuals diagnosed with schizophrenia. SPD traits often include eccentricities in thinking, perception, and behavior, along with social anxiety, unusual beliefs, and difficulties in forming close relationships. Additionally, the notion of schizotypy covers a wider continuum of experiences and behaviors present in the general population, mirroring some features associated with SSD (Raine, 1991). These traits may involve subtle perceptual distortions, unconventional beliefs, and peculiar behaviors that do not significantly impair daily functioning. Schizotypal traits exist on a spectrum, varying in intensity across individuals without meeting the diagnostic criteria for Schizophrenia. While altered perceptions and thought disturbances have long characterized SSD, recent attention has focused on understanding the complexities of cognitive impairments within this spectrum. Research suggests that deficits in cognitive functioning, particularly in attention, working memory, and executive function, are prevalent across individuals diagnosed with SSD (Mesholam-Gately et al., 2009; Fioravanti et al., 2012). These cognitive deficits contribute significantly to functional impairment and affect an individual's ability to engage in daily activities, maintain employment, and foster interpersonal relationships. Moreover, studies indicate disruptions in the integration of sensory information, leading to challenges in perceiving and processing environmental cues, could contribute to social and functional impairments observed in SSD (Javitt, 2009; Butler et al., 2008).

Bayesian inference in Autism and Schizophrenia spectra

The distinctive perceptual and decision-making styles observed in ASD and SSD have been comprehensively analysed within the predictive coding framework (Corlett et al., 2019; Kafadar et al., 2020; Lawson et al., 2014, 2017; Pellicano and Burr, 2012a; Sterzer et al., 2018; Van de Cruys et al., 2014a). For example, the hypo-priors hypothesis proposes that ASD symptoms stem from underweighting contextual information and predictions in perceptual inference (Pellicano and Burr, 2012). This aligns with the Weak Central Coherence Theory, indicating a tendency to process local details over integrating contextual information, leading to a more "realistic" but fragmented experience of the world (Happé and Frith, 2006). ASD individuals prioritize sensory information over prior expectations, potentially contributing to anxiety and insistence on sameness as predictable activities offer relief from the unpredictability of the environment (Goris et al., 2020; Grillon et al., 2017, 2008). There is also a proposal of an overly precise sensitivity to sensory prediction errors in ASD, leading to continuous updating of predictive models, possibly resulting in the formation of priors with negligible predictive value (Karvelis et al., 2018; Van de Cruys et al., 2014). According to this view (Mottron et al. 2006), the superior performance observed in tasks like visual search or identifying embedded figures in ASD might reflect the consistent and fixed strength of sensory processing mechanisms. In this view, feedforward processes take precedence over feedback processes in ASD (Mottron et al., 2006), a notion supported by increased brain activation levels during visual processing (Samson et al. 2012). Regarding of the precise underlying mechanisms (Figure 12), this collective tendency in ASD indicates a preference for relying more on sensory information than prior expectations, shaping their perceptual experiences.

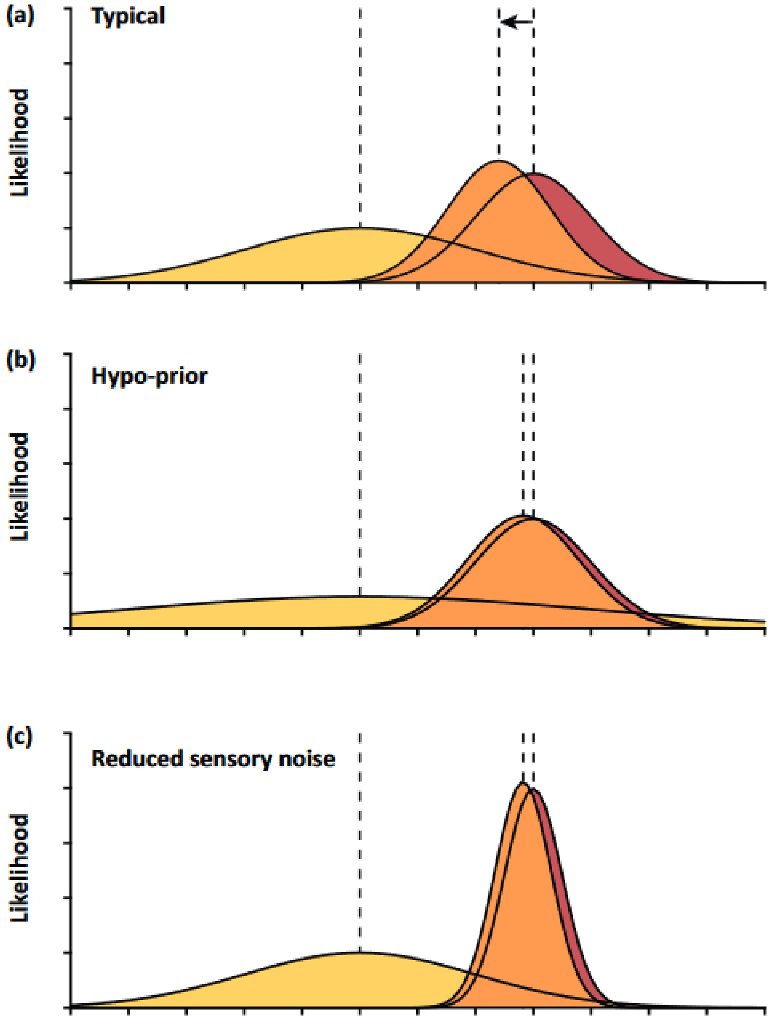

Fig xxx. Bayesian Inference in ASD spectrum

Figure 12.

a) The Bayesian perception framework initiates with a noisy sensory 'observation,' depicted by a red Gaussian curve. This observation is combined with the 'prior' knowledge, illustrated by the yellow Gaussian curve, resulting in a posterior distribution (shown in orange). The optimal estimation, marked by the centre of the posterior distribution, is shifted closer to the prior, as indicated by the arrow.

b) This panel portrays the hypo-priors account. In this instance, the prior's influence is weakened as its variance is increased, significantly bringing the optimal estimate closer to the mean of the sensory observation.

c) This panel represents the alternative bottom-up account. In this scenario, the strength of the prior remains unchanged from the original example, but there's a reduction in sensory noise, symbolized by a halving of the observation's variance. Consequently, the optimal estimate matches that of the 'hypo-priors' example. The symmetry arises due to the relative impact of the prior, which is determined by the ratio of the variance of the prior to the variance of the observation.

From https://www.cell.com/trends/cognitive-sciences/fulltext/S1364-6613(12)00241-0

Turning to SSD, different hypotheses have emerged to explain the root cause of predictive imbalances. The weaker prior hypothesis suggests an inability to anticipate sensory events, leading to over-attribution of saliency towards sensory experiences and promoting a delusional explanation of reality (Heinz, 2002). This hypothesis aligns with the idea of excessive reliance on bottom-up sensory information, leading to an imbalance in processing incoming sensory data versus top-down expectations, contributing to the formation and maintenance of psychotic symptoms (Sterzer et al., 2018). In contrast, the strong prior hypothesis suggests that the overweighting of prior information is the source of predictive imbalances observed in SSD (Corlett et al., 2019; Horga and Abi-Dargham, 2019). According to this framework, individuals with SSD are thought to possess highly rigid and ultra-precise prior beliefs about the world that exert a powerful influence on their perception and interpretation of reality. This means that individuals within the SSD tend to heavily rely on pre-existing beliefs, often to an extent that overrides or distorts incoming sensory information (Powers et al., 2017). Thus, positive symptoms of schizophrenia, such as hallucinations or delusions, are viewed as the consequence of top-down influences on perceptual processes. For example, individuals with SSD demonstrate a "hyper-mentalistic" tendency, wherein they exhibit an inclination to excessively interpret and ascribe mental states to others (Ciaramidaro et al., 2015; Crespi and Badcock, 2008). This hyper-mentalistic approach aligns with the strong prior hypothesis by suggesting that their rigid and precise prior beliefs significantly influence how they perceive and interpret social cues and interactions. Moreover, SSD shows the tendency to prioritize overarching or holistic information rather than focusing extensively on minute details (Russell-Smith et al., 2010). This inclination towards global processing can be understood through the lens of the strong prior hypothesis, wherein rigid pre-existing beliefs or expectations shape their interpretation of the world, encouraging a broader and looser perspective. Additionally, decision-making processes in SSD individuals exhibit distinctive biases, such as the "Jumping to Conclusion Bias” and the "Bias Against Disconfirmatory Evidence" that reflects their inclination to underweight evidence that contradicts their pre-established beliefs, aligning with the idea that their strong prior beliefs overshadow contradictory information (Moritz and Woodward, 2006). These decision-making biases in SSD, coupled with over-confidence in incorrect perceptual decisions (Moritz et al., 2014), could be manifestations of how their ultra-precise predictive models heavily influence their cognitive processes, guiding their interpretations and judgments in various situations.

Comparatively, both ASD and SSD exhibit deviations from normative predictive coding processes. While ASD leans towards underweighting contextual information and an inclination towards sensory data, SSD shows an overemphasis on prior information, leading to distinct perceptual distortions and the persistence of delusional beliefs. Despite these divergences, both spectra demonstrate altered perceptual processing, shedding light on the nuanced interplay between prior expectations and sensory information in shaping their cognitive experiences.

Thesis outline

The preceding points lead to several significant conclusions that shed light on the complexities of perceptual processes.

First and foremost, our perception is an active process, as suggested by the Bayesian brain theory (Rao and Ballard, 1999). This theory challenges the traditional view that sensory processing is a mere reconstruction of bottom-up signals (Gibson, 1951). Instead, it posits that perception involves active inference, utilizing prior expectations to optimize the processing of incoming information.

Secondly, brain oscillations play a pivotal role in the landscape of perceptual decision-making (Samaha et al., 2020). Notably, alpha oscillations have emerged as key influencers of decisional outcomes, with recent evidence suggests an intriguing aspect: while alpha amplitude modulation does not seem directly tied to changes in sensitivity, it does affect decisional bias (Di Gregorio et al., 2022; Iemi et al., 2017; Iemi and Busch, 2018; Kloosterman et al., 2019; Limbach and Corballis, 2016; Nelli et al., 2017; Samaha et al., 2017; Tarasi and Romei, 2023).

Third, brain rhythms are integral to implementing Bayesian inference: alpha/beta synchronization is hypothesized to convey top-down predictions from higher to lower brain regions, while feedforward gamma synchronization acts as a mechanism for conveying prediction errors in a bottom-up fashion (Bastos et al., 2020, 2015, 2012).

Fourth, disruptions in these oscillatory codes can lead to a breakdown in the brain's predictive capacity, as observed in conditions like Autism Spectrum Disorder (ASD) and Schizophrenia Spectrum Disorder (SSD). ASD tends to focus more on external sensory input (Pellicano and Burr, 2012a), while SSD tends to overly weigh prior information in their predictive inferences (Powers et al., 2017), indicative of disorders in predictive coding.

Given these foundational premises, this thesis aims, employing advanced computational models and state-of-art EEG methodologies, to delineate and differentiate the distinct oscillatory mechanisms underlying predictive processing. Furthermore, it seeks to elucidate the rhythmic underpinnings of maladaptive predictive inference observed in ASD and SSD.

Study 1 involved crafting a new bio-behavioral model outlining the Autism-Schizophrenia continuum. The study moves away from a dichotomous perspective, adopting a dimensional framework as it conceptualizes ASD and SSD within a full spectrum. Crucially, the proposed model frames ASD and SSD as predictive ability disorders that stem from disruptions in brain oscillatory patterns. The study unfolds in two key parts. Firstly, it delves into how different predictive styles related to decision-making fall along a continuum where ASD and SSD represent extremes, highlighting a contrasting approach from SSD to ASD in perceptual inference styles. Secondly, the study explores cortical oscillations as potential electrophysiological biomarkers influencing predictive signal conveyance in the brain. It seeks to bridge existing neuro-computational models with insights from brain oscillations literature, framing ASD and SSD as 'oscillopathies.' Finally, the study hypothesizes that differences in predictive approaches in the two spectra would stem from opposing underlying oscillatory imbalances, causing disruption in the processing of descending predictive signals and ascending prediction errors.

Study 2 aims to delve deeper into the brain connectivity patterns related to individual autistic traits within the general population. Derived from the hypotheses established in Study 1, this research further explores the specifics of connectivity anomalies and the directional disruption of connections present in ASD. By examining directional connectivity indices via Granger Analysis applied to EEG signal, the study specifically investigates whether the observed imbalances between feedback and feedforward pathways, noted in clinical form of Autism, are mirrored in individuals with heightened autistic traits in the general population. Notably, the findings indicate that a higher degree of autistic traits predicts a shift towards a feedforward-driven connectivity pattern. This empirical investigation not only complements the theoretical groundwork established in the previous study but also extends it, bridging the understanding gap regarding unique brain organization in individuals with ASD and its potential manifestation in those exhibiting elevated autistic traits without clinical diagnosis.

Study 3, building upon the groundwork laid by Studies 1 and 2, aims to further discern neural signatures distinguishing individuals with high and low autistic traits. Employing a larger dataset, lobe-level analysis, sophisticated graph theory indices, the study effectively delineated that individuals with elevated autistic traits showcase more pronounced bottom-up mechanisms in brain processing. This connectivity organization aligns with the prediction highlighted in study 1, suggesting that in ASD, individuals struggle to form precise predictions of the external environment as sensory input overshadows internal expectations. Study 3's results substantiate this theory by emphasizing that differences in bottom-up connectivity, specifically the impact of sensory input on the overall internal model, are notably pronounced among individuals with higher autistic traits, even within a healthy population. By reinforcing the notion presented in Study 1 and 2, Study 3's findings highlight that even within a healthy population, individuals with higher autistic traits exhibit notable differences in bottom-up connectivity, emphasizing the substantial impact of sensory input on the overall internal model. This unified perspective across the studies underscores the continuum in brain connectivity alterations associated with varying levels of autistic traits, providing deeper insights into how these neural differences manifest across diverse populations.

Study 4 investigates the behavioural and electrophysiological mechanisms underlying the integration of prior knowledge in decision-making. It reveals that individuals vary in their reliance on prior information, linking back to the concept of predictive coding outlined in Study 1, with some individuals emphasizing sensory input while others heavily exploit prior knowledge. This study manipulates prior information on a trial-by-trial basis while recording EEG, revealing that prior expectations influence response criterion without impacting objective performance. At the neural level, this perceptual bias was encoded by the amplitude of posterior alpha oscillations tracking the shifts in decisional criterion. Importantly, this mechanism was regulated by two higher-level neural mechanisms differently acting on this marker: whereas parieto-occipital alpha coupling facilitates the bias setting, fronto-parietal theta coupling dampens the impact of prior knowledge on posterior areas' activity. These findings aided in tracing, for the first time, the neurofunctional mechanisms underlying human predictive styles differences discerning between *believers* (who largely tune their responses according to prior information by means of alpha coupling) and *empiricists* (who check expectation exploitations by means of theta coupling).

Building on this, Study 5 delves into the dispositional factors, associated with autistic and schizotypal traits, able to direct the adoption of a particular predictive style. It employs a manipulation (similar to the 4th study) of perceptual strategies and EEG recordings in individuals screened for these traits. The results of this study align with the theoretical framework proposed in Study 1, highlighting the continuum model between ASD and SSD. It confirms the predictive styles observed in prior studies (*believers* vs. *empiricists*) and establishes a relationship between trait proximity and predictive strategies, revealing that those closer to the positive schizotypy pole tend to embrace a belief-based approach, while proximity to the ASD pole associates with an empiricist strategy, favouring sensory input.

Study 6 offers a unique exploration into the influence of cognitive styles, connected to schizotypal and autistic traits, on attitudes towards vaccination. While study 5 concentrated on the ASD-SSD continuum's implications in decision-making in laboratory setting, this research delves into vaccination attitudes, investigating how these traits intersect to shape ecological and real-life perspectives. The study indicates that proximity to the SSD pole, characterized by a reliance on prior models, is associated with negative vaccination attitudes. This parallels earlier findings in decision-making, hinting at a broader application of these cognitive traits in shaping beliefs. By shedding light on how these traits influence vaccination beliefs, the study expands our understanding of cognitive styles. It demonstrates their broader impact beyond perceptual decision-making task, showcasing how they can influence high-level attitudes related to health.

Together, these studies converge to unveil the intricate landscape of cognitive styles and brain oscillatory mechanisms governing perception, decision-making style, and health-related attitudes. Study 1 illustrates the manifestation of distinct cognitive styles along the ASD-SSD continuum. It emphasizes how an individual's position on this continuum is defined by the varying emphasis placed on prior knowledge versus sensory evidence. Study 2 and 3 bridge the gaps between theoretical models and empirical findings, revealing how differences in the trade-off between ascending and descending information flow within brain networks relate to individual autistic traits. Additionally, the thesis reveals the intriguing relationship between brain oscillations, predictive encoding, and decision-making strategies, solidifying the role exerted by alpha oscillations in shaping perceptual biases and predictive styles (Study 4). Importantly, the differentiation in predictive styles seems to be driven by traits associated with ASD and SSD, steering individuals toward the predictive styles aligned with their position on the continuum (Study 5). Finally, the presented work offers a holistic perspective, extending beyond laboratory settings to explore real-world implications, as evidenced in the investigation into vaccination attitudes concerning schizotypal and autistic traits (Study 6). This research introduces an innovative perspective, demonstrating how cognitive styles and ASD-SSD traits significantly shape beliefs beyond conventional decision-making contexts, with potential implications for public health intervention intentions. Overall, these studies collectively contribute to a richer understanding of how brain oscillatory mechanisms underlie cognitive styles, decisions, and attitudes, emphasizing their extensive impact across diversified contexts.

Study 1: Predictive waves in the Autism-Schizophrenia continuum: a novel biobehavioural model

from the published manuscript:

Tarasi, L., Trajkovic, J., Diciotti, S., di Pellegrino, G., Ferri, F., Ursino, M., & Romei, V. (2022). Predictive waves in the autism-schizophrenia continuum: A novel biobehavioral model. *Neuroscience & Biobehavioral Reviews*, *132*, 1-22.

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; Kõlves 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.

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). 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; Massrali 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).

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 ≃ 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).

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-mentalistic" 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 *Social Rigidity* and *Perceptual Oddities* 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	Explorator y factor analysis & Confirmat ory 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.

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).

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.

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).

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 (Alderson-Day et al., 2017; Partos et al., 2016). 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 these 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.

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).

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.

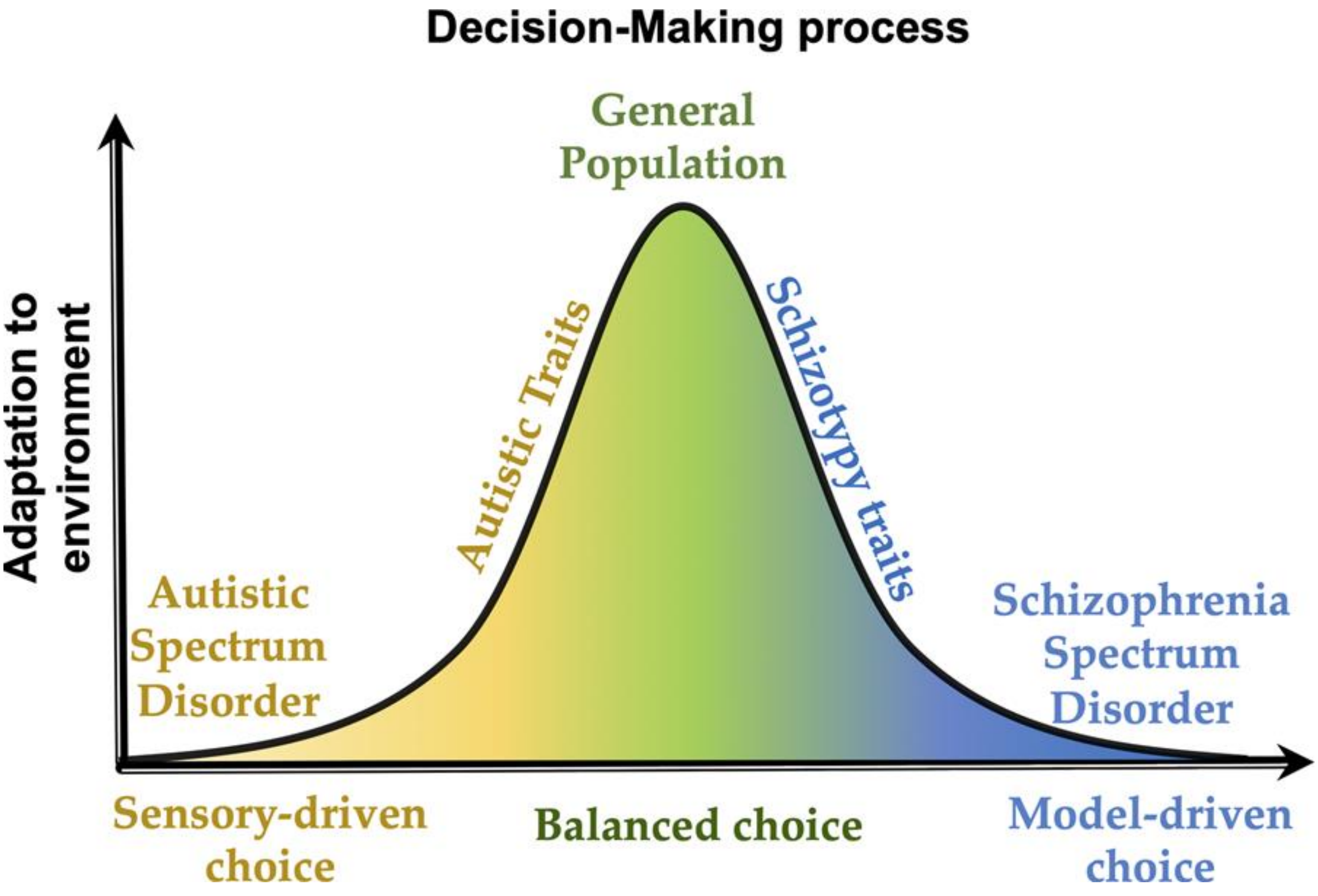

Figure 1. ASD-SSD continuum

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.*

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).

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.

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

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 feed-back information flows (Kessler et al., 2016; Mamashli et al., 2021; Seymour et al., 2017; Varela et al., 2001).

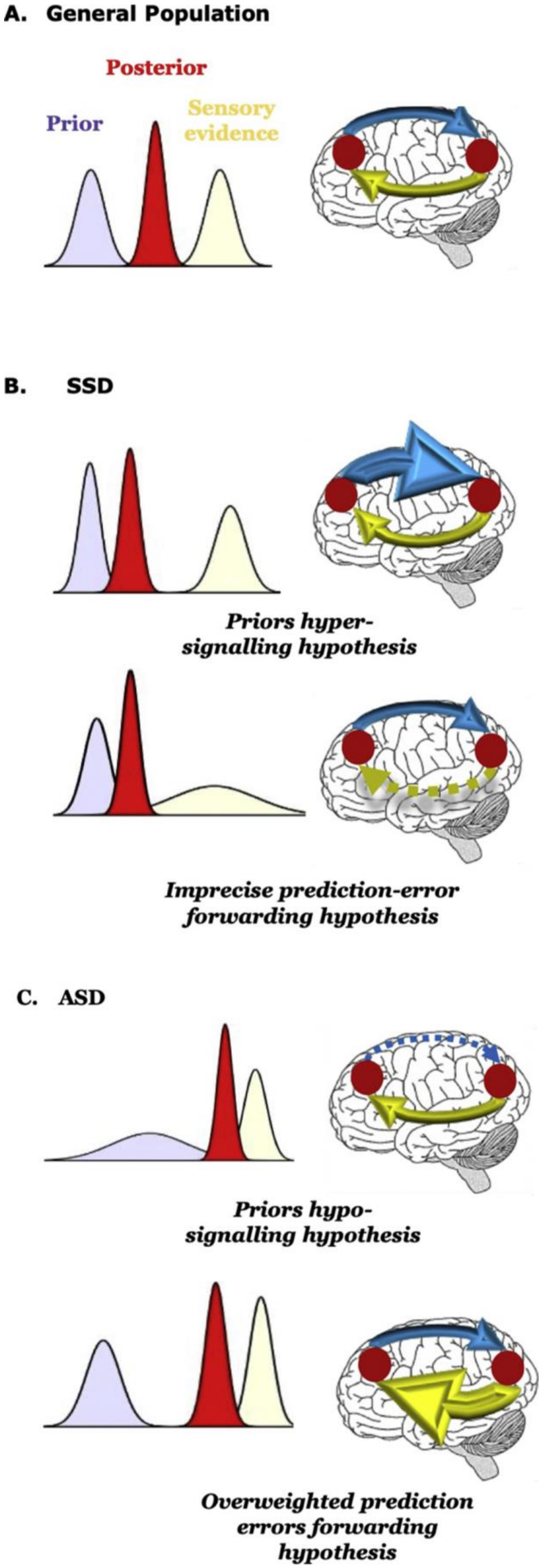
A. General Population
Posterior
Prior
Sensory evidence
B. SSD
Priors hyper-signalling hypothesis
Imprecise prediction-error forwarding hypothesis
C. ASD
Priors hypo-signalling hypothesis
Overweighted prediction errors forwarding hypothesis

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).

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	
Background: 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).	Hypothesis: The alpha-based predictive signaling would be fixedly low regardless of the contextual volatility in ASD
4. Rigid (over)-signaling of prediction error in ASD	
Background: 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).	Hypothesis: The gamma-based prediction error response would fixedly high regardless of the contextual volatility in ASD.

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).

Study 2: The directionality of fronto-posterior brain connectivity is associated with the degree of individual autistic traits

from the published manuscript:

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Abstract

Altered patterns of brain connectivity have been found in autism spectrum disorder (ASD) and associated with specific symptoms and behavioral features. Growing evidence suggests that the autistic peculiarities are not confined to the clinical population but extend along a continuum between healthy and maladaptive conditions. The aim of this study was to investigate whether a differentiated connectivity pattern could be also tracked along the continuum of autistic traits in a non-clinical population. Granger Causality analysis conducted on resting-state EEG recording shows the presence of an opposite pattern of connectivity along the anterior-posterior axis according to the degree of the individual autistic trait. Specifically, participants with higher autistic traits were characterized by a prevalence of ascending connections starting from posterior regions ramping the cortical hierarchy. In contrast, the stream of information in individuals with lower autistic traits flowed from the top to the bottom of the cortical hierarchy. These findings point to the presence of a tendency within the neural mapping of individuals with higher autistic features in conveying proportionally more bottom-up relative to top-down information. This pattern of findings mimics those found in clinical forms of autism, supporting the idea of a neurobiological continuum between autistic traits and ASD.

Keywords: Autism Spectrum Disorder; Autistic Quotient; EEG; Granger Causality; Bottom-Up and Top-Down Connectivity

INTRODUCTION

Autism spectrum disorder (ASD) is a biologically based condition characterized by the presence of restricted and rigid behavior (fixations on certain activities, specific routines or rituals) and deficits in socio-communication abilities (inappropriate social interaction, deficiencies in developing and maintaining social relationships). The whole conceptualization of this condition has changed in recent years: the dichotomous (i.e., absent or present) approach has been replaced by a dimensional (continuum) perspective (Tanguay, 2011). This change in perspective stems from the presence of a constellation of heterogeneous clinical manifestations that can be placed in the autistic boundaries (Baker, 2013). In recent years, the dimensional conceptualization of autism has been further extended. Indeed, several lines of research claim that there are no definite boundaries separating autism from the rest of the general population, as symptoms span from overt clinical manifestations to trait-like expression of this condition (autistic trait) (Simon Baron-Cohen et al., 2001b). The existence of an extended autistic phenotype is confirmed by studies showing a similar genetic basis in individuals within the general population who express autistic traits and in those with diagnosed autism (J Bralten et al., 2018), and by the presence of a substantial overlap in their neurocognitive peculiarities.

Similar to clinical ASD individuals (Frith, 2003), individuals with high level of autistic traits are faster and more accurate in task measuring visuospatial ability, such as the Embedded Figures Test and the Block Design Task (Stewart et al., 2009) and both show an enhanced reliance on details in perceptual processing (Alink and Charest, 2020a) as well as a preference for predictability (Goris et al., 2020). Neuroscientific research has been studying the neural determinants of autism for decades. Individuals within the general population with high autistic traits represent an opportunity to increase knowledge about the neurobiological mechanisms underlying autism, limiting confounding factors such as medication, chronicity and comorbidities that are present in overt clinical forms.

A large body of evidence has shown a close link between brain connectivity anomalies and autistic spectrum symptoms. Studies using functional magnetic resonance imaging (fMRI) have consistently indicated widespread impairment of white matter projections in ASD, mainly in the corpus callosum, bilateral frontal-occipital fasciculus, right arcuate fasciculus and right uncinate fasciculus (Dimond et al., 2019). Similarly, studies investigating connectivity patterns on faster time scales using magnetoencephalography (MEG) and electroencephalography (EEG) assert that widespread connectivity alterations are distinctive biomarkers of ASD (Kessler et al., 2016; Simon and Wallace, 2016). 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). However, the nature of these connectivity anomalies is still under debate. Several studies in the clinical ASD population have shown a weakness in functional connectivity between brain areas during cognitive tasks (Catarino et al., 2013; Just et al., 2007), leading to the development of the *underconnectivity theory* of autism (Just et al., 2012a). In a review analysis, 26 out of 33 neuroimaging studies analyzed showed the presence of reduced or lack of connectivity in ASD, especially in long-range connections (Rane et al., 2015). However, there is a whole branch of literature that points in a different direction showing the prevalence of strong brain hyper-connectivity in individuals within the autistic spectrum. Supekar et al., (Supekar et al., 2013) found functional hyper-connectivity between both proximal and distant anatomical regions, suggesting the presence of both short- and long-range aberrant integration in children with ASD. Moreover, abnormal brain connectivity could also predict autistic symptoms as children characterized by the presence of brain hyper-connectivity were more impaired in social domains and manifest greater autistic symptom severity (Keown et al., 2013).

These apparently contradictory results could be disambiguated by taking into account the directionality of the considered connections. Specifically, functional connectivity in ASD might be abnormally increased when mediated by the feed-forward pathways, but abnormally decreased when mediated by the feed-back pathways. This pattern of over-representation of feed-forward information flow and weak top-down signaling would be congruent with the sensory peculiarities observable in ASD individuals. In fact, compared to control participants with typical development, children with ASD are more influenced by bottom-up visual information (conveyed through feed-forward pathways) (Amso et al., 2014) and less constrained by top-down prior information (conveyed through feed-back pathways) leading to an increased veridical representation of the external world (Karvelis et al., 2018a). Indeed, Takesaki et al. (Takesaki et al., 2016) show that increased occipito-frontal connectivity in the frequency band involved in the spreading of feed-forward information (i.e., gamma band) was associated with higher performance in a visual task in ASD participant. Another strong support for this proposal comes from a MEG study conducted by Khan et al., (Khan et al., 2015). The authors showed that, during somatosensory stimulation, ASD participants were characterized by the presence of increased long-range feed-forward connectivity from primary (S1) to secondary (S2) somatosensory cortex and this strengthened connectivity was correlated with multisensory processing abnormalities. Complementarily, the ASD participants were characterized by reduced long-range feedback connectivity (Mamashli et al., 2021). The weakness in top-down signaling in ASD was confirmed by Seymour et al., (Seymour et al., 2019) using a visual task: V4-to-V1 feedback connectivity was reduced in individuals within the autism spectrum compared to healthy controls and the strength of this feedback connectivity was inversely related to autistic quotient score.

However, although autistic traits are distributed to varying degrees in the general population, it remains unclear whether the peculiarities in brain organization found in ASD patients are also present to a lesser degree in non-clinical individuals with high autistic traits. The first studies conducted analyzing this subclinical population show that higher levels of autism features are related to decreased white matter integrity in tracts associated with visual processing and increased cortical volume in areas related to working memory (Schröder et al., 2021). Other studies show that higher autistic trait was correlated with white matter alteration in inferior fronto-occipital fasciculus (Hirose et al., 2014) and a negative correlation was found between the individual autistic trait and the efficiency of brain networks in an EEG study (Barttfeld et al., 2013). However, to date, we are not aware of other studies that have investigated the presence of a direction-dependent pattern of cortical connectivity (matching that observed in ASD) also in general population with elevated autistic traits.

To fill this gap in the literature, in the present resting-state EEG study we assessed the presence of a differentiated connectivity pattern according to the individual autistic trait, using directional connectivity indices (e.g., Granger analysis). This analysis estimates the causal relationship between distinct brain areas activity measuring the extent to which one time series can predict another (Cohen, 2014; Ricci et al., 2021a). Via this data-analysis technique, we sought to determine whether the imbalances between top-down and bottom-up contributions observed in clinical forms of autism would reverberate in the general population according to the individual autistic trait.

MATERIAL AND METHODS

Participants

Twenty participants (14 female; age range 21–30) took part to the study. All participants signed a written informed consent prior to take part in the study, which was conducted in accordance with the Declaration of Helsinki, and approved by the Bioethics Committee of the University of Bologna. All participants had no neurocognitive or psychiatric disorders. All participants completed the Autism-Spectrum Quotient test (AQ) (Simon Baron-Cohen et al., 2001b). The AQ is a self-report widely used to measure autistic traits in the general population. It consists of 50 items divided into 5 subscales. Each subscale addresses a psychological domain implicated in ASD (e.g., social skills). The AQ provides a global score, with higher values indicating higher levels of autistic traits. In the present study, the total score of the AQ was considered and the Italian version of the AQ was adopted (Ruta et al., 2012).

EEG acquisition and preprocessing

Participants comfortably sat in a room with dimmed lights. EEG was recorded at rest for two minutes, while participants kept their eyes closed. A set of 64 electrodes was mounted according to the international 10–20 system. EEG was measured with respect to a vertex reference (Cz) and all impedances were kept below 10 kΩ. EEG signals were acquired at a rate of 1000 Hz. EEG was processed offline with custom MATLAB scripts (version R2020b) and with the EEGLAB toolbox (Delorme and Makeig, 2004). The EEG recording was filtered offline in the 0.5-70 Hz band. The signals were visually inspected and noisy channels were spherically interpolated. The recording was then re-referenced to the average of all electrodes. Subsequently, we applied the Independent Component Analysis (ICA), an effective method largely employed for removal of EEG artefacts. Components containing artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data.

Cortical Sources Reconstruction and ROIs definition

Since we were interested in connectivity analysis, cortical source activity was reconstructed starting from pre-processed EEG signals. To this aim, intracortical current densities were estimated using the Matlab toolbox Brainstorm (Tadel et al., 2011). Firstly, to solve the forward problem, a template head model (ICBM 152 MNI template) was used as implemented in OpenMEEG software (Gramfort et al., 2010) via the Boundary Element Method. This provides three layers representative of the scalp, the outer skull surface and the inner skull surface, and realistic anatomical information. Then, the sLORETA (standardized Low Resolution Electromagnetic Tomography) algorithm was used for cortical sources estimation. sLORETA is a functional imaging technique belonging to the family of linear inverse solutions for 3D EEG sources distribution modeling (Pascual-Marqui et al., 2002). Specifically, this method computes a weighted minimum norm solution, where localization inference is based on standardized values of the current density estimates. This method provides an instantaneous, distributed, discrete, linear solution with the property of zero dipole-localization error under ideal (noise free) conditions. For sources estimation, the choice of constrained dipole orientations was made, which models each dipole as oriented perpendicularly to the cortical surface. Hence, for each participant, we reconstructed the resting-state time series of current densities at all cortical voxels (15002 voxels). Then, the cortical voxels were grouped into cortical regions according to the Desikan-Killiany atlas (Desikan et al., 2006) provided in Brainstorm, which defines 68 regions of interest (ROIs) as reported in Table 1. At each time point, the mean activity of the voxels belonging to a particular ROI was used as waveform of the cortical activity in that ROI. It is worth noticing that some possible inaccuracies in voxel-level source reconstruction deriving from the use of a template head model for all participants (instead of subject-specific head model) were mitigated by considering the average behaviour at ROIs level.

ROI	Abbreviation	ROI	Abbreviation
Banks of Sup. Temp. Sulcus	BK	Parahippocampal	PH
Caudal Anterior Cingulate	cAC	Pars Opercularis	pOP
Caudal Middle Frontal	cMF	Pars Orbitalis	pOR
Cuneus	CU	Pars Triangularis	pTR
Entorhinal	EN	Pericalcarine	PCL
Frontal Pole	FP	Postcentral	POC
Fusiform	FU	Posterior Cingulate	PCG
Inferior Parietal	IP	Precentral	PRC
Inferior Temporal	IT	Precuneus	PCU
Insula	IN	Rostral Anterior Cingulate	rAC
Isthmus Cingulate	IST	Rostral Middle Frontal	rMF
Lateral Occipital	LO	Superior Frontal	SF
Lateral Orbitofrontal	IOF	Superior Parietal	SP
Lingual	LG	Superior Temporal	ST
Medial Orbitofrontal	mOF	Supramarginal	SMG
Middle Temporal	MT	Temporal Pole	TP
Paracentral	PAC	Transverse Temporal	TT

Table 1: *The 68 ROIs defined by the Desikan-Killiany Atlas provided in software Brainstorm and the corresponding abbreviation.*

Granger Causality Analysis

Once the time waveform in each cortical ROI was estimated (as described above), for each participant k ($k = 1, \dots ,20$) we evaluated the functional connectivity among the ROIs, in order to investigate the relationship between the resting-state cortical communication and the AQ score. To this aim, we adopted Granger Causality (GC) that provides directional metrics of functional connectivity and it is based on the autoregressive (AR) modeling framework. Let's indicate with $x_{k,i}[n]$ and $x_{k,j}[n]$ two time series representing the activity of two distinct cortical ROIs (ROI_i and ROI_j) for participant k. The Granger Causality quantifies the causal interaction from ROI_i to ROI_j as the improvement in predictability of $x_{k,j}[n]$ when using a bivariate AR representation (based on past values of $x_{k,j}$ and also on past values of $x_{k,i}$) compared to a univariate AR representation (based only on past values of $x_{k,j}$). Mathematically, the following two equations hold for the univariate and bivariate AR model, respectively

$$x_{k,j}[n] = \sum_{m=1}^{p} a_{k,j}[m]\, x_{k,j}[n-m] + \eta_{k,j}[n] \tag{1}$$

$$x_{k,j}[n] = \sum_{m=1}^{p} b_{k,j}[m]\, x_{k,j}[n-m] + \sum_{m=1}^{p} c_{k,ji}[m]\, x_{k,i}[n-m] + \varepsilon_{k,j}[n] \tag{2}$$

where index m represents the time lag, p is the model order, a, b, c are model's coefficients (dependent on time lag) and the time series $\eta_{k,j}[n]$ and $\varepsilon_{k,j}[n]$ represent the prediction error of the AR model in each case. The variance of the prediction error quantifies the prediction capability of the model based on past samples: the lower the variance the better the model's prediction. The GC from $x_{k,i}$ to $x_{k,j}$ is defined as the logarithm of the ratio between the variances of the two prediction errors, i.e.

$$GC_{k,ROI_i \to ROI_j} = \ln \frac{var\{\eta_{k,j}[n]\}}{var\{\varepsilon_{k,j}[n]\}} \tag{3}$$

The measure in (3) is always positive, and the larger its value (i.e. the larger the improvement in $x_{k,j}[n]$ prediction when using information from the past of $x_{k,i}$ together with the past of $x_{k,j}$) the larger the causal influence from ROI_i to ROI_j. Similarly, Granger Causality from $x_{k,j}$ to $x_{k,i}$, $GC_{k,ROI_j \to ROI_i}$, is computed via the same procedure, building the AR models for the time series $x_{k,i}$.

For each participant k, we computed the two directed measures of GC for each pair of ROIs, overall obtaining 68 x 67 connectivity values. In all cases, the order p of the AR models was set equal to 30; this value was determined on the basis of a preliminary analysis where we tested different values for the order to the model, obtaining that GC results did not change substantially for $p \geq 30$. Then, for each participant, the total connectivity (GC_k^{TOT}) was computed as the sum of all connections values, and each connection value normalized to the total connectivity, according to the following equations:

$$GC_k^{TOT} = \sum_i \sum_{j,j \neq i} GC_{k,ROI_i \to ROI_j} \tag{4}$$

$$\widetilde{GC}_{k,ROI_i \to ROI_j} = \frac{GC_{k,ROI_i \to ROI_j}}{GC_k^{TOT}} \cdot 100\,; \qquad \forall\, i,j \text{ with } i \neq j \tag{5}$$

In Eq. (4), the summations extend over all the 68 ROIs; moreover, we have $\sum_i \sum_{j,j \neq i} \widetilde{GC}_{k,ROI_i \to ROI_j} = 100$ (i.e., from the adopted normalization, the sum of all connections among the 68 ROIs resulted equal to 100 within each subject). Subsequently, for each participant k, we characterized each $i-th\ ROI$ ($i = 1, \dots, 68$) in terms of the overall (normalized) connectivity outflowing from that ROI ($\widetilde{GC}_{k,ROI_i}^{OUT}$) and inflowing into that ROI ($\widetilde{GC}_{k,ROI_i}^{IN}$). Specifically, we computed

$$\widetilde{GC}_{k,ROI_i}^{OUT} = \sum_{j,j \neq i} \widetilde{GC}_{k,ROI_i \to ROI_j} = \left(\sum_{j,j \neq i} GC_{k,ROI_i \to ROI_j} / GC_k^{TOT} \right) \cdot 100 \tag{6}$$

$$\widetilde{GC}_{k,ROI_i}^{IN} = \sum_{j,j \neq i} \widetilde{GC}_{k,ROI_j \to ROI_i} = \left(\sum_{j,j \neq i} GC_{k,ROI_j \to ROI_i} / GC_k^{TOT} \right) \cdot 100 \tag{7}$$

In Eqs. (6) and (7), the summations extend over all the 68 ROIs. Based on the previous equations, $\widetilde{GC}_{k,ROI_i}^{OUT}$ (named “output sum” for ROI_i) quantifies the contribution of the overall outflow from ROI_i to the total cortical connectivity, and thus characterizes ROI_i as a *source* of causal influence; $\widetilde{GC}_{k,ROI_i}^{IN}$ (named “input sum” for ROI_i)

quantifies the contribution of the overall inflow into ROI_i to the total cortical connectivity, and thus characterizes ROI_i as a *sink* of casual influence.

Then, in order to identify possible ROIs whose role as source or sink of causal inference was modulated by the AQ score, for each ROI_i we computed the Pearson's correlation coefficient between the score values AQ_k and $\widetilde{GC}_{k,ROI_i}^{OUT}$ $(k = 1, \dots, 20)$ and between the score values AQ_k and $\widetilde{GC}_{k,ROI_i}^{IN}$ $(k = 1, \dots, 20)$. Only ROIs for which this analysis provided a correlation coefficient with absolute value above 0.4 (hereafter defined as AQ-modulated source ROIs and AQ-modulated sink ROIs) were taken into consideration, and then used for the following analysis step. In particular, participants were divided into two classes, comprehending participants with AQ score below and above a given cutoff, respectively ($Class1 = \{k{:}\, AQ_k \leq AQ_{th}\}$, $Class2 = \{k{:}\, AQ_k > AQ_{th}\}$), with the cutoff AQ_{th} set equal to 17 since this value corresponds to the average AQ score in control subjects according to the literature (Ruzich et al., 2015a). Then, we computed the average value, over Class1 and over Class2, of each outgoing connection (still normalized, i.e. as in Eq. (5)) from the AQ-modulated source ROIs, and the difference between the two classes was obtained and graphed, to assess how the output connectivity from the AQ-modulated source ROIs differ between the two groups. This same computation was replicated for each connection entering into the AQ-modulated sink ROIs, in order to assess how the input connectivity targeting these ROIs differ between the two groups of participants.

RESULTS

As described in the method section, we first normalized the connectivity matrix, so that the sum of all connections among the 68 brain regions is as high as 100 in each participant (Eqs.(4) and (5)). Then we analyzed where the connections were stronger or weaker (in the normalized scale), as a function of AQ. In particular, for each $k - th$ subject, we focused attention on the "output sum" ($\widetilde{GC}_{k,ROI_i}^{OUT}$) i.e. the sum of the connections leaving each $i - th$ ROI in the network, and "input sum" ($\widetilde{GC}_{k,ROI_i}^{IN}$), i.e. the sum of the connections entering each $i - th$ ROI. Of course, we have 68 values for both the "output sum" and "input sum" (one value for each ROI) per each participant. We assessed whether these quantities exhibit a dependence on AQ score by computing the regression coefficient between these quantities and the AQ score in the twenty participants and focusing only on those ROIs that exhibited a correlation coefficient higher than 0.4.

Results concerning the quantity “output sum” are illustrated in Fig. 1. In this case, five ROIs resulted AQ-modulated as sources of casual influence, that is exhibited a correlation between the output sum and AQ score greater than 0.4: they are the LG left, PCL right, rMF left, rMF right and TP right (see the *glossary* for the meaning of the names). From the plots we can conclude that the overall connectivity outflowing from the LG left, PCL right and TP right is stronger in participants with higher autistic traits; moreover, in each of these regions the p value of the correlation (Bonferroni uncorrected) is lower than 0.05. Conversely, the overall outflow connectivity is stronger in participants with lower autistic traits (low AQ scores) for the regions rMF left, rMF right but with a higher (i.e., less significant) p value.

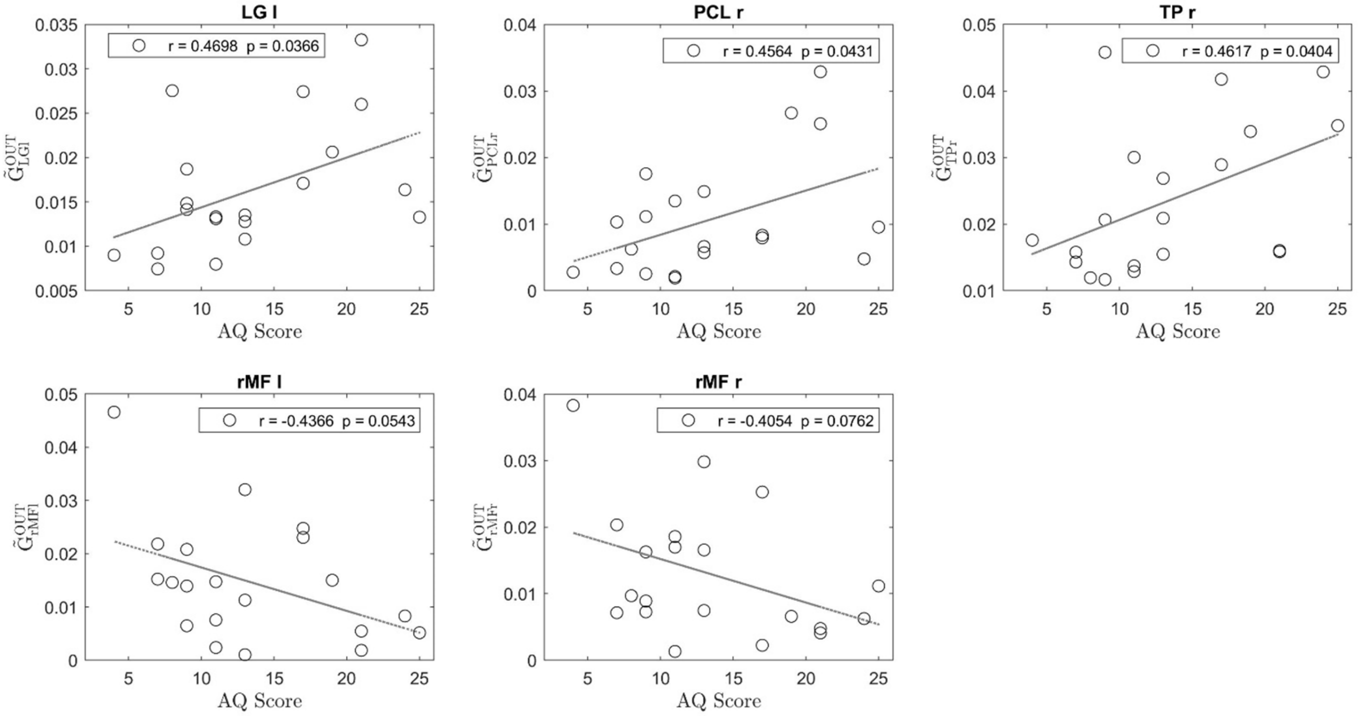

Figure 1 *– Plot of the regression lines between the sum of the normalized connections exiting from a given region (output sum $\widetilde{GC}_{ROI_i}^{OUT}$) and the Autism Spectrum Quotient (AQ) score, obtained using data from the twenty participants. Only plot in the five regions which exhibit a correlation coefficient higher than 0.4 are shown. For each plot, the regression coefficient, and the p value for testing the hypothesis of no-correlation, are shown in the label. It is worth noting that, to obtain these plots, the connection matrix for each participant was normalized, so that the total sum of connection strength is as high as 100 (see Eqs. (4) – (6)). Hence, the values in these plots*

reflect if the connections leaving the ROI are stronger (high value) or weaker (low value), compared with the total sum of the connections in the same subject.

Results concerning the quantity "input sum" are illustrated in Fig. 2. In this case, just two regions resulted AQ-modulated as sinks of causal influences, exhibiting a correlation higher than 0.4; they are the LO right (for which the overall inflow connectivity is higher in the participants with lower autistic traits, but with a higher p value) and the rMF right, (for which the overall inflow connectivity is higher in participants with higher autistic traits, with an uncorrected p value of 0.0019).

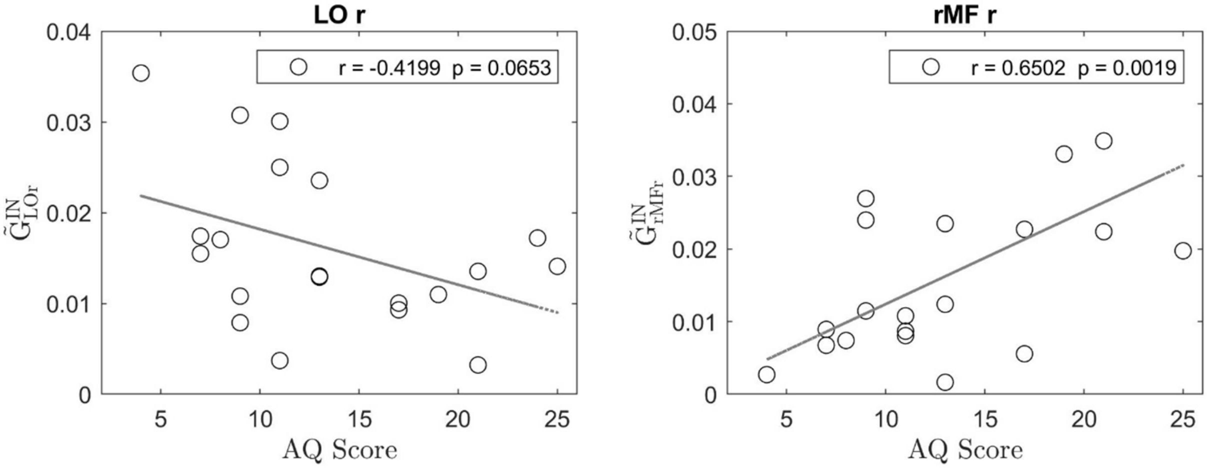

Figure 2 *– Plot of the regression lines between the sum of the normalized connections entering into a given region (output sum $\widetilde{GC}^{IN}_{ROI_i}$) and the Autism Spectrum Quotient (AQ) score, obtained using data from twenty participants. Only plot in the two regions which exhibit a correlation coefficient higher than 0.4 are shown. For each plot, the regression coefficient, and the p value for testing the hypothesis of no-correlation, are shown in the label. It is worth noting that, to obtain these plots, the connection matrix for each participant was normalized, so that the total sum of connection strength is as high as 100 (see Eqs. (4), (5), and (7)). Hence, the values in these plots summarize if the connections entering the node are stronger (high value) or weaker (low value), compared with the total sum of the connections in the same participant.*

In order to reach a better understanding of these differences, we subdivided the 20 participants in two groups (with lower and higher autistic traits) on the basis of the AQ score, using the threshold value 17 to discriminate between the two groups (see also the Methods section). It is worth noting that, according to Figs. 1 and 2, this threshold discriminates quite clearly between a group of 13 participants with AQ $\leq$ 13 (denoted participants with lower autistic traits), and a group of seven participants with an AQ $\geq$ 17 (higher autistic traits). Starting from this partition, the differences between the mean values of the connectivity matrix (still normalized) in the two groups were computed and plotted, by focusing the attention only on the AQ-modulated ROIs obtained in Figs. 1 and 2.

Figure 3 shows the differences in the connections that exit from the five AQ-modulated source regions previously identified in Fig. 1. Blue lines indicate a stronger connection in the group with higher autistic traits, whereas red lines denote a stronger connection in the group with lower AQ scores (only the connections with an absolute value difference between the two groups higher than 0.025 are plotted). As it is clear from this figure, one can observe the presence of three ROIs from which output connections are quite stronger in the group with higher autistic traits: moreover, most of the connections from LG left and PCL right (Out degree as high as 7 and 9 respectively) are directed from occipital toward higher fronto-parietal regions, while connections from the TP right (Out degree as high as 14) are mostly confined within fronto-parietal regions. However, it is worth noting the presence of several connections directed from the TP right toward regions in the left hemisphere. This may underline the presence of some lateralization from right to left in participants with higher autistic traits. Conversely, regions which exhibit stronger output connections in the group with lower autistic traits (i.e., the rMF right and rMR left) have a connectivity especially directed from top to down without any clear lateralization and exhibit a smaller Out degree (4 and 2 respectively).

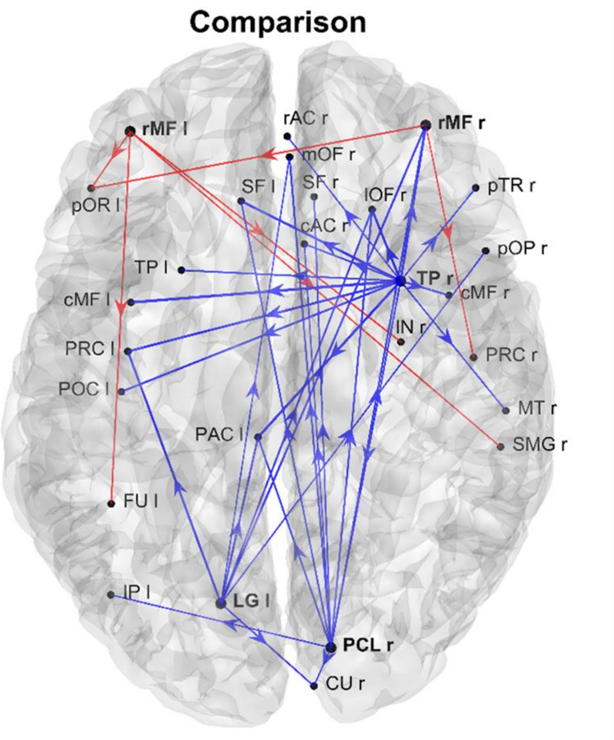

Figure 3 *– Network showing the differences between the normalized connections in the two groups, with reference to the connections that exit from the five AQ-modulated source ROIs identified in Figure 1. Only differences with an absolute value higher than 0.025 are shown. Red lines indicate that the mean value of the normalized connection is stronger in the group with lower autistic scores (AQ score<17), while blue lines denote connections higher in the group with higher autistic scores (AQ score≥17). It is evident the presence of three nodes (LG left, PCL right and TP right) with stronger output connectivity in the group with higher autistic traits.*

Figure 4 shows the differences in the connections that enter the two AQ-modulated sink ROIs previously identified in Fig. 2. In this case too, only differences higher than 0.025 (in absolute value) are shown, with blue line denoting stronger connection in the group with higher autistic traits, and red lines stronger connections in the other group. The region LO right shows a pair of connections stronger in the group with lower autistic traits (In degree 2) entering from top to bottom. Much more relevant, in the group with higher autistic traits the region rMF right exhibits a large number of stronger entering connections (In degree 24), while most of these connections originate from lower occipital-parietal regions. The presence of these bottom-up connections entering into rMF right is characterized by the highest statistical difference between the two groups (uncorrected p value of 0.0059 for the unpaired t-test between the two groups).

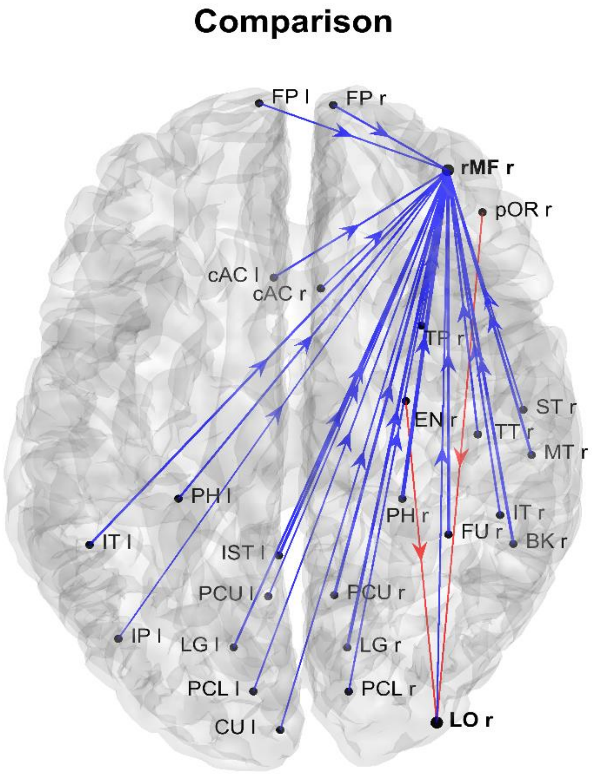

***Figure 4** – Network showing the differences between the normalized connections in the two groups, with reference to the connections that enter into the two AQ-modulated sink ROIs identified in Figure 2. Only differences with an absolute value higher than 0.025 are shown. Red lines indicate that the mean value of the normalized connection is stronger in the group with lower autistic scores (AQ score <17), while blue lines denote connections higher in the group with higher autistic scores (AQ score ≥17). It is evident the presence of a ROI (rMF right) characterized by stronger input connections in the group with higher autistic scores relative to the group with lower autistic scores.*

DISCUSSION

In the present study we demonstrated the presence of a differential connectivity pattern according to autistic traits in a non-clinical population. To the best of our knowledge, this is the first study that has exploited Granger Causality analysis to investigate the brain organization connected to autistic features in a resting-state electroencephalographic study. Although there is abundant evidence of abnormal brain connectivity in clinical forms of autism, there are limited studies investigating whether such abnormalities are also traceable in the general population with high autistic traits (Schröder et al., 2021).

In literature, ASD has been framed as either a dis-connection or over-connection disorder (O'Reilly et al., 2017a). Recent experimental evidence has shown that both hypotheses may be appropriate if weighted according to the directionality of the considered connectivity. Specifically, in ASD there would be the presence of increased functional connectivity in feedforward direction and hypoconnectivity in the feedback direction (Khan et al., 2015). The employment of a directional functional connectivity method like Granger Causality has allowed to investigate the existence of a direction-dependent connectivity pattern, that mimics that observed in ASD, even in general population depending on the autistic trait.

An important aspect of our analysis, compared with previous connectivity studies, is that we investigated the *normalized* connectivity network, i.e., the sum of the connectivity values is equal to 100 in each subject. This choice allows us to understand whether a given subject makes greater or lesser use of connections in a particular direction compared with other parts of his/her brain connectivity network, and to summarize which hubs are particularly relevant for information processing (considered either as a source to generate information to be transmitted toward other regions, or as sink to collect information from different regions). The basic idea is that a connectivity strength is not important per se, but compared with the strength of other connections within the same network, to decide where information is principally created, transmitted and manipulated within a complex and strongly interconnected processing system.

The conducted analysis has showed that connectivity along the fronto-posterior axis appears to be sensitive to the magnitude of individual autistic traits in a different way depending on the directionality (top-down or bottom-up) being considered. Indeed, high-AQ individuals are characterized by a prevalence of connections that originate from posterior brain regions ascending the cortical hierarchy in a feed-forward flow. Complementarily, there is less connectivity flowing in the opposite direction. Indeed, we proved that the number of connections outflowing from rMF left and rMF right are weakened as the autistic trait increases. rMF encapsulate several frontal Brodmann regions (including BA46; (Kikinis et al., 2010)) critical for higher order executive functions including top-down control, attention and decision making (Miller and Cohen, 2001). The reduced number of connections from this hub may suggest that top-down information-flow is limited in individuals with high- relative to low-autistic features.

Vice versa, in the high-AQ individuals the activity of these high-level areas seems to be regulated from the downstream regions as evidenced by the significant number of connections entering in rMF right deriving mainly from the occipito-parietal areas. This preponderance of signals coming from the posterior region of the brain involved in visual processing is further supported by the finding that the ROIs in which the outgoing connections are greater in the high- compared to the low-AQ score have mainly occipital origin (i.e., LG left and PCL right). Crucially, most of the connections exiting from these regions are directed toward fronto-parietal hubs. This pattern of results resembled that observed in clinical form of autism. In a resting-state functional MRI study, Keehn et al., (R Joanne Jao Keehn et al., 2019) show that a sub-group of adolescents with ASD was characterized by occipito-frontal overconnectivity, which was also associated with autism symptom severity. Interestingly, the occipito-frontal seeds associated with over-connectivity in their study (i.e., pericalcarine cortex and middle frontal gyri) are similar to those shown in our study.

Another region exhibiting increased numbers of outgoing connections according to the individual autistic trait is the temporal pole. This region is crucial for high-level semantic representation and in social-emotional processing, including mentalization ability (Olson et al., 2007). The diminished capacity to infer the mental states of others is one of the key features of the autistic spectrum (Andreou and Skrimpa, 2020). Future studies should clarify whether the observed differentiation in the connectivity profile of the right temporal pole might subtend to a peculiar social-processing also in high-AQ individuals. Noteworthy, outgoing connections from the right temporal pole were directed primarily to regions of the left hemisphere. This finding fits with the anomalies found in clinical forms of autism in the white matter pathways connecting the two cerebral hemispheres (e.g., the corpus callosum (Valenti et al., 2020)). This could imply some dysfunction in interhemispheric information transfer present along the autism continuum.

Another aspect to be addressed by further studies would be the spectral characterization of the connectivities proven to be sensitive to the autistic trait. Several studies indicate that synchronization along the alpha/beta band could serve top-down signaling whereas feedforward signaling would rely on gamma synchronization (Mayer et al., 2016; Michalareas et al., 2016a). It would be intriguing to explore whether the preponderance of feed-forward over top-down connections observed as the autistic trait increases in our non-clinical population is mirrored by an over-representation of gamma connectivity over alpha/beta connectivity.

Overall, our results highlight the presence of a predominance of bottom-up relative to top-down signaling as the autistic features raise. This finding is congruent with previous behavioral and functional research. Individuals along the autistic spectrum perform better on tasks relying on bottom-up processing and poorly on tasks where top-down coordination is required and this behavioral pattern is paired with a higher activity in occipital and posterior parietal cortex and lower activity in the frontal cortex (Manjaly et al., 2007; Samson et al., 2012a). Crucially, individuals with high autistic traits show peculiarities in information-processing qualitatively similar to those found in ASD clinical forms (Alink and Charest, 2020a; Joshua C Skewes et al., 2015). However, an important and novel aspect of these results is that these highlighted characteristics in brain organization are present even at rest. This would testify to the presence of an intrinsic and stable bias within the neural system in the signalling of bottom-up relative to top-down information in people with high autistic traits.

Since some behavioral patterns observed in ASD are also found in individuals with high autistic traits, it would be of great interest to investigate whether and how the pattern of altered directionality observed here in resting-state connectivity along the autism continuum also extends during task performance (e.g., during decision-making tasks), providing a neural substrate underlying the noted similarities at the behavioral level.

CONCLUSION

To sum up, the obtained findings testify to the presence of an opposite pattern of connectivity along the anterior-posterior gradient as the individual autistic traits increase: while the anterior areas are overwhelmed by information coming from downstream areas, the posterior areas are less regulated by top-down activity coming from superior areas. This indicates that peculiarities in brain organization are not only traceable in diagnosed autism, supporting the idea of a neurobiological continuum between autistic traits and clinical autism spectrum conditions.

Study 3: Bottom-up vs. top-down connectivity imbalance in individuals with high-autistic traits: an electroencephalographic study

from the published manuscript:

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Abstract

Brain connectivity is often altered in autism spectrum disorder (ASD). However, there is little consensus on the nature of these alterations, with studies pointing to either increased or decreased connectivity strength across the broad autism spectrum. An important confound in the interpretation of these contradictory results is the lack of information about the directionality of the tested connections. Here, we aimed at disambiguating these confounds by measuring differences in effective connectivity using EEG resting-state recordings in individuals with low and high autistic traits. Brain connectivity was estimated using temporal Granger Causality applied to cortical signals reconstructed from EEG. Between-group differences were summarized using centrality indices taken from graph theory (*in degree*, *out degree*, *authority*, and *hubness*). Results demonstrate that individuals with higher autistic traits exhibited a significant increase in *authority* and *in degree* in frontal regions involved in high-level mechanisms (emotional regulation, decision-making, and social cognition), suggesting that anterior areas mostly receive information from more posterior areas. Moreover, the same individuals exhibited a significant increase in the *hubness* and *out degree* over occipital regions (especially the left and right pericalcarine regions, where the primary visual cortex is located), suggesting that these areas mostly send information to more anterior regions. *Hubness* and *authority* appeared to be more sensitive indices than the *in degree* and *out degree*. The observed brain connectivity differences suggest that, in individual with higher autistic traits, bottom-up signaling overcomes top-down channeled flow. This imbalance may contribute to some behavioral alterations observed in ASD.

Keywords: Autism Spectrum Disorder; Autistic Quotient; Granger Causality; In Degree and Out Degree; Hubness and Authority; Bottom-Up and Top-Down connections

Introduction

Autism is a complex neurodevelopmental condition characterized by several behavioral peculiarities, involving avoidance of social interactions, reduced communication, and restricted interests (see the Diagnostic and Statistical Manual of Mental Disorders). The biological origin of this condition is a subject of active research, in an effort to understand its fundamental neural mechanisms. In this regard, a current perspective is that autistic traits could be explained by modifications in brain network characteristics, especially in the connectivity among brain areas underlying perception, social cognition, language, and executive functions (Kana et al., 2014).

Indeed, many recent studies have reported that individuals within the autism spectrum disorder (ASD) exhibit altered brain connectivity compared to typically developing individuals. However, literature reports are often inconsistent (see review papers by Maximo et al., 2014; Mohammad-Rezazadeh et al., 2016; Carroll et al., 2021). The traditional point of view, predominantly supported by studies using structural and functional MRI, hypothesizes that autism is characterized by long-range underconnectivity, potentially combined with local overconnectivity (Abrams et al., 2013; Delbruck et al., 2019; Just et al., 2012b). Conversely, there have been several more recent studies, using EEG and MEG, in which the hypoconnectivity hypothesis could not be confirmed in ASD. Rather, several studies pointed to hyperconnectivity among specific brain areas, especially between thalamic and sensory regions (Nair et al., 2013) or between the extrastriatal cortex, frontal and temporal regions (Fu et al., 2019; Murphy et al., 2012; Uddin et al., 2013). Finally, a third line of evidence points towards the existence of a more subtle mixture of hypo- and hyper-connectivity, suggesting the presence of multiple mechanisms (Abbott et al., 2018; Di Martino et al., 2011; Kana et al., 2014; Lynch et al., 2013).

Some of these differences, of course, can derive from methodological issues. Connectivity is an elusive concept that can be dramatically affected by the measurement technique adopted (for instance, fMRI vs. EEG/MEG), by the particular task involved (vs. resting state analysis), and perhaps more importantly, by the specific measure employed to estimate the connection strength (e.g., functional, effective or anatomical connectivity, directed or undirected measures, bivariate or multivariate). Indeed, most connectivity measures in literature are not-directional and hence are inadequate to discover differences in lateralization or in top-down vs. bottom-up information processing (O'Reilly et al., 2017b).

In particular, it is well-known that cognitive functions are characterized by a complex balance between integration, involving the coordination among several brain areas, and segregation, involving specialized computations in local areas. According to the predictive coding theory (Clark, 2013a), the brain continually generates models of the world by integrating data coming from sensory input with information from memory. Sensory perception is thus the result of a combination between present data from the external world (usually carried by feedforward bottom-up connectivity) and past or prior knowledge (mainly conveyed through feedback, top-down connections); hence, an equilibrium between these directional connectivity patterns is necessary to adaptatively integrate stimuli-driven and internally-driven representations, preventing their segregation or excessive bias towards one or the other.

Recent hypotheses (Pellicano and Burr, 2012a; Van de Cruys et al., 2014a) assume that ASD individuals exhibit an impaired predictive coding, characterized by an imbalance between these two processing streams, i.e., dominant bottom-up processing and relatively weaker top-down influences compared with control individuals. This signifies that people in the autistic spectrum would pose much more emphasis on present sensory stimuli and somewhat less weight on contextual information. This imbalance, in turn, may result in poor social adaptation and insufficient appropriateness to social requirements (Sinha et al., 2014). Results that support this point of view include a reduced susceptibility to illusions and top-down expectations (Crespi and Dinsdale, 2019; Joshua C. Skewes et al., 2015a) and increased local (vs. global) processing in individuals within the autism spectrum (Cribb et al., 2016a; Mottron et al., 2006) leading to a more stimulus- and detail-driven perceptual style.

The aforementioned alterations in predictive coding may be caused by altered brain connectivity, especially concerning top-down vs. bottom-up circuitry (Tarasi et al., 2022c). Additionally, alterations in connectivity patterns may involve a different transmission of brain rhythms and an impaired wave synchronization, which plays a pivotal role in several cognitive tasks, including attention, information selection, working memory, and emotion (Basar-Eroglu et al., 2007; Clayton et al., 2015).

Finally, increasing evidence both at the genetic and behavioral levels demonstrates that autism does not represent a dichotomy condition (i.e., one ON/OFF in type) but is best described as a spectrum of manifestations ranging from clinical forms to trait-like expressions within the general population (S. Baron-Cohen et al., 2001; J. Bralten et al., 2018; Cribb et al., 2016a) that share a peculiar cognitive style that distinguishes them from the rest of the clinical and nonclinical population (Tarasi et al., 2022c).

Following these ideas, in a recent paper (Tarasi et al., 2021a), we investigated whether the patterns of brain connectivity, estimated with Granger causality from EEG source reconstruction, exhibit differences in two nonclinical groups classified as low or high on autistic traits. Preliminary results suggested that connectivity along the fronto-posterior axis is sensitive to the magnitude of the autistic features and that a prevalence of ascending connections characterized participants with higher autistic traits.

The present study aims to further extend the previous work on a larger cohort allowing for an improved connectivity analysis by implementing measures taken from the graph theory. In particular, new aspects of the present study concern: i) the use of a larger data set; ii) a preliminary analysis at the lobe level; iii) the use of more sophisticated indices taken from the graph theory, such as hubness and authority; iv) the use of a more sophisticate statistical analysis (i.e., the use of sparse connectivity matrices) to better point out differences in connectivity between the two groups.

Particularly, graph theory represents a powerful tool able to summarize complex networks consisting of hundreds of edges, using a few parameters with a clear geometrical meaning. Recently, this theory has been applied with increasing success as an integrative approach, able to evaluate the complex networks that mediate brain cognitive processes (Farahani et al., 2019; Minati et al., 2013; van Wijk et al., 2010; Wang, 2010). In particular, since our attention here is primarily devoted to the presence of differences in the direction of connections (ascending vs. descending, lateralization, etc.), we focused our analysis on the *in degree* and *out degree*, defined as the sum of connection strengths entering or leaving a given node. Furthermore, we also tested whether two analogous but more specialized measures of centrality, *hubness* and *authority*, can provide additional information to better characterize directionality. The hub's index of a node is the weighted sum of the authority's indices of all its successors; hence, this measure summarizes the capacity of a node to send information to other critical, authoritative nodes. The authority's index of a node is the weighted sum of the hub's indices of all its predecessors and summarizes the capacity of a node to receive essential information from hubs. Here, we investigate whether differences in these measures, and the pattern of *out* and *in* connections from the dominant nodes, can reveal a difference in the network's topology, and alterations in information processing, as a function of the autistic trait.

2 Materials and methods

2.1 Participants

Forty participants (23 female; age range 21–30, mean age = 24.1, SD = 2.4), with no neurocognitive or psychiatric disorders, took part in the study. All participants signed a written informed consent before taking part in the study, conducted according to the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna. All participants completed the Autism-Spectrum Quotient test (AQ) (Baron-Cohen et al., 2001). The mean AQ score was 16.1 ± 6.6. The AQ is a self-report widely used to measure autistic traits in the general population. It provides a global score, with higher values indicating higher levels of autistic traits. We used the original scoring methods converting each item into a dichotomous response (agree/disagree) and assigning the response a binary code (0/1). In the present study, the total score of the AQ was considered, and the Italian version of the AQ was adopted (Ruta et al., 2012). The participants were divided into two groups, depending on their AQ score being below or above a given cutoff, with the cutoff set to 17, since this value corresponds to the average AQ score in the non-clinical population (Ruzich et al., 2015b). In the following, we will refer to the two groups of participants as Low AQ score Group (N = 21) and High AQ score Group (N = 19). The methods for EEG data collection and preparation, reconstructing cortical sources, defining Regions of

Interest (ROIs), and conducting Granger Causality Analysis in this study precisely replicate the methodologies used in study 2.

2.2 Indices Derived from Graph Theory

As previously reported by other authors (Deshpande et al., 2009; Sporns, 2018) the connectivity between the ROIs of a brain network can be described as a weighted graph, where the magnitude of the connectivity between two ROIs is represented as the weight of an edge, whilst the ROIs connected by the edge are the nodes of the graph. A most remarkable consequence of the adoption of this representation for the brain network is the introduction of several concepts and measures from Graph Theory, which allows us to achieve a better understanding of the network's topology (Farahani et al., 2019; Minati et al., 2013; van Wijk et al., 2010). For this study, we focused on centrality indices that take into account the direction of connections, specifically *authority*, *hubness*, *in degree*, and *out degree* centralities. These indices, which will be detailed in the following, were specifically selected for their focus on the ROIs' inputs and outputs, which we hypothesized could offer confirmatory evidence of connectivity patterns previously observed in individuals with low and high autistic traits (Tarasi et al., 2021a).

The Graph – A graph is the mathematical abstraction of the relationships between some entities. The entities connected in a relationship are called "nodes" of the graph and are often represented graphically in the form of points. These nodes are connected by edges. While the simplest form of a graph is undirected (i.e., the edges do not have orientation), the graph we use to describe a brain network is a weighted directed graph (or digraph), i.e., it has oriented edges, each one with a weight representing the strength of the connection.

To obtain the graphs, for each participant the connectivity matrix was normalized so that its elements provided a sum of 100 (i.e., each connectivity value was divided by the total sum of connections and multiplied by 100). Furthermore, the normalized 68 x 68 matrices (which we will be calling "complete" matrices for clarity) were turned into 68 x 68 sparse matrices by removing (i.e., setting to zero) any connection that was not significantly different between the High and Low AQ score Groups. In particular, a two-tailed Monte-Carlo testing was applied (5000 permutations) and, based on its results, not significant connections were defined as having an uncorrected p-value greater than 0.05.

Forty graphs (one per participant) were obtained both for the complete normalized and the sparse matrices. For each of these graphs, centrality indices were then computed. Although a preliminary investigation was performed on the complete matrices, our analysis is mainly focused on sparse matrices since by excluding "similar" connections we expect to better capture differences in the connectivity patterns and in graph indices between the two groups.

Centrality Indices – Graph theory defines a multitude of indices and coefficients that allow describing the topology of a network from different points of view. Centrality indices are part of these. They measure the importance of a particular node in the network. The four centrality indices considered in this study (*in degree*, *out degree*, *authority*, *hubness*) quantify the importance of a node as a source or a sink for the edges. In the following, we will first introduce the *in degree* and *out degree* centralities; then, *authority* and *hubness* will be described, stressing on how they differ from *in degree* and *out degree*.

In the following, A will always indicate a generic adjacency matrix (i.e., a matrix containing all edges' weights). In particular, the element $A_{i,j}$ of the matrix will represent the weight of the edge connecting node *i* to node *j*.

In degree is the sum of the weights of the edges entering into a node.

$$In\ degree_i = \sum_j A_{j,i} \qquad (4)$$

Out degree is the sum of the weights of the edges exiting from a node.

$$Out\ degree_i = \sum_j A_{i,j} \qquad (5)$$

As a result of their direct dependence on the strength of input and output connections, *in degree* and *out degree* provide an immediate description of the nodes most involved in the transmission (*out degree*) and reception (*in degree*) of information.

Authority and *hubness* centralities include a more refined concept compared to *in degree* and *out degree* centralities and have a distinctive feature of strict interdependence. Their mathematical formulation is the following one.

Authority (x_i) is proportional to the sum of the weights of edges entering a node, multiplied by the *hubness* of the node the edge originates from.

$$x_i = \alpha \sum_j A_{j,i} y_j \tag{6}$$

Hubness (y_i) is proportional to the sum of the weights of edges exiting from a node, multiplied by the *authority* of the node the edge points to.

$$y_i = \beta \sum_j A_{i,j} x_j \tag{7}$$

These indices were computed using the function provided by the Matlab's libraries contained in the Category "Graph and network algorithms" (Matlab R2021a), particularly the command digraph/centrality. This function sets both α and β equal to 1 and calculates *authority* and *hubness* via an iterative procedure [aggiungere altro? Michele].

Similar to *in degree* and *out degree*, *hubness* and *authority* provide a measure about which nodes of the network are primarily involved in the transmission (*hubness*) and reception (*authority*) of information, but they also mutually account for the centrality of the receiving and sending nodes. In particular, since these two centrality indices point to each other (i.e., to compute *authority*, we use *hubness*, and vice versa), they imply that strong connections exist between nodes with high *authority* and nodes with high *hubness*, and these indices may be useful to further emphasize any existing directionality in the connectivity pattern.

Connectivity Analysis - For each participant, starting from either the complete normalized or the sparse 68 x 68 matrix, the four centrality indices were computed at each of the 68 ROIs. Additionally, we computed the average complete and sparse connectivity matrix in the Low AQ score Group and in the High AQ score Group, and then their difference.

Initially, we performed an analysis at the level of macro regions (englobing several ROIs) rather than at single ROI level. To this aim, we considered 8 regions corresponding to brain lobes (frontal, parietal, temporal, and occipital lobes, both left and right). Specifically, for each participant, the 68 x 68 connectivity matrix was transformed into an 8 x 8 connectivity matrix; the elements of the 8 x 8 matrix were filled in with the mean value of all the connections going from one lobe to another. The elements of the 8 x8 matrices were subsequently tested for statistical significance across the two groups of participants, by applying a two-tailed t-test (significance level 0.05, no correction), resulting in 64 comparisons. Furthermore, the 8 x 8 difference matrix was computed, by subtracting the 8 x 8 mean connectivity matrix of the Low AQ score Group from the 8 x 8 mean connectivity matrix of the High AQ score Group. Thus, the elements of the difference matrix greater than 0 represented stronger connectivity for the High AQ score Group, while elements of the difference matrix less than 0 represented stronger connectivity for the Low AQ score Group.

Then, a more detailed analysis was performed at the level of each ROI.

In the case of the complete connectivity matrix, we identified the ROIs which exhibit a significant correlation between the centrality indices (in particular authority and hubness) and the AQ score. The p-value is computed by transforming the correlation to create a t -statistic having N-2 degrees of freedom, where N is the number of data points.

In the case of the sparse matrix, for each centrality index, we identified the ROIs that exhibited a significant difference between the two groups. ROI's significance was defined as a Bonferroni-corrected p-value less or equal to 0.05 where the p-value was obtained via Monte-Carlo testing.

Then, both in case of the complete and sparse matrix, once the significant ROIs were identified for each index, the connectivity differences between the Low and High AQ Score Group were plotted for the significant ROIs only, separately for each index (in particular in case of the *authority* index and *hubness* index); this serves to evidence differences between the two groups in the pattern of connections entering into *authority* nodes and exiting from *hub* nodes.

3 Results

3.1 Analysis on the complete connectivity matrix

A first analysis was performed on the complete normalized connectivity matrix to understand the Granger flow in some of the key regions. Normalization of the connectivity matrix was necessary to avoid that the presence of a few individuals with higher connectivity strongly affects the final results.

*Lobes' Analys*is - First, we performed an analysis at the macro region level, by computing the difference (between the two groups) of the connectivity linking the lobes of the brain (frontal, temporal, parietal, and occipital both left and right). The results are illustrated in Fig. 1, where blue lines denote connectivity higher in the Low AQ score Group (left panel), and red lines connectivity higher in the High AQ score Group (right panel). To avoid an excessive number of lines, only connections differences greater than 0.2 are shown. Results, show that top-down connections (i.e., exiting from the frontal lobes) and left to right connections (i.e., entering into the right temporal lobe) were higher in the Low AQ score Group; conversely, connectivity was especially bottom-up (i.e., entering into the frontal lobes) in the High AQ Score Group. However, these connection differences, evaluated in the complete connectivity matrix, did not reach a statistical significance (p value in the range 0.05-0.15), hence these can be only considered indicative of a main flow pattern in the groups.

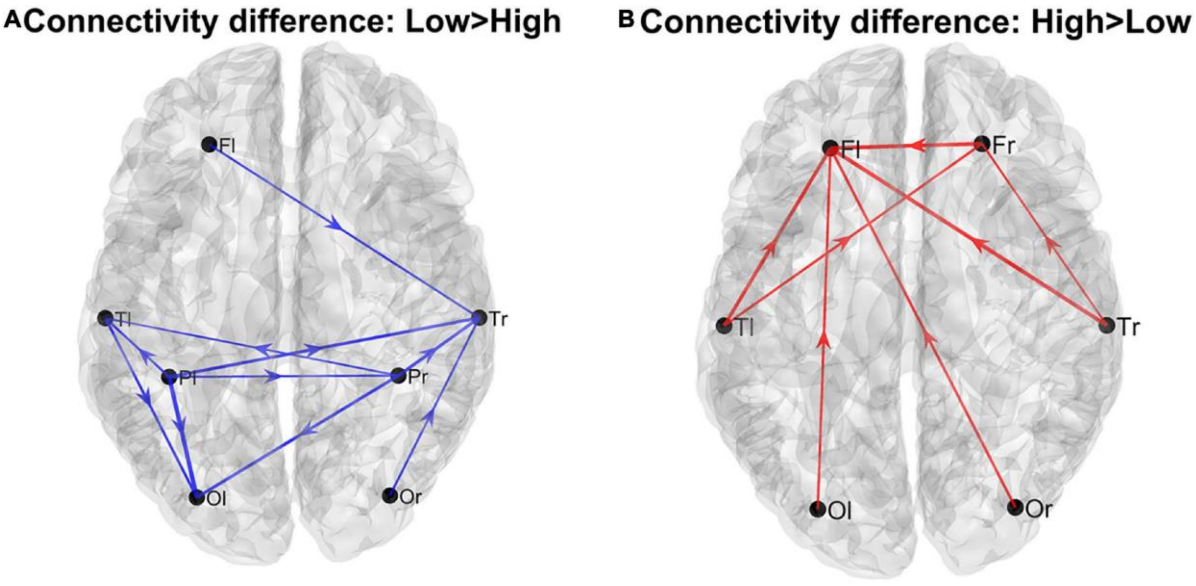


Figure 1. *Patterns of the main connection differences linking the four lobes (Frontal left and right, Fl and Fr, Temporal left and right, Tl and Tr, Parietal left and right, Pl and Pr, Occipital left and right, Ol and Or). The left panel* ***(A)*** *describes connections differences which are higher in the Low AQ score Group, while the right panel* ***(B)*** *describes connections differences which are higher in the High AQ score Group. Only connections differences with |t| > 1 (student t-test) are plotted.*

Analysis on the individual ROIs - To better clarify the dependence of the Granger flow on the autistic trait, we moved our analysis from the lobes to the individual ROIs. In particular, we computed the authority and the hubness of each ROI in each individual subject, and evaluated the correlation between these centrality indices and the AQ score.

For what concerns authority, seven regions (EN r, IST l, IST r, LO r, PH r, ST r and SMG l) exhibited a significant correlation between the AQ score and authority (see Figure 2, upper panels). It is worth noting that, in all these ROIs, correlation was negative signifying that authority increased in subjects with smaller autistic traits.

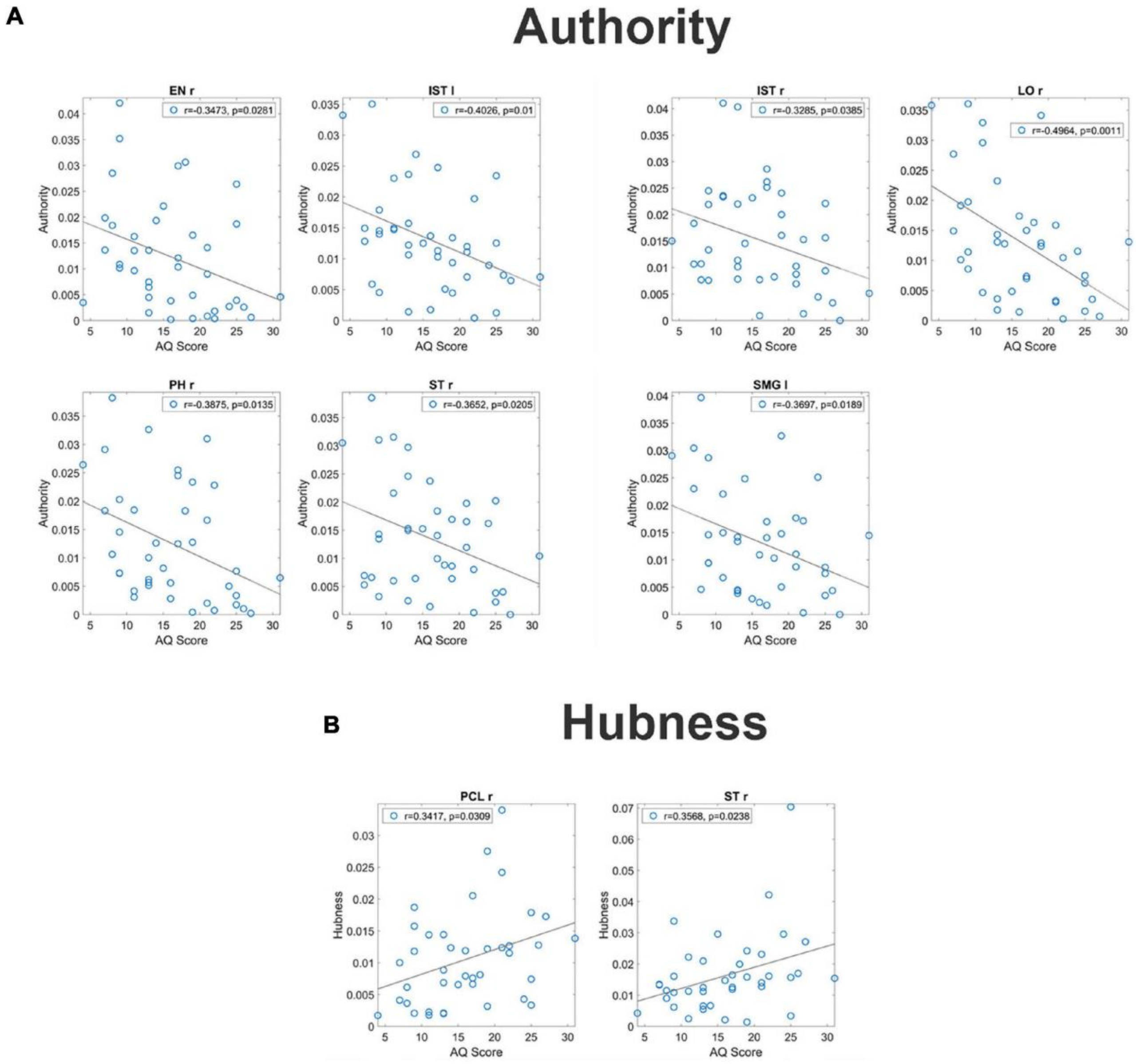


Figure 2. *Correlation between the authority and the AQ score [upper panel **(A)**] and correlation between the hubness and the autistic score [bottom panel **(B)**] for all ROIs which exhibit a significant p-value (uncorrected) for the correlation. These correlations have been computed on the complete normalized connectivity matrix. It is worth noting that the correlation is negative for the authority, denoting a more significant input flow in the Low AQ score Group, while correlation is positive for the hubness, denoting a more significant output flow for the High AQ score Group.*

For what concerns hubness, only two regions (PCL l and ST r) exhibited a significant correlation between the AQ score and hubness; in both cases, the correlation was positive, signifying that hubness increased with the autistic traits (see Figure 2 bottom panels).

Finally, to illustrate how differences in centrality index are reflected in alteration in Granger flow in the two groups of subjects, we plotted the connectivity differences for the relevant ROIs only (Figure 3: authority left panel, hubness, right panel). In particular, the left panel in Figure 3 shows the main connections differences entering into the seven regions (EN r, IST l, IST r, LO r, PH r, ST r and SMG l) whose authority was significantly correlated with the AQ score. The right panel shows the main connection differences exiting from the two regions (PCLl and STr) whose hubness was significantly correlated with AQ score. Blue lines denote higher connectivity for the Low AQ score Group, red lines higher connectivity for the High AQ score Group. Since we are working with a complete connection matrix, only connection differences above a given threshold (threshold = 0.015) are plotted to simplify the figure.

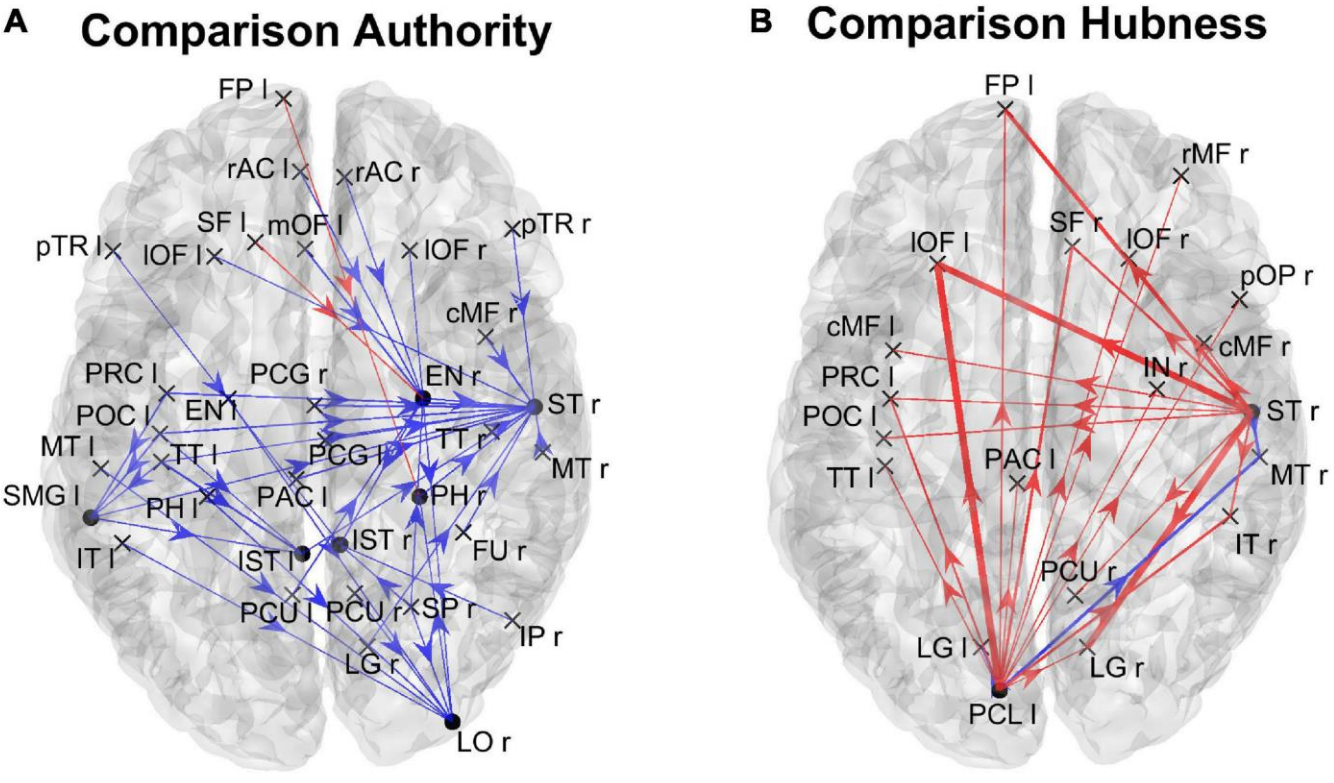


Figure 3. *Patterns of the main connection difference which exit from the ROIs with a significant correlation between authority and the AQ score [left panel **(A)**] and which enters into the ROIs with a significant correlation between the hubness and the AQ score [right panel **(B)**]. Blue lines denote correlation differences that are higher in the Low AQ score group, and red lines connections which are higher in the High AQ score group. Only connection differences higher than 0.015 on the complete connectivity matrix have been plotted. Three levels of thickness are adopted, with a larger thickness indicating a larger connectivity difference.*

The figure shows that the majority of connections entering the authority regions were stronger in the Low AQ score Group (as expected from the previous analysis), and these connections were mainly top-down in type (especially entering into the LO r) and left to right (especially entering into the EN r and the rST r). Conversely, the majority of connections exiting from the two hubs, PCL l and ST r, were stronger in the High AQ score Group (as expected from the previous analysis), with a bottom-up connectivity, especially emerging from the PCL l, and right-to left from ST r. These results are coherent with those at lobe level displayed in Figure 1.

3.2 Analysis on the sparse connectivity matrix

The previous analysis, accomplished on the overall normalized connectivity matrix, pointed out the presence of some authority nodes especially involved in top-down connectivity for the low-autistic trait population, and some hubness nodes characterized by bottom-up connectivity for the high-autistic trait population. The difficulty in the use of a complete connectivity matrix, however, derives from the presence of many connections with no clear statistical difference between the two groups. This is reflected in the poor statistical significance of the connection difference and, for what concerns the correlation, in a p value that, although significant, cannot survive the statistical correction. This means that the previous results can be considered as a mere hypothesis generated from data, requiring further more complete validation.

For this reason, in order to better unmask differences, in the following a different analysis is presented, by focusing attention only on the connections which exhibited a significant statistical difference in the two groups. Hence, as described in the Method section, we consider sparse connectivity matrices. This kind of analysis has the benefit of revealing a greater number of regions with statistical differences in connection flow.

Lobes' Analysis – Figure 4 shows the centrality indices (*in degree*, *out degree*, *authority*, *hubness*,) computed at the level of the four lobes (frontal, parietal, temporal and occipital) from the sparse matrix. The asterisks denote statistically significant differences between the two groups. As it is evident from the left panels, High AQ score individuals exhibited a statistically significant increase in the connections entering into the frontal regions, and this difference was even more marked if *authority* was used as a centrality measure instead of the *in degree*. Conversely, Low AQ score individuals exhibited more significant connections entering into the temporal regions; even in this case, the significance increased if the *authority* measure was used. For what concerns the connections emerging from regions (right panels), High AQ score individuals exhibited more significant connections emerging from the occipital regions, whereas Low AQ score individuals showed a higher significance in the parietal regions. For both emerging connection outcomes, the significance was more evident if *hubness*, instead of the *out degree* measure, was used.

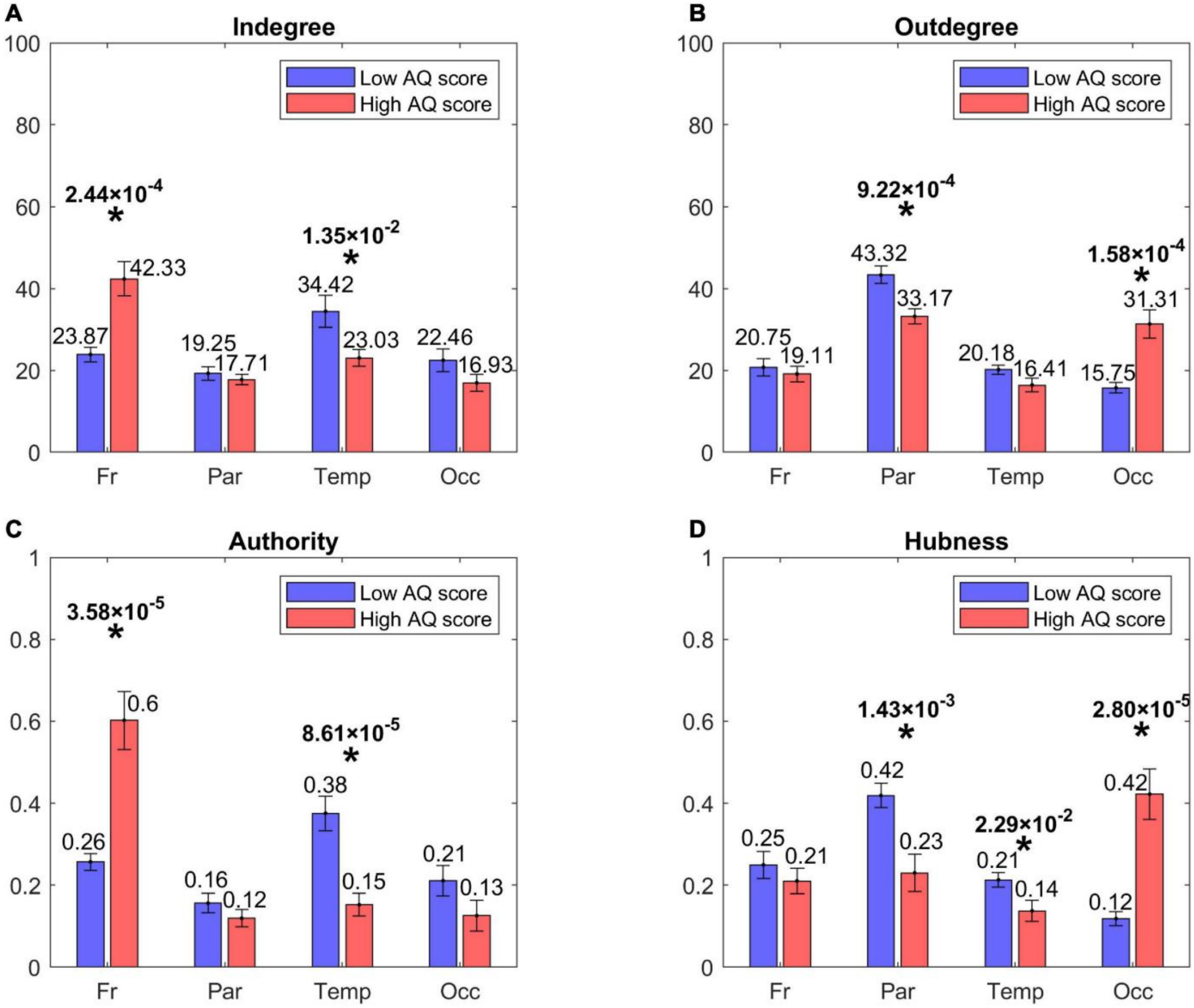


Figure 4. *Bar plots representing the centrality indices [in degree: panel* ***(A)****, out degree: panel* ***(B)****, authority: panel* ***(C)****, hubness: panel* ***(D)****] for the four lobes of the brain, i.e., Frontal (Fr), Parietal (Par), Temporal (Temp), and Occipital (Occ) in each group of participants (red bars for the High AQ score Group, blue bars for the Low AQ score Group). Each bar shows the index value (mean ± SEM) for the specific area in the specific group of participants. As per definition, the sum of the authority values and the sum of the hubness values across all areas provide a total of 1, while the sum of the in-degree values and the sum of out-degree values across all*

areas is equal to 100. The asterisks indicate the presence of a statistically significant difference between the two groups ($p < 0.05$, uncorrected).

In order to further investigate the results arising from the above histograms, Figure 5 represents the statistically significant connections (i.e., those which exhibited significant differences between the two groups) linking the eight lobes of the brain; in this case, the homologous regions in the left and right hemisphere were considered separately. The upper panel displays the p value of all significant connections using a color scale, while the bottom panel shows the connection differences (in red the connections which were significantly stronger in High AQ score individuals, in blue the connections significantly stronger in Low AQ score individuals). The results confirm those reported in Figure 4, showing that, in the High AQ score Group, significantly stronger connections were mainly directed from the occipital toward the frontal regions. The pattern in the Low AQ score Group showed significantly stronger connections emerging from the left parietal lobe, directed toward the right parietal, left temporal and left occipital regions.

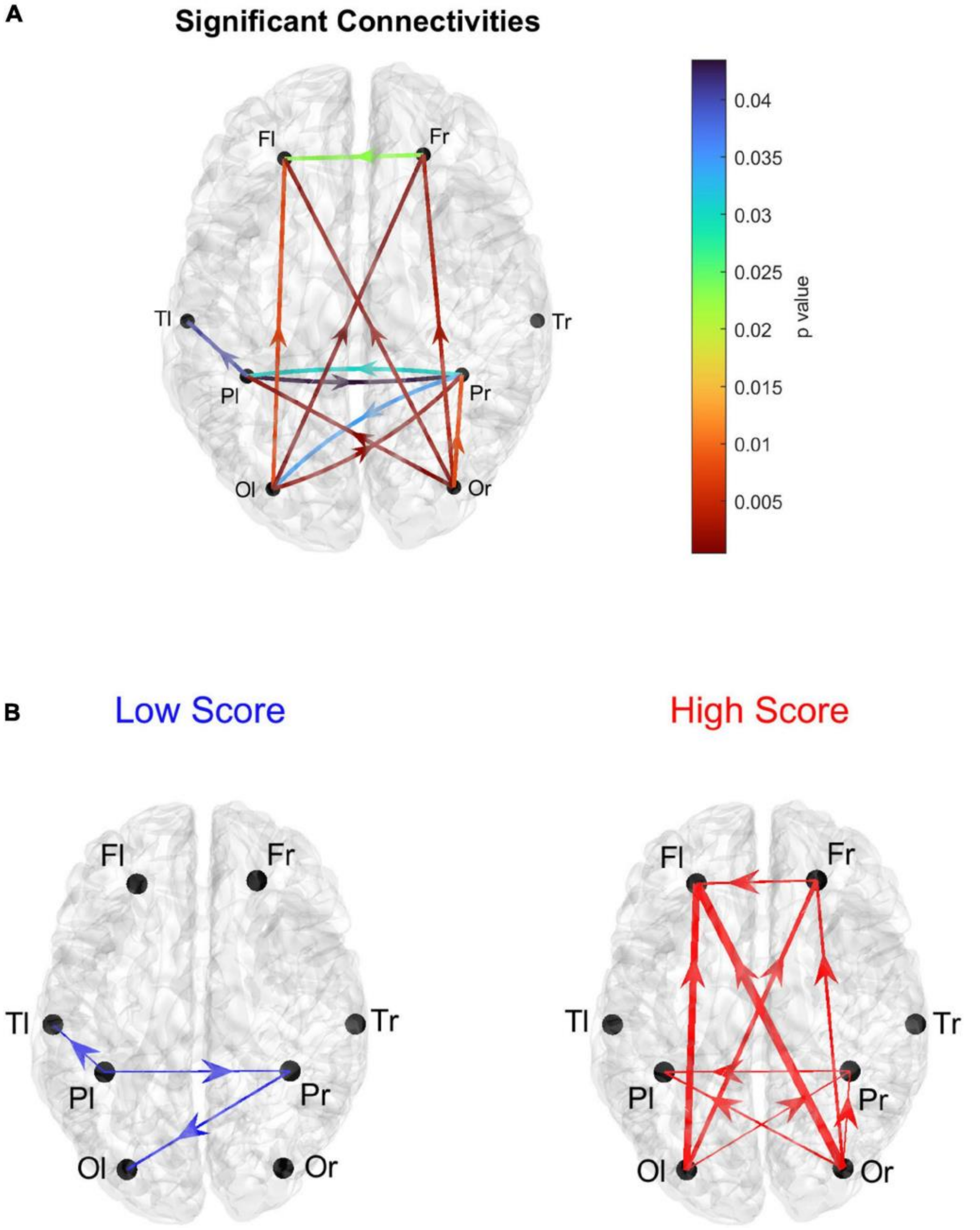


Figure 5. *Representation of the connections linking the eight lobes of the brain, Frontal (F), Parietal (P), Temporal (T), and Occipital (O), considering separately the right (r) and left (l) hemispheres. Only the connections that exhibited a statistically significant difference between the two groups ($p \leq 0.05$, uncorrected) are represented. The upper panel* ***(A)*** *shows the p-values of the significantly different connections. The lower panels* ***(B)*** *represent the differences in connectivity strength: the blue diagram (Low > High) shows the connection differences for those connections that resulted significantly stronger in the Low AQ score Group compared to the High AQ score Group; the red diagram (High > Low) shows the connection differences for those connections that resulted significantly stronger in the High AQ score Group compared to the Low AQ score Group. The thickness of each link varies according to the value of the connection difference. Three levels of thickness are adopted, with a larger thickness indicating a larger connectivity difference.*

Analysis of the individual ROIs – Figure 6 shows the positions of the ROIs which exhibited a significant difference (Bonferroni corrected) in the *in degree* (upper panels) and in the *authority* (bottom panels) indices between the two groups. The right upper panel evidences that in the High AQ score Group the *in degree* index was significantly higher (compared to the other group) especially in the frontal ROIs. This pattern was even more evident if *authority* index was used (bottom right panel). Conversely, the Low AQ score Group did not exhibit any appreciable increase in the *in degree* index, while some regions in the temporal, parietal and frontal lobes exhibited an increased *authority* without a clear topological organization.

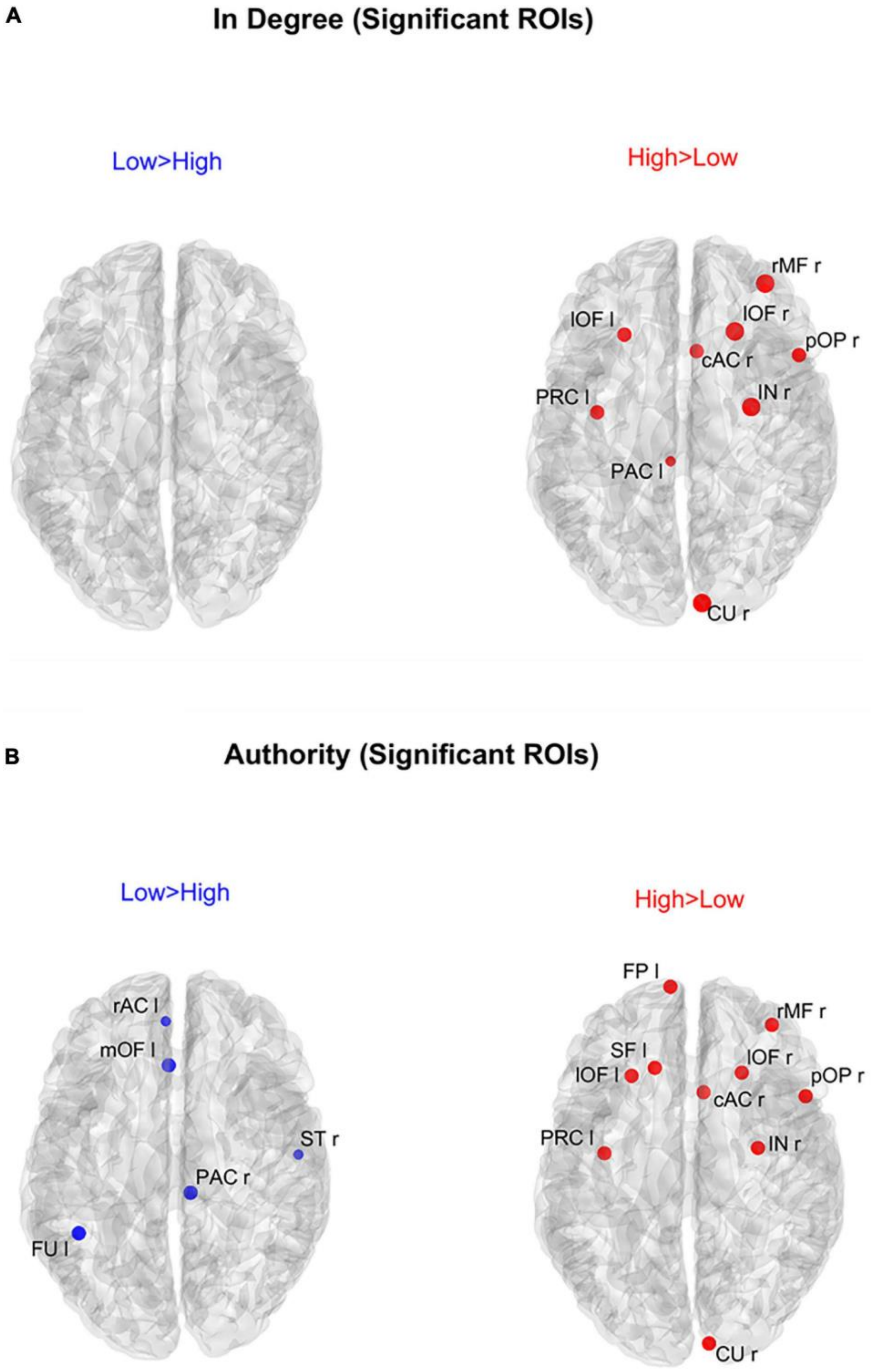


Figure 6. *Positions of the ROIs which exhibited a significant difference in the in degree index [upper panels* ***(A)****] or in the authority index [lower panels* ***(B)****] between the two groups (p-value < 0.05, Bonferroni corrected). The left panels in blue (Low > High) display the ROIs having significantly higher centrality index in the Low AQ score Group compared to the High AQ score Group. The right panels in red (High > Low) display the ROIs having significantly higher centrality index in the High AQ score Group compared to the Low AQ score Group.*

The significant ROIs are shown as simple dots and represent regions to which important information enters. Three levels of dots' size have been adopted: the larger the dot size, the more significant the centrality difference. For the panels where no dot appears over the brain map (i.e., in degree for Low > High), the constraint of significance was not satisfied by any of the 68 ROIs.

In order to gain a deeper understanding of the previous patterns (limited to *authority* only), Figure 7 shows the connection differences entering into all ROIs with significantly higher *authority* in either group. In the High AQ score Group, these connections mainly linked the two occipital regions PCL (right and left) toward frontal regions: particularly evident were the connections entering the two lOF (left and right), and the right rMF. Thus, a clear bottom-up pattern of connections emerged, supporting the results in Figure 5. Conversely, in Low AQ score individuals the pattern of connections entering into nodes with higher *authority* was less structured, showing connections directed to frontal (PAC r), right temporal (ST r) and left temporal (FU l) regions.

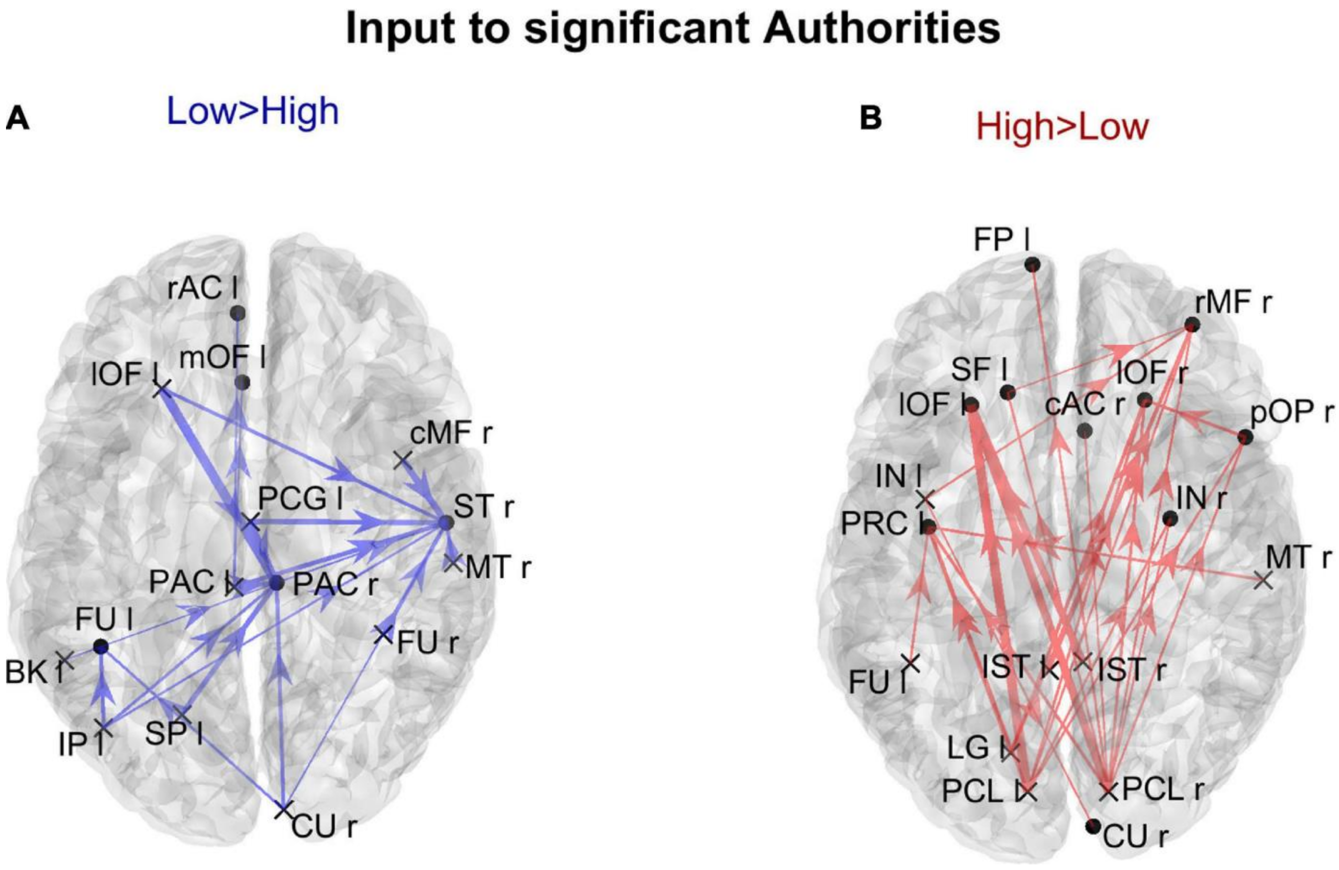


Figure 7. *Representation of the connection differences entering into the ROIs which exhibited significant differences of authority between the two groups. The left panel in blue [Low > High, panel **(A)**] displays the connection differences entering into the "Low > High" authority ROIs (the ROIs shown in the left lower panel in Figure 6), for connections higher in the Low compared to the High AQ score Group. The right panel in red*

[High > Low, panel ***(B)****] displays the connection differences entering into the "High > Low" authority ROIs (the ROIs shown in the right lower panel in Figure 6), for connections higher in the High compared to the Low AQ score Group. The plotted connections run from a generic output ROI (marked with a cross) toward the ROIs with significantly different authorities (marked with a dot). The thickness of each link varies according to the value of the connection difference. Three levels of thickness are adopted, with a higher thickness indicating a larger connectivity difference.*

Figure 8 shows the positions of the cortical ROIs that exhibited a significant difference (Bonferroni corrected) in the *out degree* (upper panels) and *hubness* (bottom panels) indices between the two groups. As shown in the right panels, in the High AQ score Group, both the above-mentioned centrality measures were significantly higher (compared to the other group) in the occipital PCL regions of both hemispheres and in the occipital left LG region. Moreover, some frontal regions also exhibited increased *hubness*, a result apparently in contradiction with previous figures. However, as will be clarified when discussing Figure 9 below, connections originating from these hubs were less significant than those originating from the occipital regions. The Low AQ score Group exhibited an appreciable increase in the *hubness* of parietal and temporal regions, especially in the left hemisphere, whereas no significant increase emerged from the *out degree* index. It is interesting to note that also an occipital region (the CU right) exhibited an increased *hubness* in the Low AQ score Group.

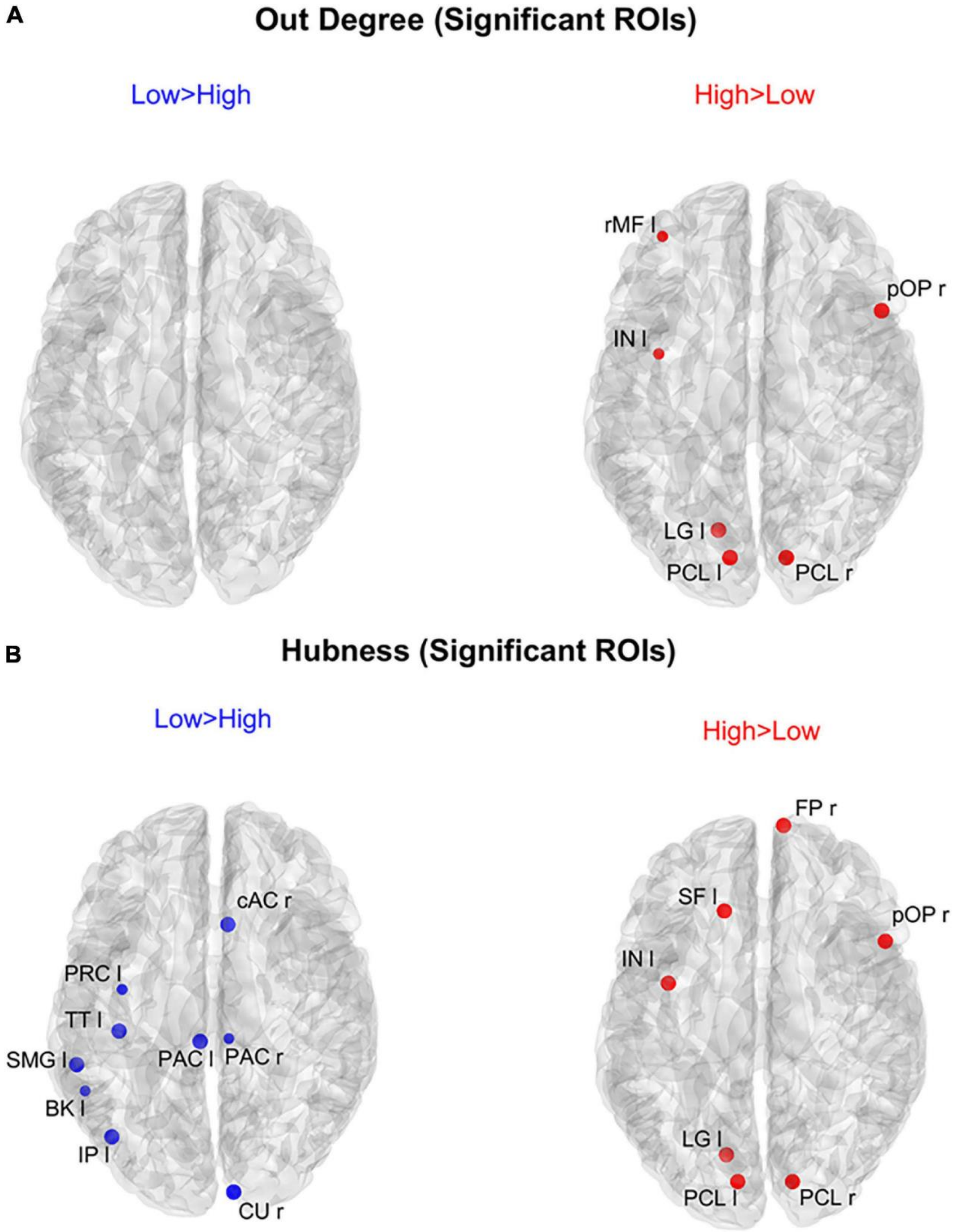


Figure 8. *Positions of the ROIs which exhibited a significant difference in the out degree index [upper panels* ***(A)****] or in the hubness index [lower panels* ***(B)****] between the two groups (p-value < 0.05, Bonferroni corrected). The left panels in blue (Low > High) display the ROIs having significantly higher centrality index in the Low AQ*

score Group compared to the High AQ score Group. The right panels in red (High > Low) display the ROIs having significantly higher centrality index in the High AQ score Group compared to the Low AQ score Group. The significant ROIs are shown as simple dots and represent regions from which important information originates. Three levels of dots' size have been adopted: the larger the dot size, the more significant the centrality difference. For the panels where no dot appears over the brain map (i.e., out degree for Low > High), the constraint of significance was not satisfied by any of the 68 ROIs.

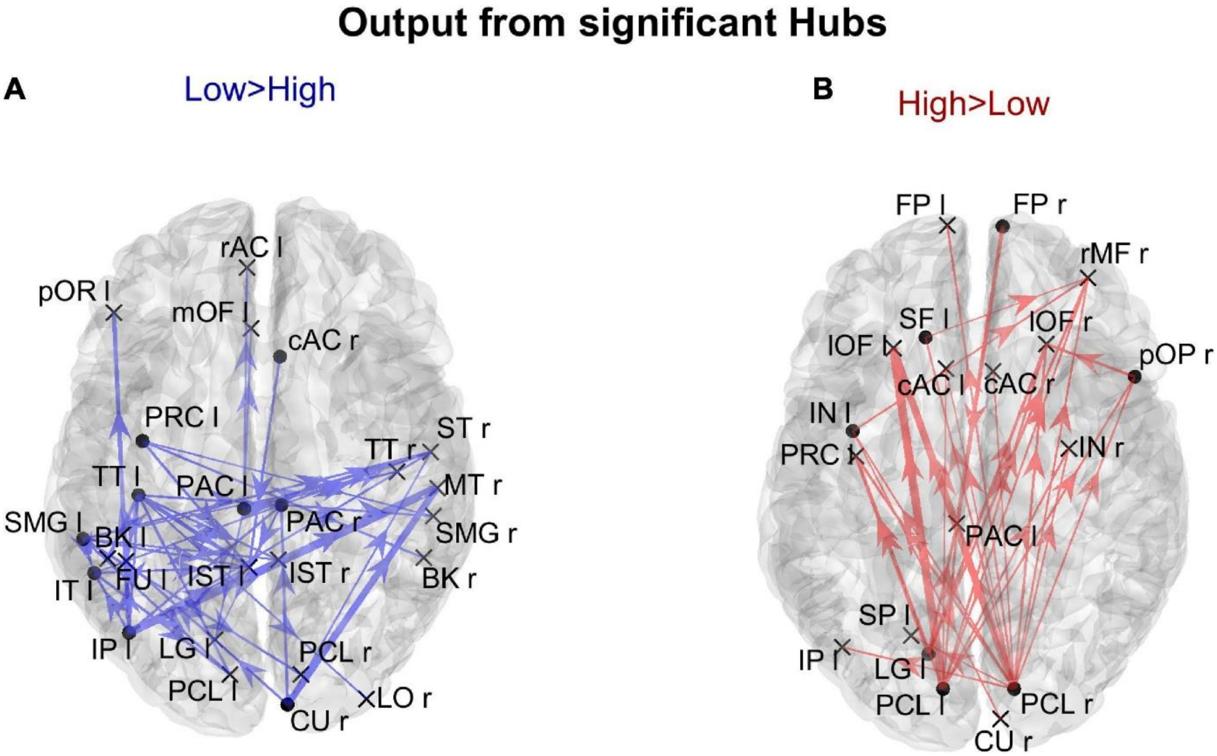


Figure 9. *Representation of the connection differences exiting from the ROIs which exhibited significant differences of hubness between the two groups. The left panel in blue [Low > High* ***(A)****] displays the connection differences exiting from the "Low > High" hubness ROIs (the ROIs shown in the left lower panel in Figure 8), for connections higher in the Low compared to the High AQ score Group. The right panel in red [High > Low* ***(B)****] displays the connection differences exiting from the "High > Low" hubness ROIs (the ROIs shown in the right lower panel in Figure 8), for connections higher in the High compared to the Low AQ score Group. The plotted connections run from the ROIs with significant hubness (marked with a dot) toward generic input ROIs (marked with a cross). The thickness of each link varies according to the value of the connection difference. Three levels of thickness are adopted, with a higher thickness indicating a larger connectivity difference.*

The results illustrated in Fig. 8 are further clarified in Figure 9, which shows the connection differences exiting from the nodes with significant higher *hubness* in either group. Once again, a clear bottom-up pattern is evident in the High AQ score Group. It is worth noting that, in this group of individuals, the front-parietal regions with increased *hubness* (i.e., the SF l, FP r, pOP r and IN l) generated only weak output connections (when compared to the other group). These were sufficient to make the *hubness* of these ROIs significantly higher, without altering the general bottom-up pattern of the overall circuitry. In fact, much stronger connections exited from the two PCL regions, defining a clear bottom-up trend. The pattern of connections originating from significant hubs in the Low AQ score Group were mainly directed from temporal and parietal left regions to the right ones, with some connections also directed downwards to the occipital nodes. As anticipated above, also the right CU exhibited a clear bottom-up function in this group, while, in agreement with Figure 7, the right temporal regions received most of the significant connectivity originating from the hubs. It is worth noting that connections toward frontal regions were less significant in this group.

4 Discussion

The present paper analyzes the differences in brain connectivity between two groups of non-clinical individuals who differ in the degree of autistic traits (low vs. high), as classified based on the Autistic Quotient (S. Baron-Cohen et al., 2001) score. Results have two main important aspects of interest. First, we confirm that autistic traits can be observed within a wide spectrum encompassing both clinical and non-clinical populations. Specifically, the degree of autistic traits clearly differs in the non-clinical population between low and high AQ scores. Second, we show that these differences can be quantified as alterations in brain connectivity. In particular, we show that Granger Causality, computed from neuroelectric signals reconstructed in the cortex (Cekic et al., 2018; Deshpande and Hu, 2012; Stokes and Purdon, 2017), together with indices taken from the Graph Theory (Farahani et al., 2019; Minati et al., 2013; van Wijk et al., 2010), can represent a valuable tool to characterize differences in brain networks and deepen our analysis of the neurobiological bases of brain disorders. Further, we confirm a previous hypothesis (Tarasi et al., 2021a, 2022c) that individuals with higher autistic traits are characterized by more evident bottom-up mechanisms for processing sensory information.

A critical point may be the selection of the threshold used to discriminate between the two classes. Despite the inherent arbitrariness of the choice, we used as a discriminative threshold the average AQ score obtained in a nonclinical population from the large-sample work of Ruzich et al. (2015), and this seems the most natural choice. Moreover, using this value, the present population of 40 subjects is subdivided in 19 and 21 subjects, i.e., the threshold we chose is quite proximal to the median of the considered population. It is worth noting that similar approaches of partitioning the sample around a threshold have been used previously in the literature (Alink and Charest, 2020b).

In the following, we will first analyze methodological issues, then the neurophysiological significance of the obtained results will be explored. Finally, limitations of the present study will be analyzed.

Granger Causality – In this work, we have chosen temporal Granger causality as a tool to reconstruct brain connectivity from EEG data. This measure mathematically represents the impact that knowledge of an upstream signal can have on the prediction of a downstream temporal signal. Thus, it represents a causal directed index of connectivity. Indeed, Granger Causality is widely employed in neuroscience today (Cekic et al., 2018; Deshpande and Hu, 2012; Seth et al., 2015; Stokes and Purdon, 2017). Moreover, in a recent paper, using artificial signals produced by a neurocomputational model as ground truth, we demonstrated that the Granger Causality overcame other functional connectivity estimators in terms of accuracy and reproducibility (Ricci et al., 2021b). This method has evident computational advantages compared with other suitable methods (such as Transfer Entropy, see (Ursino et al., 2020)).

The analysis was initially performed (see Section 3.1) on the complete normalized connectivity matrix, to show the main characteristics of the Granger flow in the two groups. Then, to improve the significance of the results, we considered only connections which exhibited a significant statistical difference between the two populations, thus working with a sparse matrix (i.e., all connections which did not show statistically significant differences between the two groups were set at zero). In other terms, the graphs in Section 3.2 do not represent the overall connectivity patterns, but rather highlight the differences between the two populations.

The connectivity matrices so obtained were then used to compute some indices taken from Graph Theory.

Graph Theory – Several studies using Graph Theory in ASD have appeared in recent years: most of them suggest that ASD individuals exhibit alterations in modularity (i.e., densely connected modules that are more segregated), in global efficiency (i.e., average path length required to go from one node to another), in betweenness (the capacity of a node to connect to other nodes) or in connection density (L. Chen et al., 2021; Keown et al., 2017; Redcay et al., 2013; Rudie et al., 2012; You et al., 2013). EEG and MEG connectivity studies using graph analysis generally report autism to be associated with sub-optimal network properties (less clustering, larger characteristic path, and architecture less typical of small-world networks) (Barttfeld et al., 2011; Boersma et al., 2013; Leung et al., 2014; Peters et al., 2013; Soma et al., 2021; Takahashi et al., 2017; Tsiaras et al., 2011). This, in turn, results in a less optimal balance between local specialization (segregation) and global integration (Sporns and Zwi, 2004). Although of particular significance, we think that these indices do not consider the fundamental problem of directionality in the processing pathway and the different importance that bottom-up and top-down connectivity plays in several brain processing.

Accordingly, an essential novelty of the present study concerns the use of some specific centrality indices (*in degree*, *out degree*, and above all, *hubness* and *authority*) to characterize group differences in network directionality. The basic idea is that the directionality of the processing streams plays a major role in determining group differences (at least for what concerns autistic traits), rather than other indices like betweenness, path length, or clustering, more frequently adopted in the characterization of brain networks. In particular, by considering macro-regions and sparse connectivity matrices, these indices provided highly significant statistical differences and provided a precise scenario to distinguish the two groups.

Connectivity among macro-areas (lobes) - The connectivity analysis was performed at two levels. First, we concentrated on the connectivity among macro-regions (lobes) of the cortex, the frontal, parietal, temporal, and occipital zones, to discover the main traits of connectivity differences.

This analysis confirms the result of a previous preliminary study (Tarasi et al., 2021a), i.e., individuals with higher autistic traits exhibit stronger outgoing connections from the occipital regions and stronger incoming connections toward frontal areas (i.e., bottom-up) compared to those observed in individuals with lower autistic traits. In addition to confirming the results of our previous study, as a new significant result of the present study we propose that two other centrality measures, i.e., *hubness* and *authority*, allow for a finer discrimination of connectivity directionality. The reason for this improvement will be critically analyzed in the next section. If these two measures are used, significant statistical differences can be observed to characterize the directionality of the connections in High AQ score vs. the Low AQ score individuals. In particular, using sparse matrices statistically significant differences were evident between the *hubness* of the occipital regions in the two classes, with much stronger *hubness* for individuals with high autistic traits. Looking at *authority*, a significant increase in the *authority* of the frontal region was observed in the group with higher autistic traits.

The same patterns were confirmed by computing (from the sparse matrices) the connectivity among the macro-regions and plotting only those which exhibited a significant statistical difference. As shown in Figure 5, increased bottom-up connectivity from occipital to frontal regions was evident in individuals with high autistic traits.

Connectivity among individual ROIs – Besides connectivity analysis at lobe level, we performed connectivity analysis at single ROI level. To this aim, *centrality indices* were computed by considering all the 68 ROIs in the Desikan-Killiany atlas. It is interesting that the results obtained on the overall connectivity matrix and on the sparse matrix provide similar indications, emphasizing the presence of bottom-up connections in the high-score group and top-down connections in the low-score group. However, analysis performed on the overall connectivity matrix did not reach a significant level, whereas a greater significance was obtained from sparse matrices. For this reason, in the following we will mainly refer to the results of sparse matrix.

An important result of our study is that hubness and authority provided more significant differences compared with in degree and out degree, respectively; hence we suggest that these indices should be used to characterize the flow in a network of multiple ROIs. In particular, by comparing in degree vs. authority in Figure 6 we can observe that the results are quite similar for what concerns the High AQ score Group (authority produces just one more significant frontal node compared with in degree), whereas significant differences can be observed in the Low AQ score Group (no significant node is evident if in degree is used, compared with five nodes using authority). Consequently, authority allowed the detection of a clear left to right connectivity in the Low AQ score Group. Similarly, only moderate differences can be observed using hubness vs. out degree in the High AQ score Group (Figure 8, hubness detects two additional regions in the frontal cortex, allowing a better analysis of top-down influences). Also in this case, hubness provided a significant improvement compared with the out degree in the Low AQ score Group (nine significant ROIs are detected by hubness, mainly located in left and medial parietal and temporal regions, vs. no significant region by the out-degree). These differences suggest that the overall graph is more complex in the Low AQ score Group compared with the High AQ score one, requiring more sophisticate indices for detecting the flow of transmitted information.

To understand why authority and hubness are more powerful compared with in degree and out degree, we remind that authority not only takes into account the number and strength of the connections entering a node but also weights these connections by the *hubness* of the upstream nodes. Similarly, *hubness* does not only takes into account the number and strength of connections exiting from a node but also weights these connections by the *authority* of the downstream nodes. Of course, these measures need to be computed together via recursive formulas, as illustrated in Eqs. 6-7. Briefly, the importance of the information exiting from a node (or the importance of the information entering into a node) is not simply the sum of its output connections (or the sum of the input connections), but also depends on the role played by the sending nodes (or by the receiving nodes). For instance, a connectivity of value 0.04 reaching an almost completely isolated node (one which does not send information to others nodes in the network) can be scarcely important compared with a connection of value 0.02, which reaches a crucial node. Hubness is able to quantify this difference compared with a simple sum of outgoing connectivity. Similarly, authority is more able to summarize the effective significance of the incoming flow compared with the simple sum of entering connections.

Using these indices, we then mapped the stronger connections that exited from ROIs with higher *hubness* and entered into the ROIs with greater *authority*. These results computed on each ROI extend the lobe analysis to several aspects: i) The main hubs for High AQ score individuals were located in the left and right PCL regions. A pattern of bottom-up connections emerging from these two regions seems to be the dominant feature that characterizes this group. Left and right PCL are the ROIs in which the primary visual cortex is located. These areas handle the transmission of incoming visual inputs from the thalamus to higher-order processing regions. The enhanced bottom-up signaling arising from this site resembles the pattern observed in individuals with clinical form of autism characterized by hyper-engagement of sensory regions (Jao Keehn et al., 2017; R. Joanne Jao Keehn et al., 2019) that could underpin the sensory and visuospatial peculiarities typically observed in ASD (Mottron et al., 2006; Samson et al., 2012b). ii) The leading *authorities* for High AQ score individuals were located in the frontal and prefrontal regions, particularly in the left and right lOF. These two ROIs encapsulate frontal sites involved in high-level mechanisms such as emotional regulation, decision-making and social cognition (Rolls, 2004). Crucially, these domains tend to be altered in ASD individuals. Excessive information inflow in brain areas related to emotional and social processing could be implicated in the difficulty to manage complex and multifaceted social interactions typically observed in this spectrum. This could also explain why ASD individuals tend to prefer less social-demanding environments as they are linked to a lower risk of over-stimulation. iii) The previous connections were distributed bilaterally, from both PCLs to both homolateral and contralateral frontal hemispheres. iv) Conversely, the pattern of connectivity in Low AQ score individuals exhibited a broader and less defined distribution, involving several connections in the temporal, parietal, and occipital lobes, with hubs mainly located in the left hemisphere and a direction from left to right. This suggests that the pattern of inter-areas communication in low-AQ individuals is more distributed and varied and not rigidly channeled into narrow pathways.

We remind, however, that these connectivity patterns reflect *differences* between the two groups, hence a relative role in one population vs. the other, not the absolute impact that connections have on the overall brain network. In other words, it is possible that some strong connections did not appear in our graph since they were equally relevant in both populations, hence without significant difference (this is the reason why the overall connectivity matrix provides less significant results). Moreover, we remind that trials were performed at rest. Thus, the examined connectivity reflects differences in a resting state.

In general, the present results support the findings obtained in our previous study on a smaller population (Tarasi et al., 2021a), even though the exact position of the ROIs representing the increased bottom-up connectivity is not identical. In our previous study, we observed increased connectivity from the right PCL and the left LG (instead of the left PCL as found here). Still, these differences can be explained based on minor variances in source reconstruction and grouping among proximal voxels. Moreover, in our previous study, the bottom-up connectivity in High-AQ score individuals was especially evident in the right hemisphere (particularly toward the right MFr, a region that still plays e significant role among the authorities in the present study). In contrast, this connectivity seems to be more bilaterally distributed in the current results.

These results support the idea that the brain network in individuals with higher autistic traits vs. individuals with lower autistic traits is not characterized by a general reduction in connectivity (as hypothesized in some theorizations) but rather that mixed patterns of under- and over-connectivity can be appreciated. Over-connectivity is evident in the fronto-posterior axis, involving bottom-up influences, whereas hypoconnectivity involves many tempo-parietal regions, especially in the left hemisphere.

Neurophysiological meaning - Several hypotheses on brain connectivity in ASD have been formulated in past years, with apparently contradictory outcomes: while some authors hypothesized more robust connectivity in ASD, others reported reduced connectivity (see Introduction). These contradictions, however, can be reconciled by thinking that differences between control and individuals within the autistic spectrum can especially reflect a directionality in the connections rather than the number and total strength of edges in the overall network. Furthermore, a mixed pattern of increased connectivity among some regions and decreased among others probably characterizes the autistic brain. Directionality in the connectivity patterns, in turn, may reflect a hierarchical organization of the processing stream, with bottom-up connections (especially from the occipital towards the frontal lobes) involved in sensory processing and top-down connections reflecting context modulation, and prior knowledge, planning, and attention. This connectivity organization agrees with the so-called predictive coding theory, which assumes that environmental and internal signals are joined together to form a unified model of reality. In particular, the predictive coding theory of ASD (Tarasi et al., 2022c; Van de

Cruys et al., 2014a) hypothesizes that ASD people do not form accurate predictions of the external environment since sensory information supersedes the internal expectation. Our results support this theory, showing that differences in bottom-up connectivity (hence, in the impact that sensory input can have on the global internal model) are stronger in individuals with higher autistic traits, even within a population of healthy individuals.

Limitations of the present study – A limitation of the present study may be the limited sample size (19 vs 21 participants). Actually, this number is in line with (and in many cases higher than) the sample employed in published works that use similar experimental procedures and investigate similar phenomena (see (Carter Leno et al., 2018; Harris et al., 2021)). However, the complexity of the analysis performed and, in particular, the study accomplished on the complete connectivity matrix, reveal the necessity of a larger number of participants to achieve statistically more solid results. Hence, future studies on a large cohort can allow a more detailed comprehension of the problem.

In this study, we did not include participants with a diagnosis of ASD, hence we cannot be confident that the present results would stand up also in a clinical population. However, the results obtained go exactly in the direction hypothesized by theoretical and empirical work on connectivity features in clinical ASD. Moreover, substantial behavioral (Alink and Charest, 2020b), genetic (J. Bralten et al., 2018) and neural (Aykan et al., 2022) evidence suggests that ASD is a continuum of conditions ranging from trait-like expression to the diagnosed clinical form of autism. Of course, additional studies on a clinical population are required to definitely support the present initial results and definitely validate the hypothesis of a continuous spectrum ranging from normality to ASD.

An interesting point concerns the relationship between the Granger connectivity, evaluated in this study, and the structural connectivity (i.e., the physical traits that connect brain regions, generally estimated by diffusion-weighted imaging). Some studies (e.g.,(Hermundstad et al., 2013)) have shown that there is significant overlap between neuroanatomical connections and correlations of functional brain signals. Conversely, other recent studies of our group, using neural mass models as a ground-truth, showed that in some conditions the two aspects may differ, as a consequence of non-linear phenomena (Ricci et al., 2021b; Ursino et al., 2021, 2020).

Hence, it is still unclear how the brain network interacts during specific tasks or at rest, accounting for all structural and functional aspects in terms of causality, given the many nonlinear dynamics that characterize brain functioning. Moreover, the present results show some connections crossing the midline. Regarding this point, although the connections traveling through the corpus callosum typically connect homotypic areas, a substantial number of traits connecting heterotypic areas in the two cerebral hemispheres have been observed (e.g. (De Benedictis et al., 2016)). Of course, without structural data, it remains difficult for the current study to formulate more precise hypotheses about this issue.

Finally, in the present study we have observed differences in bottom-up and top-down connectivity in the two groups. Works in the literature emphasize that these connections can be implicated in sensory processing, especially in multisensory conditions (Choi et al., 2018) or after sensory deprivation (Yusuf et al., 2022). Furthermore, several studies suggest that atypical sensory processing is a common characteristic of ASD and that sensory traits have important implications in the developmental phase of this pathology (Marco et al., 2011; Robertson and Baron-Cohen, 2017). The present experiments were performed in a resting condition, so it would be difficult to make strong inferences about sensory processing from the current data. Further studies, examining the response to sensory stimuli, are required to test whether these neural signatures of autistic traits (more bottom-up processing in high AQ score, more top-down processing in low AQ score) have an impact at the behavioral level, for example to explain the observed differences in sensory profile.

Study 4: Neural signatures of predictive strategies in humans

from the published manuscript:

Tarasi, L., di Pellegrino, G., & Romei, V. (2022). Are you an empiricist or a believer? Neural signatures of predictive strategies in humans. *Progress in Neurobiology*, *219*, 102367.

Abstract

Predictive coding theory suggests that prior knowledge assists human behavior, from simple perceptual formation to complex decision-making processes. Here, we manipulate prior knowledge by inducing uninformative vs informative (low and high) target probability expectation in a perceptual decision-making task while simultaneously recording EEG. We found that priors did not impact sensitivity (d') but did shape response criterion (c), being more liberal for high expected trials and more conservative for low expected trials. Importantly, we mapped the neural signature of this criterion shift, with liberal and conservative trials characterized by low and high posterior alpha amplitude, respectively. Moreover, we demonstrated that inter-areas communication along the fronto-parietal-occipital pathway is linked to the strategic tuning of sensory areas. Specifically, whereas parieto-occipital alpha synchronization facilitates the exploitation of expectancy-type information by shaping pre-stimulus alpha amplitude in a prior-dependent fashion, fronto-parietal theta coupling mediates a supervisory process on the predictive machinery, attenuating the impact of prior on sensory processing. These findings aided us in tracing the neurofunctional mechanisms underlying the differences in predictive styles existing in the general population. Crucially, an imbalance between alpha and theta synchronization leads to interindividual differences favoring priors overweighting (believers) vs. prioritization of sensory input (empiricist) strategy, respectively.

Highlights

1) Probabilistic prior shapes the decision criterion, not perceptual sensitivity

2) Shift in posterior alpha amplitude tracks the modulation in decisional bias

3) Parieto-occipital alpha coupling aids in biasing posterior alpha amplitude

4) Fronto-parietal theta coupling dampens the bias on posterior alpha amplitude

5) An imbalance between alpha vs theta coupling leads to different predictive strategies

Introduction

Perception goes beyond what hits the eyes and human decision does not result from a faithful integration of external inputs. According to predictive coding (Clark, 2013b), they both emerge from an inferential-like process in which stimuli are conditionally interpreted considering prior and contextual information. This feature is able to explain several empirical evidence. For example, the presence of a stimulus is judged as a function of its probability of occurrence or recent sensory history (de Lange et al., 2018; Urai et al., 2019). There are individual differences in the tendency to favor prior knowledge over incoming sensory evidence that explain heterogeneity in decision-making styles and underlie some psychopathological symptoms (Tarasi et al., 2022d; Teufel et al., 2015). For example, recent empirical works have shown that strong predictive models can exert an undue influence on perceptual inferences causing hallucinatory phenomena (Corlett et al., 2019; Powers et al., 2017). Therefore, the process of exploiting prior knowledge needs to be monitored and controlled to ensure its adaptivity and flexibility. However, despite the role of predictive processing in explaining many decision-making phenomena and inter-individual differences in cognitive style, the understanding of the neural mechanisms involved is limited. Predictive coding states that models about the environment are processed by higher cortical areas and conveyed to lower-level regions for shaping the perceptual process (Boly et al., 2011; Rao and Ballard, 1999). At the electrophysiological level, these interactions would be carried out through phase synchronization of inter-area oscillatory activity (Engel et al., 2001; Fries, 2015, 2005). In particular, mounting evidence suggests that inter-regional alpha phase coupling is one of the ideal biological substrates for prediction conveyance given its role in neural information transfer (Arnal and Giraud, 2012): alpha oscillations carry the top-down signaling (Michalareas et al., 2016b) and the strength of inter-areal alpha synchronization tracks the predictability of the stimulus (Bastos et al., 2020). The aim of this rhythmic transmission would be to regulate the activity of low-level areas by targeting markers involved in the modulation of decision outcomes, such as the amplitude of alpha oscillations (Di Gregorio et al., 2022; Samaha et al., 2020). Specifically, it is conceived that states of increased alpha power reflect a state of reduced neural excitability within and across participants (Romei et al., 2008b, 2008a), which in turn would inhibit stimulus processing (Jensen and Mazaheri, 2010; Klimesch et al., 2007). This hypothesis derives from a large body of studies reporting that increased alpha power in sensory regions is associated with reduced hit-rate (Romei et al., 2010; van Dijk et al., 2008) and number of phosphenes evoked by transcranial magnetic stimulation (Romei et al., 2008b, 2008a; Samaha et al., 2017a). However, the early findings were not able to disambiguate whether alpha fluctuations exert an influence on the objective ability to sample sensory stimuli [sensitivity (*d'*)] or rather modulate response bias [criterion (*c*)]. Crucially, a recent study addressed this issue demonstrating that alpha amplitude modulations are associated with response bias and not sensitivity (Limbach and Corballis, 2016). Specifically, when pre-stimulus power is low, observers have a higher proneness to see a target (i.e., more liberal criterion), regardless of its actual presentation. Accordingly, several recent studies have shown that alpha amplitude modulates the tendency to report the presence of the target (Iemi et al., 2017), the confidence associated with the choice (Samaha et al., 2017b) and visual awareness (Benwell et al., 2021), without affecting perceptual acuity. Nevertheless, the role of alpha in shifting the decision bias was mainly inferred by analyzing the relationship between spontaneous trial-by-trial fluctuations preceding the presentation of near-threshold stimuli and perceptual outcomes. It remains still unknown whether deliberate criterion modulation induced by prior information is supported by alpha shifting at the sensory areas level.

Furthermore, it is currently unclear which neural network would be accountable for the rhythmic transmission of prior-related information to the low-level areas. The parietal lobe may represent one of the seeds. Its activity has been associated with the extent to which the perceiver tuned its decision based on prior knowledge or task payoff (Hanks et al., 2011; Martijn J. Mulder et al., 2012; Platt and Glimcher, 1999; Rao et al., 2012). Moreover, rTMS over the right parietal cortex has been shown to disrupt the desynchronization of anticipatory alpha rhythms in the parieto-occipital cortex (Capotosto et al., 2009). In addition, alpha synchronization between parietal and visual cortex supports anticipatory visuospatial attention (D'Andrea et al., 2019; Siegel et al., 2008) by regulating alpha amplitude at posterior sites (Lobier et al., 2018). Here, in line with this evidence, we first decided to investigate whether alpha coupling between parietal and visual cortex could be responsible for predictive information signalling, by tuning the excitability of sensory cortices in a prior-dependent fashion.

Moreover, for predictive models not to override the information carried out by the sensory input, which may lead to dysfunctional processes such as hallucinatory phenomena (Powers et al., 2017), a supervisory system on the perceptual inference process could be conceived. Several lines of evidence would point to theta synchronization as a promising candidate crucially implicated in this monitoring process. Theta acts as an 'alarm signal', pointing to the need to engage cognitive control, whose implementation emerges from inter-site theta phase synchrony (Cavanagh and Frank, 2014). Indeed, theta has been shown to be involved in decisional adjustments (Cavanagh et al., 2009) through the functional interaction with posterior activity (Nurislamova et al., 2019), increasing when participants are induced to adopt a liberal criterion (Kloosterman et al., 2019) so as to prevent impulsive and biased responses (Cavanagh et al., 2013, 2011; Swart et al., 2018). Therefore, theta activity could underpin a higher-order mechanism subserved by a fronto-parietal executive network (López et al., 2019; Sauseng et al., 2005) that monitors the exploitation of predictive models.

In the current study, we explicitly probe these potential mechanisms by manipulating the expectation of target occurrence in a detection task with the aim of inducing response bias, while keeping sensitivity unchanged, to investigate 1) whether the alpha amplitude tracks the voluntary modulation of the decision bias, 2) the differential role of neural coupling along the theta and alpha bands in preparing sensory areas activity to strategically shape perceptual decisions and 3) the role of these neural signatures in explaining individual differences in the handling of predictive information.

Materials and Methods

Participants

Sixty-eight participants (35 female; age range 18-35) signed a written informed consent prior to take part in the study, which was conducted in accordance with the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna (protocol code 201723, approved on 26 August 2021).

Stimuli

Stimuli were presented on a 18' CRT display (Cathode Ray Tube, CRT, display resolution of 1280 x 1024 pixels, refresh rate 85 Hz) at a distance of 57 cm in a dimly lit room. Participants sat in a comfortable chair in front of the monitor. The stimuli were generated and presented using Matlab (version 2016, The MathWorks Inc., Natick, MA) and the Psychophysics toolbox. Visual stimuli were checkerboards appearing on the lower left visual field. The checkerboards presented could contain grey circles within each of the cells (target) or not (catch trials) (See figure S1). Participants were instructed to indicate via the keyboard the presence (by pressing key 'k' with the middle finger) or absence (by pressing key 'm' with the index finger) of the grey circles inside the checkerboard as quickly and as accurately as possible. Participants were instructed to give the response with their right hand to avoid confounding effects related to motor programming, as it was executed by the hemisphere opposite (i.e., the left) to the one responsible for sensory processing in the task (i.e., the right).

Experimental design.

The study was divided in two phases. In the first, each participant underwent an adaptive titration procedure to determine the contrast of the grey circles for which the detection accuracy was at ~ 70% when an equal number of target-present and target-absent trials (catch trials) was presented. We opted to include the presentation of catch trials to avoid confounding effects related to the difference response tendency adopted by the participants. In fact, by presenting only target-presence trials, it is not feasible to discriminate whether different threshold values depend on the effective perceptual ability since the absolute number of hit-rates may vary significantly despite an equal sensitivity when controlling for the number of false alarms (Green and Swets, 1966). The second phase comprised 6 blocks of 90 trials each (Figure 1). Each trial started with the appearance of the probability cue presented at the center of the screen. The cue was presented for 1 s followed by a fixation dot. After a variable delay of 1.2–1.5 s a checkerboard containing (or not) grey circles at the titrated contrast within it appeared at the bottom left of the monitor for 60 ms. We opted to present the stimulus in only one hemifields to prevent spontaneous fluctuations in attention between the two hemifields in the prestimulus period from interfering with the results. Participants had to determine the presence or absence of the grey circles within the checkerboard and press the button associated with their choice. No timeout has been set for the response. After collecting the response, the screen appeared black for 1.9-2.4 s in the inter-trial interval. The cue was a rectangle with its bottom colored in red and its top colored in blue. The percentage of the red shading to the entire rectangle indicated the probability that the checkerboard contained the grey circles (target) within it. There were three level of cues. Cue high and cue low (informative cues) indicated the probability of the presence of the target of 67 and 33%, respectively. Instead, the neutral cue (un-informative cue) equally predicted (50%) the presence and absence of the target. The actual probability of target presentation was in accordance with the probability indicated by the cue. Participants were also explicitly told that the probabilistic cue was congruent with the actual probability of stimulus presentation.

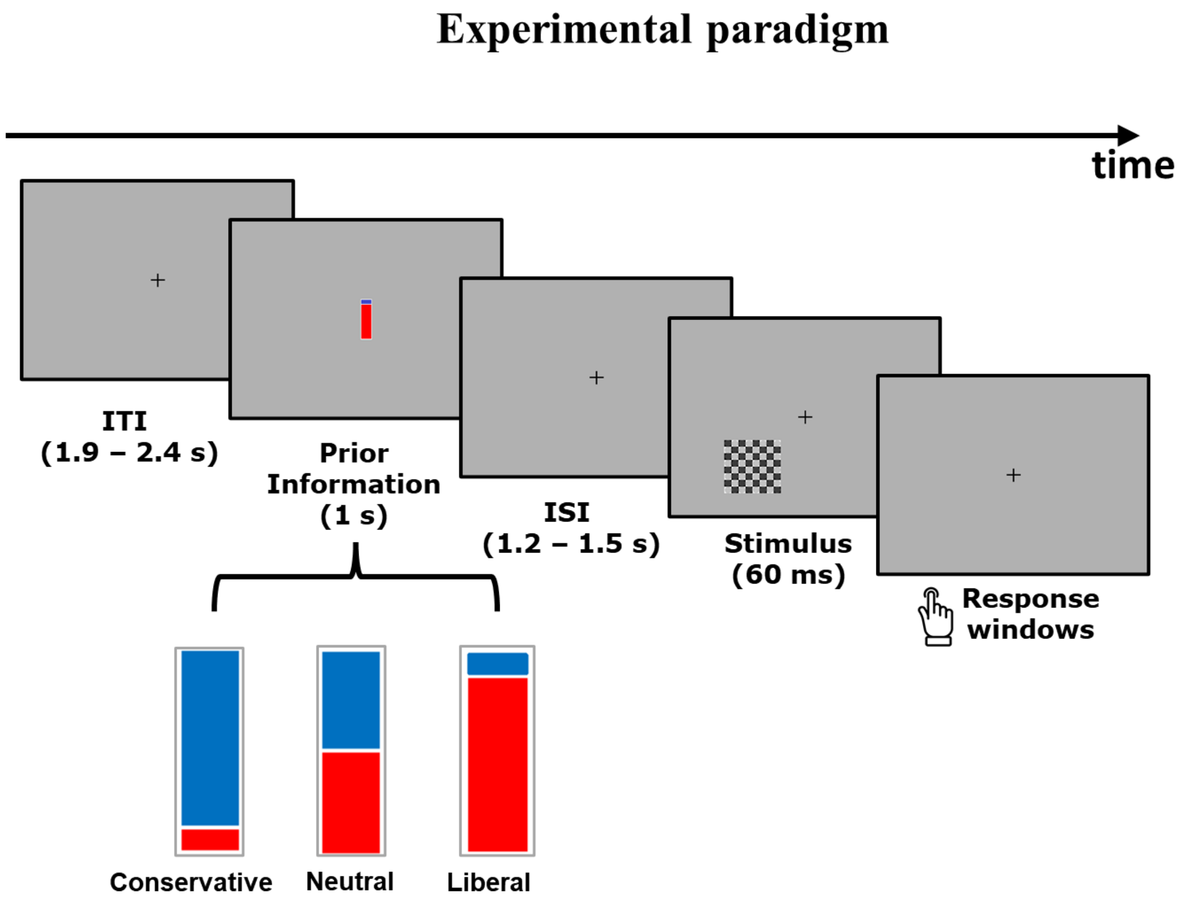


Figure 1. Experimental design. *A. EEG data were collected during a simple visual detection task. Each trial started with a fixation cross, after which a probabilistic cue appears in the center of the screen. After this, a checkerboard containing (or not) grey circles at the titrated contrast within it appeared at the bottom left of the monitor for 60 ms. The cue was a rectangle with its bottom colored in red and its top colored in blue. The percentage of the red shading to the entire rectangle indicated the target-probability. There were three cue levels. The high and low probability cues indicated the probability of the presence of the target of 67 and 33%, representing the liberal and the conservative conditions, respectively. The neutral cue equally predicted the presence (50%) vs. absence (50%) of the target.*

Signal-detection theory (SDT) modeling

We computed the SDT measures *d'* and *c* (Green and Swets, 1966). *d'* quantifies a participant's stimulus sensitivity (higher *d'* values are indicative of higher sensitivity), whereas *c* quantifies a subject's decision criterion (*c* value different from 0 implies the presence of choice bias). These measures were calculated based on the proportion of hits and false alarms. To evaluate the effect of the probabilistic cue on sensitivity and criterion, we computed *d'* and *c* separately for trials preceded by low, high, or neutral probability cues. To statistically investigate a cue-related effect on sensitivity and criterion, *d'* and c were subjected to a repeated-measures ANOVA with the cue type as within-factors (3 level: high, low and neutral probability). In order to interpret the results derived from the conducted ANOVA, post-hoc analyses were carried out using paired sample t-test by correcting the p-value for the number of comparisons made (p value corrected = 0.017). We have used customized functions taken from the gramm toolbox (Morel, 2018) for data visualization.

Drift diffusion modeling (DDM)

We fitted the drift diffusion model to RT distributions for 'stimulus presence'- and 'stimulus absence'-choices, separately for trials preceded by low, high, or neutral probability cues. We fitted the model using a hierarchical Bayesian parameter estimation of the Drift Diffusion Model using the HDDM toolbox (Wiecki et al., 2013). In HDDM, Bayesian inference through Markov chain Monte-Carlo (MCMC) sampling is used to approximate posterior distributions for each parameter at both the individual and group levels. The priors' distributions for each parameter were informed by a pool of 23 studies reporting the best fitting DDM parameters retrieved on a set of decision-making tasks (Matzke and Wagenmakers, 2009); see the supplement by (Wiecki et al., 2013) for visual representations of these priors. We initialized HDDM to draw 20000 posterior samples for each data with the first 2000 samples discarded as burn-in. We have fitted the model to RT distributions for 'stimulus presence'- and 'stimulus absence'-choices as opposed to the more common fits of correct and incorrect choice RTs to estimate the bias parameters (i.e., starting point [*z*]). In our fits, we allowed the following parameters to vary simultaneously according to probabilistic cue: (I) the mean drift rate (*v*); (II) the separation between both decision bounds (*a*); (III) the starting point of the accumulation process (*z*). We inspected traces of model parameters and their autocorrelation to ensure that the models had properly converged. We examined the overlap of the posterior distributions for the estimated parameters, defining significance as less than 5% overlap. Because these are comparisons of Bayesian posterior distributions, we report the HDDM outcomes as *q*- rather than *p-values*. To further evaluate the best-fit model, we performed posterior predictive checks, averaging 50 simulations generated by the posterior distribution of the fitted parameters, to verify the match between these simulated data sets and the actual data. Specifically, we first evaluated whether the reaction time pattern of the simulations reproduced that of the empirical data. In addition, we have ascertained through Pearson correlation analysis whether the average simulated response times were associated with the observed response times and whether the sensitivity/criterion indices calculated on the simulated data were matched to the actual values measured in the participants. Finally, we fitted an HDDM model using a simulated dataset as input to check the correspondence of the parameters extracted using the empirical data with those extracted from the simulated sample.

EEG preprocessing and time frequency decomposition

Participants comfortably sat in a room with dimmed lights. A set of 64 electrodes was mounted according to the international 10–20 system. EEG signals were acquired at a rate of 1000 Hz and all impedances were kept below 10 kΩ. EEG was processed offline with custom MATLAB scripts (version R2021a) and with the EEGLAB toolbox (Delorme and Makeig, 2004). The EEG recording was filtered offline in the 0.5-100 Hz band and a notch-filter at 50 Hz was applied. The signals were visually inspected, and noisy channels were spherically interpolated. Epochs spanning −4100 to 2000 ms relative to checkerboard onset were extracted and individual trials were visually checked and those containing excessive noise, muscle or ocular artefacts discarded. An average of 470 trials per subject passed this stage. Next the recording was then re-referenced to the average of all electrodes, and we applied the Independent Component Analysis (ICA), an effective method largely employed for removal of EEG artefacts. Components containing artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data. After these steps, we downsampled the signals to 256 Hz and a Laplacian transform was applied to the data using spherical splines. The Laplacian is a spatial filter that aids in topographic localization by attenuating artifacts attributable to volume conduction, rendering the data more suitable for performing connectivity analyses. (Cohen, 2014). Subsequentially, we implemented time-frequency analysis by convolving the time series data with a set of complex Morlet wavelets (whose cycles increased between three and eleven cycles as a function of frequency), defined as complex sine waves tapered by a Gaussian. Convolution was performed via frequency-domain multiplication, in which the Fourier-derived spectrum of the EEG data was multiplied by the spectrum of the wavelet, and the inverse Fourier transform was taken. Then, we obtained the phase extracting the angle relative to the positive real axis and the amplitude by extracting the absolute value of the resulting complex time series. Amplitude was then condition-specific baseline-corrected using a decibel (dB) transform: $dB\ amplitude = 10 \times \log_{10}(amplitude\ /\ baseline)$. Baseline amplitude was defined as the average amplitude in the period ranging from -3100 to -2700 ms before stimulus onset.

EEG analysis - Oscillatory amplitude *analysis*

We focused the amplitude analysis on a cluster of central and right posterior electrodes (as the visual stimuli were presented in the left visual field) by averaging the amplitude of the following electrodes to avoid the potential issues inherent in selecting a restricted number of sensors: Oz, POz, Pz, O2, PO4, PO8, P2, P4, P6, P8. In order to specifically investigate the pre-stimulus oscillatory activity related to the prior use, a frequency per time nonparametric cluster-based permutation tests (n = 1.000) was performed on the amplitude difference between the high- and low- probability trials in all time points ranging from -600 to 0 ms relative to the checkerboard appearance by shuffling the type of trials for each individual for each permutation in order to create a dummy distribution of amplitude difference. This method is data-driven and allows to test point-by-point the significant differences between the two types of prior information in the entire time interval considered and for all the frequencies included controlling for multiple comparisons (Maris and Oostenveld, 2007). Furthermore, to check that the effects did not depend on the unequal number of trials in which the target was present in the different conditions, the above analyses were repeated by equating the number of trials by sub-sampling. Specifically, we subsampled an equal number of target trials and catch trials from each condition so that the number of trials per condition matched that in the condition of the fewest trials. Crucially, the pattern of results points in the same direction to that highlighted when considering the entire dataset. Subsequently, we extracted, for each individual, the mean amplitude value of the time-frequency cluster resulted most significantly modulated by the prior (~8 - 14 Hz; ~ -400 - 0 ms). The difference between the amplitude values extracted in the conservative and the liberal trials (Δ amplitude) expresses the degree to which each participant regulates alpha pre-stimulus in a different way in the two conditions and was used in subsequent correlation analyses.

EEG analysis – brain-to-behavior analysis

To assess whether there was a relationship between the modulations at the behavioral level induced by the expectancy cue and the modulations at the oscillatory level, we conducted several correlation analyses. We have taken the difference between the criterion (Δ criterion) adopted in conservative trials and the criterion adopted in liberal trials (i.e., $c_{cons} - c_{lib}$) as a proxy of criterion modulation (for a similar approach, see (de Lange et al., 2013). Analogously, in the Drift Diffusion domain, we have taken the difference between the starting point (Δ starting point) adopted in liberal trials and the starting point adopted in conservative trials (i.e., $z_{lib} - z_{cons}$) as a proxy of bias induction. The larger these shifts were, the more the subject adjusted their behavior based on the predictive cue. We have ascertained the presence of a relationship between these behavioural metrics and the alpha modulation in cue low- vs high- expectancy trials by computing Pearson (r_p) and Spearman (r_s) correlations between Δ amplitude and Δ criterion as well as between Δ amplitude and Δ starting point. Moreover, we have run the skipped, both Pearson ($r_{p\ skipped}$) and Spearman ($r_{s\ skipped}$), correlation to ascertain the robustness of the association using the Robust Correlation toolbox (Pernet et al., 2013) conducing null hypothesis statistical significance testing using the non-parametric bootstrap percentile test (2000 samples, 95% confidence interval, corresponding to an alpha level of 0.05). With this method, outliers are removed guaranteeing a more robust estimate of the association between the variables under consideration. As a control analysis, we used the same correlational approach to assess any association between the difference in alpha amplitude and the difference in d' ($d_{cons} - d_{lib}$) and drift rate ($v_{lib} - v_{cons}$) in the two conditions. Both Pearson's and Spearman's correlations, as well as the skipped correlations, found no association between alpha adjustment and the difference in objective performance indices in the conservative vs. liberal trials (all $p > .52$).

EEG analysis – Functional connectivity

Functional interactions between oscillatory activity were captured by quantifying the inter-areas phase relationship. Specifically, we used the weighted phase lag index (wPLI) (Vinck et al., 2011) to evaluate the degree of synchronization between the signals. wPLI is based on the phase lag index (PLI) (Stam et al., 2007), which defines connectivity as the absolute value of the average sign of phase angle differences (+1 or −1, relative to the real axis). In contrast to the PLI, however, wPLI gives maximal weighting to phase differences that are far from the real axis, and hence omits all signals associated with artificial synchrony/volume conduction. wPLI values range between zero (random relationship between phases) and one (total phase synchronization). Phase connectivity was estimated in the pre-stimulus time (~ -600 to 0 ms) in the theta (~5-8 Hz) and in the alpha (~8-14 Hz) frequency band. We grouped the electrodes into 3 regions of interest (ROIs) in the right hemisphere going from rostral to caudal (frontal, parieto-central and occipital) by relying on the nomenclature of the International Standard 10-20 system, which associates labels with electrodes according to the cortical area on which they are situated. The frontal ROI comprises: FC2, FC4, FC6, FT8, F2, F4, F6, F8 electrodes. The parieto-central ROI comprises: Pz, P2, P4, P6, P8, CP2, CP4, CP6 electrodes. The occipital ROI comprises: Oz, O2, POz, PO4, PO8 electrodes. We selected a consistent number of sensors to be included in each ROI to avoid the potential pitfalls inherent in selecting a limited number of electrodes on which to perform analyses. We statistically evaluated whether prior knowledge was reflected by changes in pre-stimulus brain connectivity in the fronto-parietal and parieto-occipital network using an approach similar to Alekseichuk et al., (2016). The method employed is data-driven and allows to test electrodes-by-electrodes the significant differences between the two types of prior information in the synchronization index controlling for multiple comparisons (critical alpha = 0.05). First, we conducted, for each electrode's pairs within the investigate ROIs, a paired t-test to compare weighted phase-lag index between the conservative vs liberal condition. The connectivity index was then estimated for every condition as follows: $CI = \frac{sp\_sig}{sp\_total}$, where sp_sig is the number of sensor pairs that demonstrates the significant modulation of connectivity between the two conditions and sp_total is the total number of sensor pairs considered. A permutation test was then introduced to estimate the level of significance. To this end, for each individual, the wPLIs values associated with the two conditions (i.e., liberal and conservative) were randomly permuted to generate dummy data. These data entered the analysis as described above. The procedure was repeated 1.000 times, and the resulting distribution of the dummy connectivity indices was used to estimate the 95% confidence interval; if the connectivity indices calculated on the real data exceeded this interval, they were considered statistically significant. This procedure was carried out separately for the two-frequency band (i.e., theta and alpha) and for the two networks (i.e., fronto-parietal and parieto-occipital) considered.

Investigate the relation between connectivity indices and amplitude modulations.

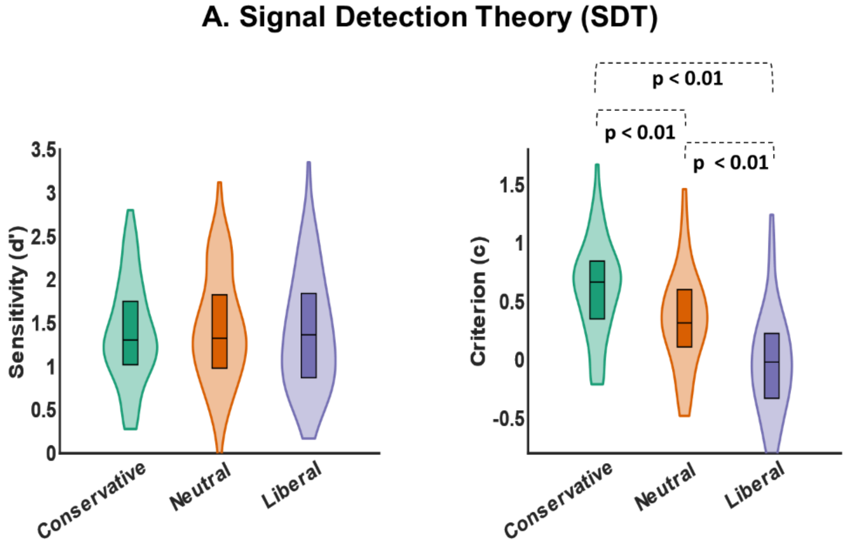
Since we hypothesize that the synchronization along the fronto-parieto-occipital axis was crucial to shape the activity at the level of sensory cortex, we assessed whether the changes in connectivity indices observed in the fronto-parietal and parieto-occipital networks were associated with the prior-related alpha amplitude modulation. First, we hypothesized that the differentiation observed in parieto-occipital alpha coupling between conservative and liberal conditions would support a rhythmic modulation of sensory excitability to predispose perception. Thus, we extracted, for each participant, the mean wPLI values of the significant connections (sp_sig) along the parieto-occipital circuit that emerged from the previously conducted analysis. Next, we took the difference between the extracted wPLI values in the conservative - liberal conditions (Δ alpha coupling) as predictors of pre-stimulus alpha amplitude modulation (Δ amplitude). Secondly, we asserted that fronto-parietal theta synchronization would represent a predictive control mechanism that set the perceptual areas in an un-biased state. Therefore, we expected that the increased fronto-parietal theta synchronization observed in liberal vs. conservative trials underlies reduced pre-stimulus alpha amplitude differentiation between conditions. Thus, we extracted, for each individual, the mean wPLI values of the significant pairwise connections (*sp_sig*) along the fronto-parietal circuit that emerged from the previously conducted analysis. Next, we took the difference between the extracted wPLI values in the liberal - conservative conditions (Δ theta coupling) as predictors of pre-stimulus alpha amplitude modulation (Δ amplitude). We have ascertained the presence of a relationship between Δ alpha connectivity and Δ alpha amplitude as well as between Δ theta connectivity and Δ alpha amplitude by computing Pearson and Spearman correlations. Moreover, we have runned the parametric skipped (both Pearson and Spearman) correlation to ascertain the robustness of the association using the Robust Correlation toolbox (Pernet et al., 2013) conducing null hypothesis statistical significance testing using the non-parametric bootstrap percentile test (2000 samples, 95% confidence interval, corresponding to an alpha level of 0.05).

Individual differences in predictive style are predicted by synchronization along the rostro-caudal axis

To investigate whether a differential weight assigned to the outlined neurofunctional mechanisms might underpin the differences in predictive style adopted, we used a median split approach to separating individuals that showed large (vs. low) prior-based pre-stimulus differentiation in alpha amplitude. Specifically, we have calculated the median of Δ alpha amplitude index (median = 0.12) that aided us to divide the subjects in two groups: the high alpha amplitude modulators (i.e., individuals which show above-median Δ alpha index) and low alpha amplitude modulators (i.e., individuals which show below-median Δ alpha index). To assess whether the two groups showed specific differentiation related to criterion shift, we assessed with an independent samples t-test whether the Δ criterion index was different in the two groups. As a control analysis, we tested whether the two groups showed differentiation in discriminative ability. To this end, we used an independent-samples t-test with dependent variable the overall d' of the participants (the cue factor was collapsed since previous analyses clarified its nonimpact on sensitivity). Furthermore, to ascertain the relationship between the modulation of connectivity indices along the rostro-caudal axis and the inter-individual difference in the shaping of alpha amplitude due to the prior knowledge, we conducted two ANOVAs. As dependent variable, we extracted, at the individual level, the mean wPLI values of the pairwise connections (sp_sig) that exceeded the significance threshold in the previously conducted non-parametric analysis. Since there were two significant prior-related effect on connectivity metrics (i.e., theta in the fronto-parietal network and alpha in the parieto-occipital network), we conducted two mixed ANOVAs. Both ANOVAs take into account a between-subjects independent variable, the group type (two levels: high vs low alpha modulators), and a within-subjects independent variable, the trial type (liberal vs conservative). In order to interpret the results derived from the conducted ANOVAs, post-hoc analyses were carried out using t-test by correcting the p-value for the number of comparisons made (4 comparison, p value corrected = 0.0125).

Results

Human participants (n = 68) performed a simple detection task. In each trial, a checkerboard was presented on the lower left visual field. The checkerboards presented could contain isoluminant grey circles within each of the cells (target) or not (catch trials). Participants were instructed to indicate via the keyboard the presence vs. absence of the target. In the first phase, each participant underwent an adaptive titration procedure to determine the contrast of the grey circles for which the detection accuracy was at ~ 70%. The overall accuracy value in the main task was close to 70% (namely, 71.9%), testifying to the effectiveness of the titration phase. In the second phase, the checkerboards were preceded by a symbolic cue indicating the probability of the target's presence. There were three cue levels. The high and low probability cues indicated the probability of the presence of the target of 67 and 33%, representing the liberal and the conservative conditions, respectively. The neutral cue equally predicted the presence (50%) vs. absence (50%) of the target. The actual probability of target presentation was in accordance with the probability indicated by the cue. Participants were also explicitly told that the probabilistic cue was congruent with the actual probability of stimulus presentation.



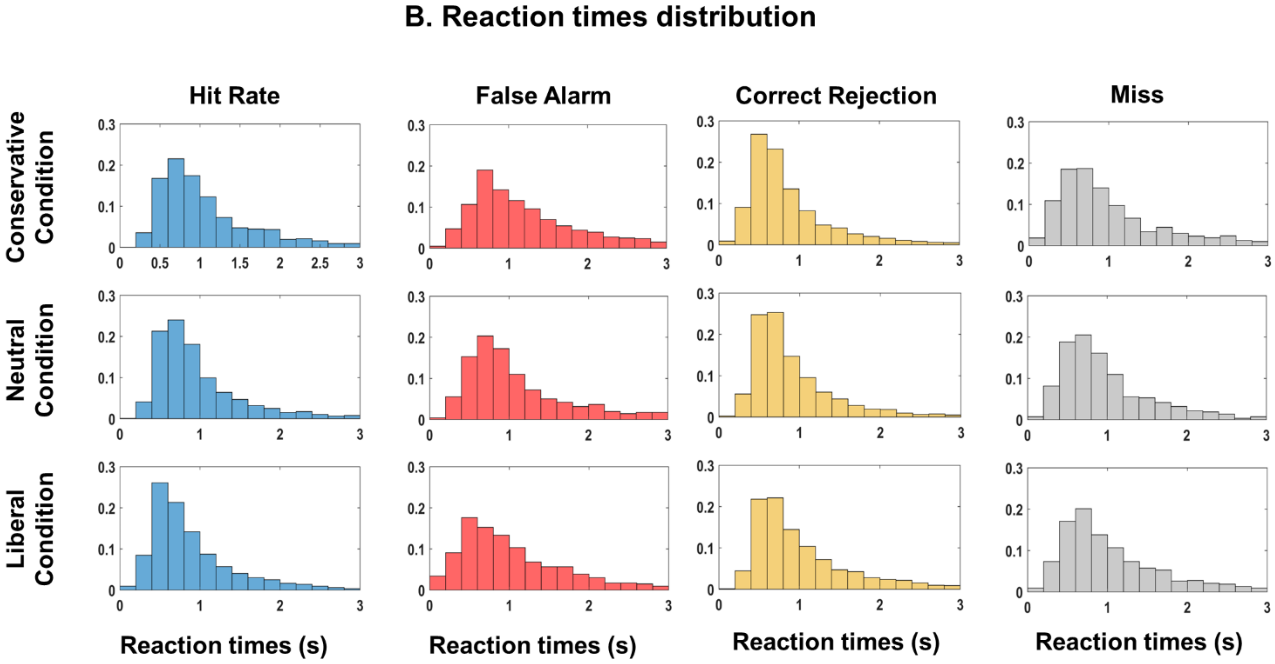


Figure 2.

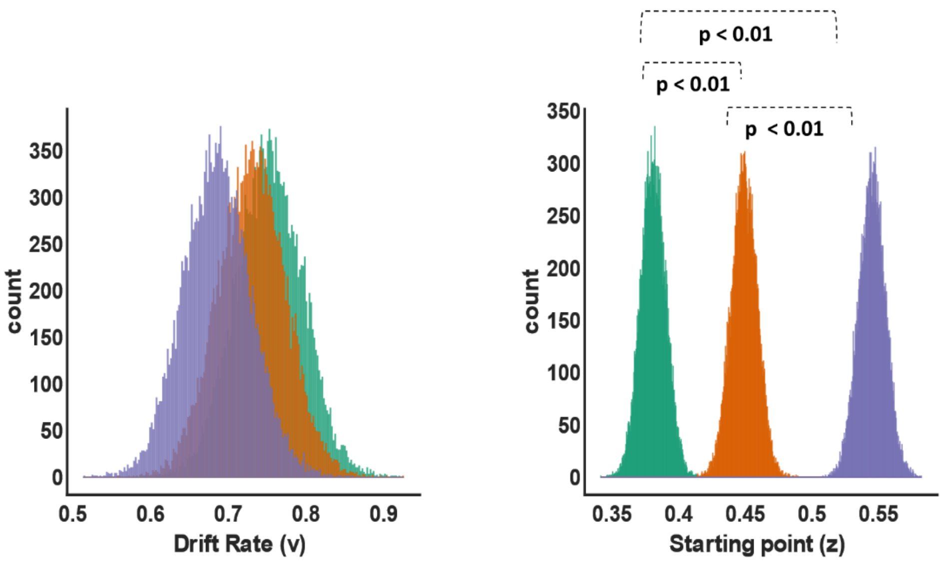
A. *Signal Detection Theory. Sensitivity (d') and Criterion (c) indices are represented separately for trials preceded by low, high, or neutral probability cues. Prior information had no effect on sensitivity. In contrast, the probabilistic cue significantly shapes the decision criterion: a more liberal criterion was adopted when trials were preceded by high probability cue relative to both trials preceded by neutral and low probability cue, whereas the criterion was more conservative when low probability cue precedes the checkerboard appearance relative to neutral cue.*

B. *RT distributions of hit rates, false alarms, correct rejections, and misses are shown in the panels. The reaction times were grouped into 15 bins starting at 0 and ending at 3s, each of which considers an interval of 0.2 s. The height of each bin represents the density of observations in that interval. By qualitative inspection of the graphs, there is an acceleration effect of both the accurate and inaccurate response if they are congruent with the prior. For example, there are faster hit rates in the liberal condition* *matched by faster false alarms. Conversely, in the conservative condition, there are faster correct rejections as well as faster misses.*

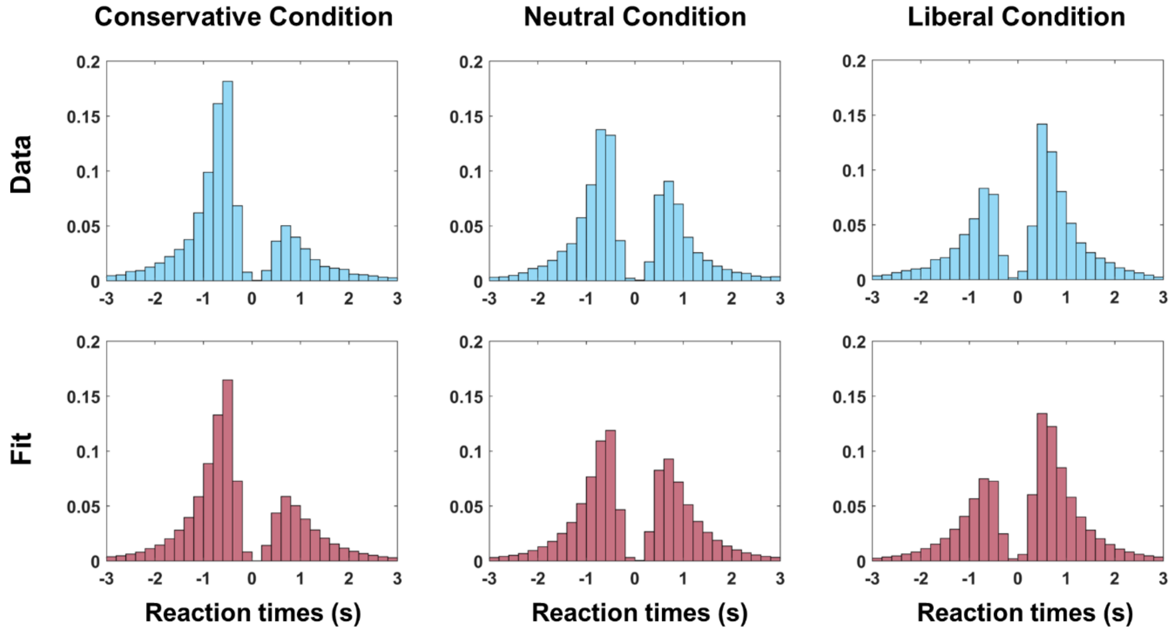
Prior information modulates the decisional bias

We computed the signal detection theory indices *d'* (sensitivity) and *c* (criterion) (Green and Swets, 1966) separately for trials preceded by low, high, or neutral probability cues (Figure 2A). The conducted repeated-measures ANOVA did not find any impact of probabilistic cue on sensitivity ($F_{2,134} = 1.13$; $p > 0.32$). In contrast, the cue significantly shapes the decision criterion ($F_{2,134} = 107.44$; $p < 0.01$) : a more conservative criterion was adopted when trials were preceded by low probability cue ($c_{low} = 0.61 \pm 0.05$) relative to both trials preceded by neutral cue ($c_{mid} = 0.34 \pm 0.05$; $t_{67} = 7.4$, $p < 0.01$) and high probability cue ($c_{high} = - 0.03 \pm 0.05$; $t_{67} = 11.14$, $p < 0.01$), whereas the criterion was more liberal when high probability cue precedes the checkerboard appearance relative to neutral cue ($t_{67} = -10.91$, $p < 0.01$). Focusing on the distribution of reaction times (Figure 2B, Table S1), it can be observed that expectation-like information prioritizes congruent decision outcomes rather than accelerating correct/wrong responses. For example, hit rates are faster in the liberal trials than in the other conditions, but this is coupled with the presence of faster false alarms. A Bayesian parameter estimation of the Drift Diffusion Model parameters using the HDDM toolbox (Wiecki et al., 2013) (Figure 3A) confirm these patterns of results: the posterior distributions revealed higher starting point in the high probability trials relative to both mid probability trials ($q < 0.01$) and low probability trials ($q < 0.01$) and lower starting point in the low probability trials relative to mid probability trials ($q < 0.01$). No difference was found both in drift rate and in threshold separation (all qs > 0.05). This implies that the speed of accumulation (v) and the amount of evidence that needs to be accumulated until a decision is taken (a) do not differ according to conditions. We also confirmed the goodness of the fitting procedure. Specifically: 1) the pattern of simulated response times with posterior prediction check were very similar to those empirically collected (Fig. 3B); 2) the simulated mean response times were correlated with the observed response times ($r = .97$; $p < .01$); 3) the sensitivity/criterion indices calculated on the simulated data were significantly associated with the actual values measured in participants; 4) there were no significant differences between real vs. estimated DDM parameters using a simulated sample (all qs ≥ .17), which are further found to be strongly associated. Therefore, both posterior predictive checks and correlation analyses suggested that the model fit the data properly.

Overall, the behavioral results indicate that the experimental paradigm used was able to manipulate response bias without affecting other decision-making parameters.



A. Drift Diffusion Model (DDM)



B. Empirical RT vs Fitted RT

Figure 3.

A. *Drift Diffusion Model. A Bayesian parameter estimation of the Drift Diffusion Model parameters revealed the presence of higher starting point in the liberal relative to both neutral and conservative trials and lower starting point in the low probability trials relative to mid probability trials. No difference was found in the drift rate parameter.*

B. *The upper panel shows the distribution of the empirical RTs under the three experimental conditions, while the lower panel shows the distribution of the simulated RTs using the fitted parameters. The reaction times were grouped into 30 bins starting at -3s and ending at 3s, each of which considers an interval of 0.2s. The height of each bin represents the density of observations in that interval. The RT distribution for no target response is plotted negatively, so the RT distribution for no target presence response trials is given on the left side of zero, while the distribution for target presence response trials is shown on the right side of zero. In general, we can see that no target presence response is overrepresented in the conservative condition, while target presence response become the majority in the liberal condition. Notably, the empirical and simulated data show extremely similar and overlapping trends, testifying to the goodness of fit obtained with the HDDM model.*

Pre-stimulus alpha oscillations affect perceptual bias.

We assessed whether preparatory activity in the posterior regions was modulated by prior information by running a frequency per time non-parametric permutation test on the amplitude difference between the liberal and the conservative trials across the 600-millisecond pre-stimulus window and a broad range of frequencies (2–50 Hz). The conducted analysis revealed a significant effect in the pre-stimulus period, particularly pronounced in the alpha range (Figure 4A). Specifically, there was greater amplitude suppression in the liberal relative to the conservative condition. To demonstrate the spatial specificity of this neural effect, we conducted a control analysis to ascertain whether there was a similar modulation of the time-frequency representation in the left posterior electrodes. The cluster-based analysis did not reveal the presence of significantly different clusters that distinguished the liberal from the conservative condition. Furthermore, to mitigate the possibility that the effect was due to a choice-predictive motor activity (Donner et al., 2009), we assessed whether there was a differentiation in the time-frequency representation in the sensors representing the motor areas activity [electrodes C1 and C3 (Shibata et al., 2021; Thut et al., 2000)]. Again, the conducted analysis did not individuate any clusters that differentiated the two conditions. In addition, to further confirm the spatial specificity of the neural effects, we have depicted (Figure 4B) the topography of the differential pre-stimulus activations between the liberal and conservative condition in the alpha range. The posterior areas, especially those located to the right hemisphere, are the only showing consistent pre-stimulus differentiation between the conditions, testifying to the presence of spatial segregation of the effects.

Next, we analyzed the functional significance of this neural differentiation. If, as hypothesized, the highlighted voluntary modulation of the amplitude of alpha fluctuations is linked to prior-dependent behavioral changes, it is reasonable to expect an association with response bias. Indeed, Pearson and Spearman's correlation analyses showed a positive correlation between Δ criterion (i.e., how much individual shift the criterion) and Δ alpha amplitude (i.e., how much individual shift the alpha amplitude) ($r_p = .32$, $p < 0.01$; $r_{p\ skipped} = 0.35$, CI = [0.15 0.49]; $r_s = .38$, $p < 0.01$; $r_{s\ skipped} = 0.41$, CI = [0.16 0.56]; Figure 4C) as well as between Δ starting point (i.e., how much individual shift the starting point) and Δ alpha amplitude ($r_p = .26$, $p < 0.05$; $r_{p\ skipped} = 0.37$, CI = [0.17 0.55]; $r_s = .3$, $p = 0.01$; $r_{s\ skipped} = 0.39$, CI = [0.18 0.58]). These findings showed that alpha modulation is linked to the shaping of subjective response criterion as well as with a shifting of the starting point of the accumulation process congruent with the probabilistic information received. Specifically, the greater the alpha amplitude adjustment, the greater the response bias triggered. Thus, these results suggested that alpha amplitude regulation is a crucial marker of response strategy tuning. Furthermore, the relationship between the magnitude of alpha and the criterion adopted is present beyond the condition considered, with higher alpha associated with a more conservative criterion in both the liberal and conservative conditions.

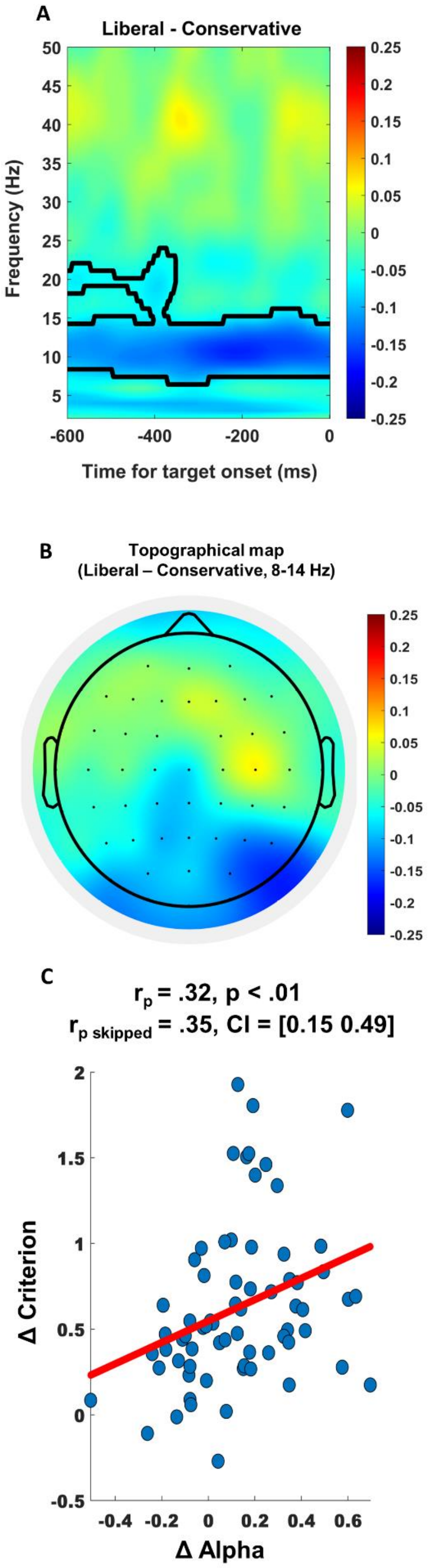


Figure 4. Alpha amplitude tracks perceptual bias.

A. Time-frequency map of the pre-stimulus (- 600, 0 ms) amplitude difference between liberal and conservative trials registered in regions involved in visual processing. Time 0 refers to stimulus onset. Black contours denote cluster resulting significant from statistical analysis. It is noticeable a reduction in the pre-stimulus alpha amplitude in the liberal vs. conservative conditions, prominently in the alpha band.

B. Topography of the differential activations between the liberal and conservative condition in the alpha range (8-14 Hz) in the pre-stimulus window (-600 - 0 ms). Oscillatory activity in the alpha band diverges in the two conditions precisely in the posterior electrodes and peaks predominantly in the right hemisphere. The rest of the brain activations appear comparable in magnitude. This indicates a spatially localized effect that prepares cortical activity specifically in regions dedicated to stimulus detection.

C. Association between behavioral and neural markers of prior information. It is observable a significant positive correlation between individual differences in prestimulus alpha amplitude between conservative and liberal trials (Δ amplitude) and the behaviorally prior-induced criterion shift (Δ criterion).

Inter-areas couplings in theta and alpha bands shape predictive processes

Next, we evaluated the neurofunctional role of fronto-parietal-occipital interplay in theta and alpha bands in predictive processing. Functional interactions between oscillatory activity were captured by quantifying the phase relationship between the neural signals using the weighted phase lag index (wPLI) (Vinck et al., 2011).The non-parametric analysis conducted showed that the connectivity index (CI), which expresses the proportion of sensor pairs exhibiting a significant difference in connectivity between liberal and conservative trials, showed a clear differentiation between conditions and networks (Figure 5). Regarding the fronto-parietal network, the permutation test indicated that CI = 0.094 corresponds to the 5% significance level. Accordingly, there is a significant increase in theta connectivity in the liberal condition compared to the conservative condition (CI θ liber. > θ cons. = 0.156) while all other comparisons do not exceed the threshold value (all CI < 0.032). A diametric pattern of results emerged when considering the synchronization along the parieto-occipital circuit in which the permutation test indicated that CI = 0.1 corresponds to the 5% significance level. Indeed, the conducted analysis showed increased alpha synchronization when participants expected a low vs. high probability of stimulus presence (CI α cons. > liber. = 0.125). No other comparisons within the parieto-occipital network exceeded the threshold value (all CI = 0). Furthermore, we ruled out that the synchronization effect could be explained by the simultaneous increase in the amplitude of alpha oscillations in the conservative condition.

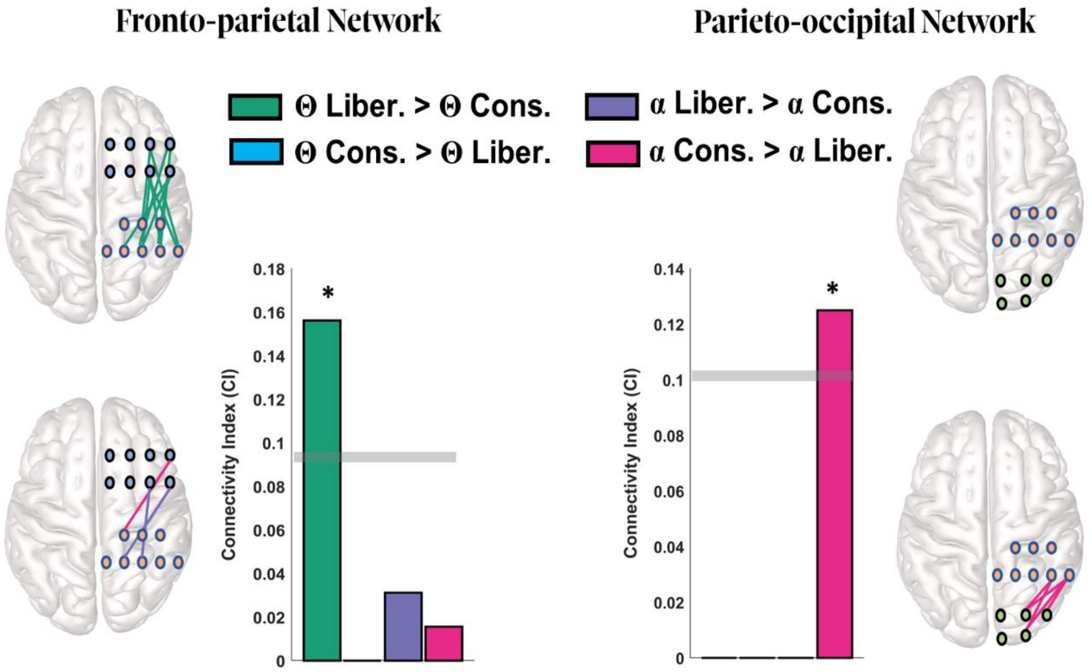


Figure 5. Fronto-parietal-occipital interplay in theta and alpha bands is shaped by predictive processing.

A. In the fronto-parietal network, theta coupling is enhanced in the liberal condition compared to the conservative condition while all other comparisons do not exceed the threshold value (gray line denotes the level of statistical significance).
B. In the parieto-occipital network, alpha coupling is enhanced in the conservative condition compared to the liberal condition while all other comparisons do not exceed the threshold value (gray line denotes the level of statistical significance).

Subsequently, we assessed the functional role of these inter-area dynamics. Recent evidence posits that high-level predictive information is transmitted across the alpha band to influence simpler processes occurring at earlier hierarchical nodes (Bastos et al., 2020). Thus, we argued that the differentiation observed in alpha coupling between conservative and liberal conditions would support a rhythmic modulation of sensory excitability to predispose perception. Specifically, the greater the increase in parieto-occipital synchronization in conservative vs liberal trials, the more there is a congruent shift in cortical excitability indexed by alpha amplitude regulation. The correlational analysis conducted (Figure 6) confirmed this assumption highlighting a significant relationship between alpha coupling shift and alpha amplitude regulation ($r_p = .26$, $p < 0.05$; $r_{p\ skipped} = .37$, CI = [0.12 0.56]; $r_s = .27$, $p < 0.05$; $r_{s\ skipped} = .35$, CI = [0.11 0.56]). Specifically, the more the participants showed increased alpha coupling in the conservative compared with the liberal condition, the more their pre-stimulus alpha amplitude was modulated in a prior-dependent fashion (i.e., higher in the conservative condition, lower in the liberal condition). In contrast, we hypothesize that fronto-parietal theta synchronization would represent a complementary process that controls the predictive process by setting the visual cortex in an un-biased state that allows for a more veridical representation of the external world. Therefore, we expect that the increased theta synchronization observed in liberal vs. conservative trials underlies reduced pre-stimulus alpha amplitude differentiation between conditions. Indeed, the correlational analysis conducted (Figure 6) showed that the increased theta synchronization observed in the liberal vs. conservative condition was associated with reduced pre-stimulus alpha amplitude regulation ($r_p = -.28$, $p < 0.05$; $r_{p\ skipped} = -.37$, CI = [-.55 - 0.16]; $r_s = -.3$, $p = 0.01$; r_s skipped = - .35, CI = [-.56 -0.13]). Specifically, the more individuals increased coupling in theta in the liberal compared to conservative trials, the less differentially visual cortices responded to probabilistic information prior to target onset.

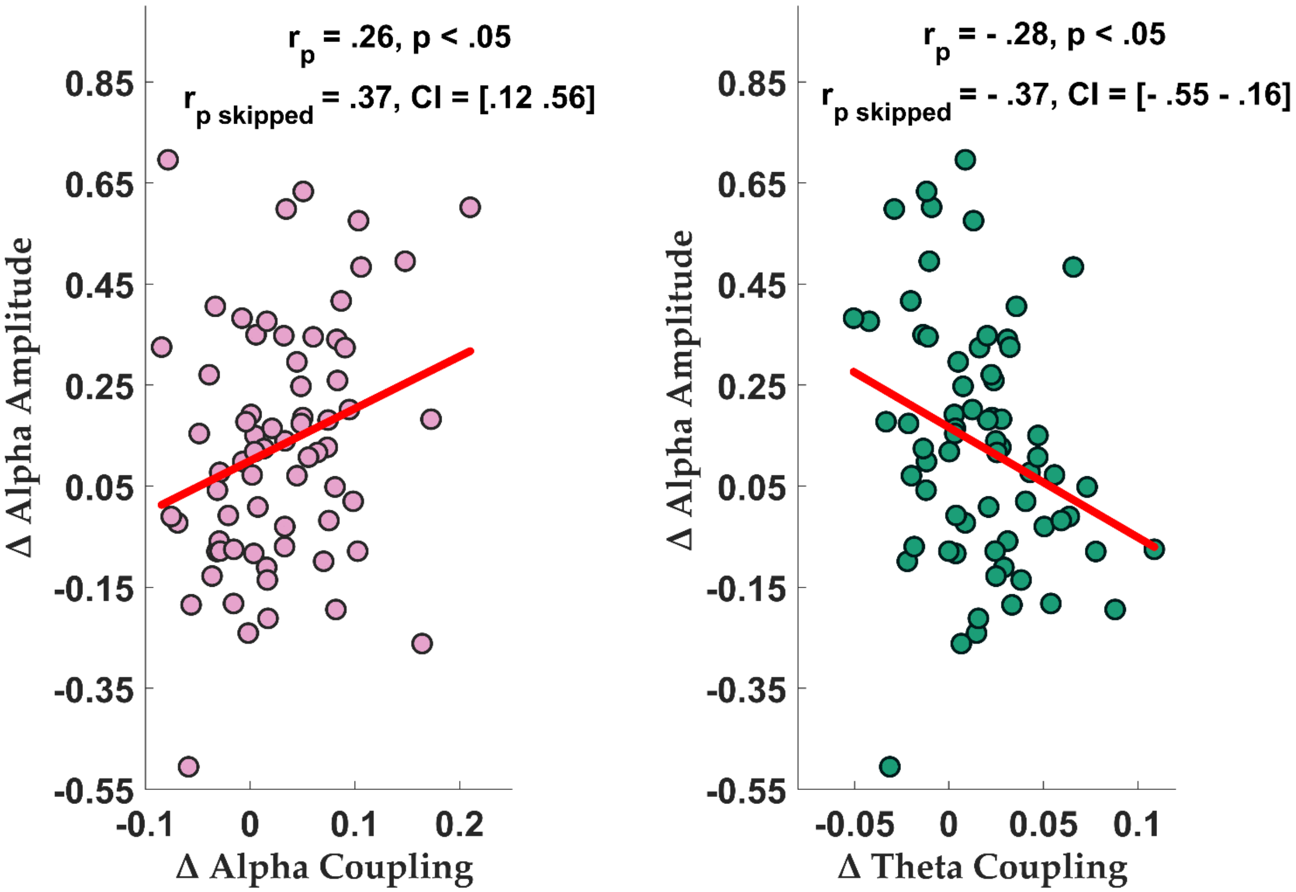


Figure 6. Alpha and theta synchronization play a diametrical role in cortical excitability setup.

A. Association between parieto-occipital alpha coupling and alpha amplitude regulation. It is observable a significant positive relationship between alpha coupling shift and alpha amplitude modulation. Thus, the increased alpha alignment in the conservative vs. liberal condition supports the priors-dependent modulation of pre-stimulus alpha amplitude.
B. Association between fronto-parietal theta coupling shift and alpha amplitude regulation. It is observable a significant negative relationship between theta coupling shift and alpha amplitude modulation. Thus, the increased theta synchronization in the liberal compared to conservative trials subtends a lower prior-based differentiation of posterior cortex excitability.

Synchronization along the rostro-caudal axis accounts for individual differences in sensory bias setting

The analyses conducted showed that alpha and theta synchronization play a diametrical role in cortical excitability setup. The presence of neural phenomena that facilitate vs. dampen predictive processing couples well with behavioral and computational evidence showing significant interindividual differences in prediction handling (Tulver et al., 2019). Indeed, people could be distributed within a predictive continuum at the poles of which are placed individuals who make an overuse (vs. underuse) of predictive information (Tarasi et al., 2022d). Thus, we hypothesized that the different weight assigned to the outlined neurofunctional mechanisms might underpin the differences in predictive style adopted. Specifically, individuals who tend to modulate sensory cortex activity more according to priors (prior-prone individuals) would be dominated by the alpha-based prediction transmission mechanisms, whereas individuals who tend to discount predictive information (prior-resistant individuals) would place the areas involved in stimulus encoding in a neutral state of expectation through strong regulation of theta coupling. To test this hypothesis, we have used a median split approach by subdividing the participants in two groups based on their (prior-based) alpha amplitude modulation (Δ alpha amplitude). We would expect a differential connectivity pattern in subjects who heavily adjust visual cortex excitability (High Modulators) as a function of the prior knowledge compared to those who show less modulation (Low Modulators). According to these premises, above-median alpha amplitude modulators should be associated with a higher modulation of alpha coupling, whereas below-median alpha amplitude modulators should exhibit a higher regulation of fronto-parietal theta communication. First, we replicated the relevance of alpha modulation specifically in the change of criterion since the high- alpha modulators (Δ criterion$_{\text{high alpha modulators}} = 0.80 \pm 0.09$) show greater shift in the bias measures relative to low- alpha modulators (Δ criterion$_{\text{low alpha modulators}} = 0.46 \pm 0.06$, $t_{66} = 3.23$, $p < 0.01$), while no difference in perceptual sensitivity can be tracked in the two groups ($d'_{\text{high alpha modulators}} = 1.39 \pm 0.09$; $d'_{\text{low alpha modulators}} = 1.40 \pm 0.11$; $t_{66} = 0.06$, $p > 0.96$). Furthermore, the conducted ANOVA proved the presence of a significant interaction term between trials type (liberal vs conservative) and group (low- vs high- modulators) when considering the fronto-parietal theta connectivity ($F_{1,66} = 8.47$, $p < 0.01$). Post-hoc analysis revealed that, while the low-alpha modulators group showed enhanced synchronization in the liberal relative to conservative condition (liberal = 0.16 ± 0.01, conservative = 0.13 ± 0.01, $t_{33} = 4.73$, $p < 0.01$), the high-alpha modulators showed a comparable level of coupling in the two types of trials (liberal = 0.14 ± 0.01, conservative = 0.13 ± 0.01, $t_{33} = 1.39$, $p > 0.17$). A different pattern of results emerged considering the parieto-occipital alpha connectivity. Indeed, the conducted ANOVA replicated the presence of a significant interaction term between trials type and group ($F_{1,66} = 4.30$, $p < 0.05$) and highlighted the significance of the group factor ($F_{1,66} = 7.24$, $p < 0.01$). Post-hoc analyses revealed the presence of a general increase in alpha connectivity in the high modulator group (Conservative trials: high modulators = 0.36 ± 0.03, low modulators = 0.26 ± 0.02, $t_{66} = 2.95$, $p < 0.01$; Liberal trials: high modulators = 0.32 ± 0.02, low modulators = 0.24 ± 0.02, $t_{66} = 2.30$, $p < 0.05$), which also increased synchronization on conservative trials compared with the liberal condition ($t_{33} = 3.95$ $p < 0.01$), whereas the low-modulators show no differentiation between the two conditions ($t_{33} = 1.44$, $p > 0.16$). These results demonstrated that the synchronization along the fronto-parietal-occipital axis is associated to inter-individual differences in perceptual bias setting. Specifically, modulation in theta connectivity is associated with a lack of expectancy-dependent bias in pre-stimulus activity. Conversely, individuals which showed greater prior-based regulation of visual cortex excitability are characterized by the presence of a significant modulation in alpha phase synchrony. Overall, these results suggest that the phase aligning along the alpha and theta bands mediates frequency-specific dissociated processes on posterior alpha amplitude that could underpin the differential use of probabilistic models in individuals within the general population (Figure 7).

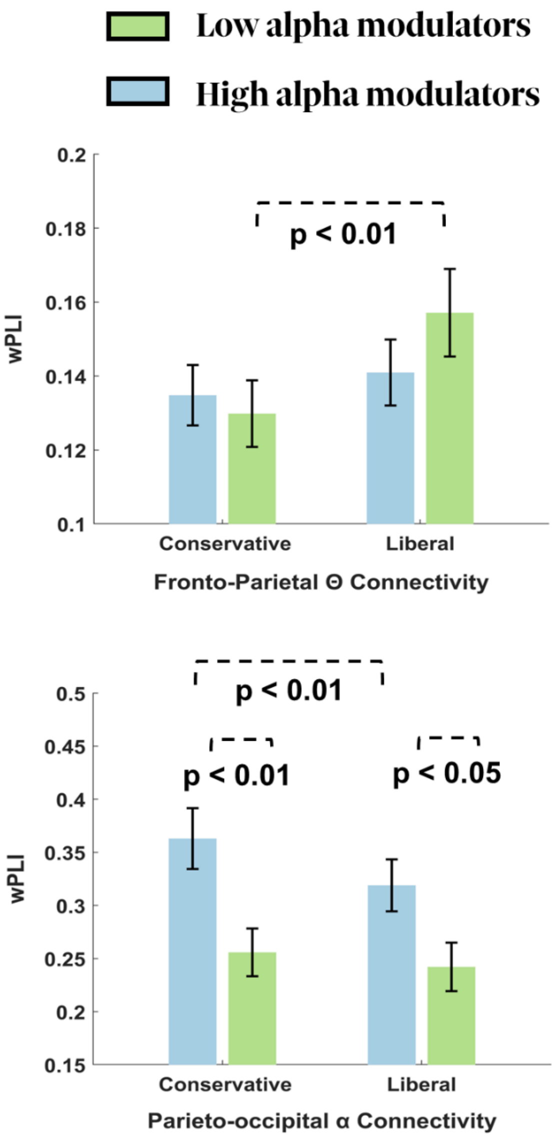


Figure 7. Synchronization along the rostro-caudal axis accounts for interindividual differences in predictive style.

A. Individuals who weakly set the posterior alpha amplitude as a function of expectation showed reduced response bias and increased fronto-parietal theta synchronization in the liberal compared to conservative condition.

B. Participants characterized by greater alpha amplitude regulation showed large criterion shift paired with a general increase in parieto-occipital coupling in the alpha band and enhanced alpha synchronization in conservative vs liberal trials.

Discussion

To investigate the behavioural and neural correlates of the predictive processing in the visual modality, we recorded the brain activity of human observers while performing a probabilistic detection task. Behavioural results indicate that participants were able to incorporate expectation-related information into their decision-making process. Specifically, the manipulation of perceptual expectations was able to elicit a response bias (i.e., shaping the *criterion* and *starting point*) while leaving the objective performance (i.e., *d-prime* and *drift rate*) unchanged. At the neural level, the perceptual prior resulted in a change in posterior alpha oscillatory pattern along with a reconfiguration of long-range connectivity in the rostro-caudal axis in the alpha and theta bands. Prior information plays a key role in optimising perceptual decision making. However, it was not clear whether the functional role of expectations is to increase perceptual sensitivity to the expected stimuli or to influence what is perceived. Literature studies indicate that priors affect response rate (Bang and Rahnev, 2017), reaction times (Martijn J. Mulder et al., 2012), and metacognition (Sherman et al., 2015) but have a negligible (Wyart et al., 2012) or even detrimental effect on perceptual sensitivity (Rahnev et al., 2011). The behavioural results described strengthen the idea that expectations drive the content of perception: providing the probability of target-presence induces the participant to respond congruently to the prior information received regardless of the objective occurrence of the stimulus. At the neural level, the induction of response bias was reflected in the change in pre-stimulus alpha amplitude. Alpha rhythm is a key predictor of trial-by-trial variability in decision outcomes (Di Gregorio et al., 2022; Samaha et al., 2020). Indeed, spontaneous alpha suppression has been related to increased tendency to report the presence of the target, even when no stimulus was presented (Iemi et al., 2017; Limbach and Corballis, 2016). The results of the presented study extend this range of findings as it shows that alpha oscillations are also implicated in voluntary modulation of the decision criterion. Indeed, an increased anticipation of target-presence is associated with a greater suppression of the amplitude of pre-stimulus alpha oscillations. Crucially, the differentiation of alpha wave amplitude in the liberal vs. conservative condition was associated with the magnitude of change in the criterion at the individual level. Thus, this biological marker appears to be related to the choice bias induced on the behavioural side. Furthermore, this result prompts the question of how much the fluctuation in pre-stimulus alpha amplitude highlighted in previous literature reflects a trial-by-trial variations in self-generated expectations about the presence of the stimulus in the upcoming trial rather than a stochastic process. It should be noted that the highlighted neural effects emerge considering the sensors placed in the right hemisphere, as the presentation of the checkerboards was left lateralized. Follow-up studies should involve the presentation of the stimuli in both visual fields to rule out the possibility that the observed effects are hemisphere-specific. Furthermore, it is noteworthy that this result points in a different direction from that outlined in a recent study (Zhou et al., 2021) in which modulation of the decision criterion due to expectancy induction was not reflected in a concordant modulation of the alpha amplitude. However, the experimental paradigms differ in two main aspects: a) in our study, perceptual expectations have been modulated trial-by-trial, whereas Zhou et al., (2021) have employed a block-by-block approach and b) in our design, probabilistic contingencies were maintained continually valid, whereas in Zhou et al., (2021) they were reliable only in the first phase of each block. Thus, it can be assumed that these crucial variations in the experimental design employed explain the differential findings from the two groups.

How would voluntary regulation of pre-stimulus alpha oscillations impact the response criterion? According to the SDT framework, observers evaluate the presence vs. the absence of the stimulus by assessing whether the strength of the internal responses exceeds the decisional criterion. Any mechanism that magnifies the internal response is likely to cause exceeding the decision-making criterion. According to the Gating by Inhibition theory (Jensen and Mazaheri, 2010), alpha rhythms play a fundamental role in maintaining an active and flexible inhibition mechanism capable of modulating the excitability of the cerebral cortex. Thus, the mechanism behind the liberalization of the decisional criterion may depend on a deliberate release from inhibition by alpha desynchronization in visual regions as the probability of the target appearance increases (Foxe and Snyder, 2011). The consequent increase in neural excitability would affects not only the interpretation of signal but also noise, facilitating the internal response to exceed the decisional criterion under the same input stimulation, without actually affecting perceptual performance (Iemi et al., 2019, 2017; Samaha et al., 2020; Vugt et al., 2018).

Having highlighted that alpha amplitude in posterior regions could be regulated by voluntary top-down processes related to prior, we subsequently analysed which brain networks were engaged in this alpha rhythm tuning. Electrophysiological evidence indicates that different neuronal assemblies exchange information through phase synchronisation of oscillatory activity (Canolty et al., 2010; Fries, 2015; Varela et al., 2001). If two different brain networks oscillate in phase, they are more likely to influence each other because their excitatory state is concordant in time. Thus, we have investigated whether the long-range phase coupling along the theta and alpha bands between fronto-parietal and parieto-occipital regions come into play in the regulation of sensory oscillatory activity. The results showed that synchronization along the parieto-occipital circuit is increased in the conservative condition compared with the liberal condition along the alpha band, whereas in the fronto-parietal circuit there is an increase in theta synchrony in the liberal trials. Crucially, we isolate different influences subserved by theta and alpha synchronization on the alpha amplitude recorded in posterior regions. Interregional alpha-band phase synchronization underpins numerous cognitive processes including top-down processing, perception, attention selection, cross-modal integration and working memory (Bastos et al., 2020; Doesburg et al., 2009; Michalareas et al., 2016b; van Driel et al., 2014; van Kerkoerle et al., 2014; Zanto et al., 2011). Our results expand this literature by showing that alpha coupling is involved in the transmission of predictive-like information in human observers. Indeed, enhanced alpha synchronization in the conservative vs. liberal condition underlies a magnified prior-dependent regulation of pre-stimulus alpha amplitude. This synchronization shift may induce a modulatory effect on the levels of inhibition in the sensory cortex, making it more difficult (vs. easier) for the internal response to subsequently overcome the decision criterion. Therefore, these results point toward a crucial role of parieto-occipital interaction in exploiting perceptual expectations through controlling the level of excitation of visual areas (indicated by modulation of alpha amplitude). On the contrary, the results indicated that theta synchronization may play a diametric role in predictive processes since increased phase aligning in the liberal vs. conservative condition inhibits the prior-based differentiation of pre-stimulus alpha amplitude. Fronto-parietal theta coupling has been related to a performance monitoring system in context that require increased cognitive efficiency (López et al., 2019; Nurislamova et al., 2019). Although early studies focused on the reactive role of theta rhythm (i.e., increase after the occurrence of a cognitively challenging event), recent evidence shows that theta regulation can also be employed proactively, pre-setting the system to be sensitive to cognitively demanding events (Cooper et al., 2015) and especially when preparing to override a pre-potent response tendency (Cavanagh et al., 2013; van Noordt et al., 2017). For example, theta increase in the frontal areas act as an inhibitory control mechanism that reduce the influence of salient attribute in value-based decision making that predicts regulatory success (HajiHosseini and Hutcherson, 2021). Crucially and in agreement with what we have observed, theta oscillations are able to interplay with alpha parameters in posterior regions to implement high-level processing (Jiang et al., 2018; Min and Park, 2010; Popov et al., 2018). Thus, these results suggest that the exploitation of predictive models might be overseen by an executive mechanism traveling at slower frequencies that monitors and controls the process. Why is this dynamic required mainly in the liberal condition? The human cognitive system has an inherent bias that tends to conservative criterion placement (Rahnev and Denison, 2018) since missing the target is less detrimental than incurring frequent false alarms (Zenger and Fahle, 1997). Thus, it can be hypothesized that under conditions in which this error is more likely to emerge, a higher level of control could be required. Moreover, there is a close link between frontal functionality and false alarms (Festini and Katz, 2021) as frontal damages are associated with the establishment of a liberal response bias (Biesbroek et al., 2015).

Finally, the existence of neural mechanisms involved in the facilitation vs. attenuation of predictive processing prompted the investigation of their ability to intercept interindividual differences in prediction handling. Specifically, individuals lie along a continuum of predictive styles at the poles of which stand the decision makers who are more inclined to use prior information vs. the observers who adopt an empirical strategy that dampens prior information in favor of sensory inputs. We have assumed that the latter (*empiricists*) would be characterized by intense use of the predictive control mechanism, placing the sensory cortex in a state of waiting for stimulation rather than prompting it in a particular state of excitability. In contrast, prior-prone individuals (*believers*) might use an intense bias mechanism in visual cortex to modulate perception in an expectation-congruent modality. Using a median split approach, we partitioned the sample according to the prior-relation alpha amplitude modulation. We demonstrated that individuals who weakly set the posterior alpha amplitude as a function of expectation showed reduced propensity to biased response coupled with an increase in fronto-parietal theta synchronization in the liberal condition. This modulation was abolished in the high alpha modulator group, which instead are characterized by a greater response bias paired with a general increase in parieto-occipital coupling in the alpha band and enhanced alpha synchronization in conservative trials compared with the liberal condition. These findings aided us in tracing the neural mechanisms potentially underlying the differences in predictive style existing in the general population. Interestingly, the two groups do not show dissimilarity in sensitivity index (d’). Hence, in the experimental context explored, both approaches succeed in ensuring adaptive behavior. Future studies should investigate whether in settings in which prior models are hyper (vs hypo) accurate (e.g., 90 vs 55% of predictive power), objective performance may diverge depending on the predictive strategy employed. Furthermore, the under-exploitation (vs. over-exploitation) of the mapped neurofunctional mechanisms could account for the behavioral failures observed in some clinical populations that are placed at maladaptive extremes of the predictive continuum (Tarasi et al., 2022d). For example, reduced alpha synchronization could underlie the reduced use of prior information observed in autism (Pellicano and Burr, 2012b), whereas a deficit in theta alignment could explain the lack of supervision in the utilization of priors in hallucinators (Corlett et al., 2019).

Conclusion

To sum up, the current work investigated the processes behind predictive perception showing how expectations are integrated into the human perceptual process. Results indicate that prior knowledge shapes the content of perceptual representations rather than their fidelity and that this process is enacted through a preparatory mechanism that modulates cortical oscillations, particularly in the alpha band, in perceptual regions. Inter-areas communication along the fronto-parietal-occipital pathway is crucially linked to this strategic tuning of sensory area activity and in explaining inter-individual differences in the way prior knowledge is used. Specifically, fronto-parietal theta coupling would mediate a supervisory process of the predictive machinery (enhanced in prior-resistant individuals), whereas parieto-occipital alpha synchronization would underpin the conveyance of expectation-like information (enhanced in prior-prone individuals).

Study 5: Neural Signatures of Predictive Strategies Track Individuals Along the Autism-Schizophrenia Continuum

from the published manuscript:

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Abstract

Background and Hypothesis

Humans develop a constellation of different representations of the external environment, even in the face of the same sensory exposure. According to the Bayesian framework, these differentiations could be grounded in a different weight assigned to prior knowledge vs. new external inputs in predictive inference. Since recent advances in computational psychiatry suggest that autism (ASD) and schizophrenia (SSD) lie on the two diametric poles of the same predictive continuum, the adoption of a specific inferential style could be routed by dispositional factors related to autistic and schizotypal traits. However, no studies have directly investigated the role of ASD-SSD dimension in shaping the neuro-behavioral markers underlying perceptual inference.

Study Design

We used a probabilistic detection task while simultaneously recording EEG to investigate whether neurobehavioral signatures related to prior processing were diametrically shaped by ASD and SSD traits in the general population (n = 80).

Study Results

We found that the position along the ASD-SSD continuum directed the predictive strategies adopted by the individuals in decision-making. While proximity to the positive schizotypy pole was associated with the adoption of the predictive approach associated to the hyper-weighting of prior knowledge, proximity to ASD pole was related to strategies that favored sensory evidence in decision-making.

Conclusions

These findings revealed that the weight assigned to prior knowledge is a marker of the ASD-SSD continuum, potentially useful for identifying individuals at-risk of developing mental disorders and for understanding the mechanisms contributing to the onset of symptoms observed in ASD and SSD clinical forms.

Keywords: Alpha oscillations, Perceptual decision-making, Predictive coding, Computational psychiatry

Introduction

The Bayesian approach conceptualizes the brain as an inferential organ(Helmholtz, 1867) that optimizes perception by integrating sensory information coming from the outside world with prior knowledge structured through experience. This framework aids in understanding the generative mechanisms underpinning the constellation of predictive styles observable in the general and psychiatric populations, that would derive from a different weight each individual assigns to priors vs. new sensory information(Corlett et al., 2019; Pellicano and Burr, 2012b). In a recent paper(Tarasi et al., 2022a), we shed light on these inter-individual differences by identifying predictive styles marked by the tendency to overweight vs underweight prior information. Using a probabilistic detection task, we induced a perceptual expectation by informing the participants, on a trial-by-trial basis, about the probability of target occurrence. We demonstrated that prior knowledge does not affect objective performance (i.e., sensitivity and drift rate). Instead, it induces a significant shift in response strategy, being more liberal for highly expected target trials and more conservative for low expected target trials. Crucially, we observed significant variations in the magnitude of bias shifting across participants, testifying that there is wide heterogeneity regarding the weight assigned to prior knowledge within the general population. At the neural level, the amplitude of the posterior alpha oscillations (8-14 Hz) allowed us to intercept these inter-individuals' differentiations: participants (*believers*) who exhibited a massive suppression in the amplitude of alpha oscillations in the high- versus low-probability condition showed a concurrent strong bias shift, whereas individuals (*empiricists*) who exhibited a reduced modulation of alpha amplitude showed a dampened criterion shifting. These findings are in the vein of recent studies revealing that alpha desynchronization is associated with decision-making confidence(Samaha et al., 2017b), visual awareness(Benwell et al., 2022a), and bias in reporting target-presence(Limbach and Corballis, 2016), but is not associated with increased perceptual performance(Bertaccini et al., 2023; Di Gregorio et al., 2022; Tarasi and Romei, 2023).

However, we did not investigate which factors might drive the adoption of a particular predictive strategy. According to the autism-schizophrenia continuum model(Tarasi et al., 2022d), the cognitive-perceptual styles observable in the Autistic Spectrum Disorder (ASD) and in the Schizophrenic Spectrum Disorder (SSD), may represent one of the critical determinants in this process. ASD has been associated to overweighting of external evidence compared to prior knowledge(Karvelis et al., 2018b; Van de Cruys et al., 2014b). For example, perception in individuals with high autistic traits is more constrained by the stimulus objectively displayed rather than expectations about its presence(Joshua C. Skewes et al., 2015b). Moreover, ASD relies less on anticipatory neural response in multisensory integration tasks(Ronconi et al., 2023) and did not show posterior alpha desynchronization to behaviorally-relevant targets(Keehn et al., 2017). In contrast, in SSD, ill-adaptive perceptual inference would be due to overweighted priors over sensory evidence(Kafadar et al., 2022; Schmack et al., 2013). Powers et al.(2017) identified that, in a visual-auditory conditioning task, the number and confidence of conditioned hallucinations were positively correlated with the severity of hallucinations, and that this inclination relies on the overweighting of priors' information in the perceptual process. A comparable result was obtained in individuals at high clinical risk for psychosis who showed behavioral performance consistent with the presence of hyper-precise priors(Kafadar et al., 2020). Moreover, an abnormal modulation of alpha activity has been related to maladjustment expectation in social interaction in schizophrenic patients(Billeke et al., 2015).

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

Methods

Participants

80 participants (43 female, age range 18-35) completed a visual detection task (Fig.1A) in which prior knowledge was manipulated by inducing expectations of target probability. All participants signed a written informed consent prior to take part in the study, which was approved by the Bioethics Committee of the University of Bologna. Part of the sample (n=66) is drawn from a previously published dataset(Tarasi et al., 2022a).

Computational modeling on decision-making process

Both Signal Detection Theory (SDT)(Green and Swets, 1966) and Drift Diffusion Model (DDM)(Wiecki et al., 2013) were used to unravel which decision-making parameter was influenced by prior information. The SDT measures *d'* (sensitivity) and *c* (criterion) were calculated based on the proportion of hits and false alarms separately for trials preceded by low, high, or medium probability cues (See Table S1). A rm-ANOVA was employed to investigate a cue-related effect on SDT indices. The following DDM parameters were allowed to vary according to conditions: drift rate, distance between decisional bounds, starting point of the accumulation process. Traces of model parameters and their autocorrelation have been inspected to evaluate that the models had properly converged.

EEG analysis

In order to confirm the central role of alpha oscillations in tracking the voluntary modulation of decision bias, we have replicated the EEG analyses strategy performed in our previous study(Tarasi et al., 2022a) with this enlarged sample by 1) conducting a time-frequency analysis on the amplitude difference between high- and low-probability trials and 2) assessing whether the degree of criterion shifting due to prior knowledge was related to pre-stimulus alpha amplitude modulation. Moreover, building from the previous work, we separated the participants as a function of their prior-based pre-stimulus differentiation in alpha amplitude, to investigate whether large vs. small modulation of alpha could underlie the differences in the predictive style adopted.

Specifically, for each individual, the mean alpha (~8 - 14 Hz) amplitude value in the pre-stimulus time (~-400 - 0 ms) was considered and the *Δ alpha amplitude* was computed by taking the difference between the alpha amplitude extracted in low- and high-probability trials. This metric was used to delineate two types of predictive styles: the *believers* (i.e., individuals showing an above-median Δ alpha amplitude) and the *empiricists* (i.e., individuals showing a below-median Δ alpha amplitude). To reconfirm that the two clusters of individuals showed specific differentiation related to bias-shift, we assessed with an independent-samples t-test whether the SDT and DDM indices were differently modulated by the group factor.

Autism-schizophrenic continuum

The autistic traits in our sample were measured using the Autism-Spectrum Quotient test (AQ) (Simon Baron-Cohen et al., 2001), while schizotypy was assessed using the Schizotypal Personality Questionnaire (SPQ) (Raine, 1991). An independent-samples t-test was employed to explore which specific subscales of the AQ and SPQ had different magnitude between the group of believers and empiricists. Moreover, in order to identify where individuals on the autism-schizophrenia axis lay, a principal component analysis (PCA) was performed on the correlation matrix of the AQ and SPQ subscales. The first two principal components were extracted and the second one (PC2) was selected for subsequent analyses because, according to previous literature (Del Giudice et al., 2014; Dinsdale et al., 2013; Nenadić et al., 2021; Zhou et al., 2019), it is supposed to capture the diametric relationship between these two conditions. Then, to assess whether the predictive style adopted by the participants could be related to the individual position along the autism-schizophrenia axis, independent-sample t-tests were employed to investigate whether the individual PC2 score showed statistically significant differences between the believers and empiricists group. We checked that the results obtained from the median-split analysis remained valid even when using the continuous variables Δ alpha amplitude and Δ criterion as dependent variables and the PC2 score as a predictor. Finally, a mediation analysis was conducted to probe effects of ASD-SSD continuum factor on Δ criterion, mediated by any effects exerted by it on *Δ alpha amplitude* regulation. All the analyses were carried out with standardized values for all the variables, and we report 95% confidence interval based on 5000 bootstrap iterations (bias-corrected).

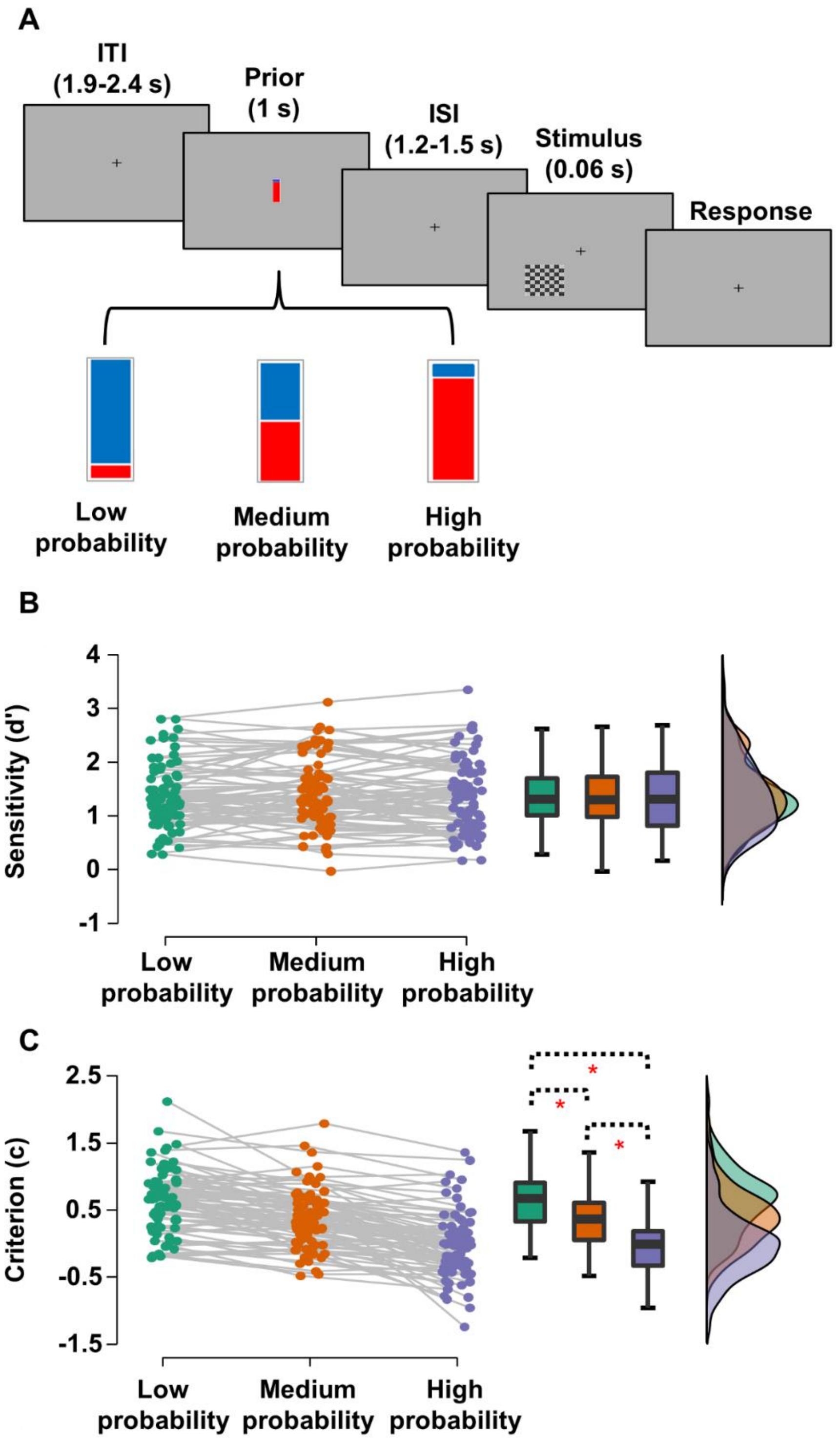

Figure 1.

A. Each trial started with the appearance of the cue presented at the centre of the screen for 1 s. The cue was a bar with its bottom colored in red and its top colored in blue. The amount of red in the bar indicated the probability of target's occurrence. High and low cue indicated the probability of target occurrence of 67 and 33%, respectively. Instead, the neutral cue equally predicted (50%) the target presence and absence. After a *variable delay of 1.2–1.5 s a checkerboard containing (or not) grey circles appeared on the monitor. Participants pressed with the right hand the button associated with the choice. After response collection, the screen turned black for 1.9-2.4 s. The actual probability of target presentation was in accordance with the probability indicated by the cue, and participants were informed of this.*

B. Prior information had no effect on perceptual sensitivity. C. On the contrary, the probabilistic cue shaped the decision criterion that gradually became more liberal as the probability of target presentation increased.

Results

Expectations modulate decision-making strategies

We computed the SDT indices *d'* and *c* to investigate the effect that prior information has on perceptual decision-making (Fig.1). The conducted analysis replicates the previous study by showing that priors affected the criterion ($F_{2,158} = 88.73; p < 0.01; \eta_p^2 = 0.53$) but not the sensitivity ($F_{2,158} = 1.22; p > 0.30; \eta_p^2 = 0.015$). Specifically, the participants adopted a more liberal criterion in trials preceded by high-probability cue ($c_{high} = - 0.02 \pm 0.05$) relative to trials preceded by medium- ($c_{mid} = 0.37 \pm 0.05$; $t_{79} = -9.76, p < 0.01; d = -1.10$) and low-probability cue ($c_{low} = 0.63 \pm 0.05$; $t_{79} = -9.87, p < 0.01; d = -1.10$), in which the criterion were located in more conservative position relative to the neutral condition ($t_{79} = 7.15, p < 0.01; d = 0.80$). DDM parameters confirm these patterns of results: individuals increased the starting point in the high-probability trials relative to both medium- ($q < 0.01$) and low-probability trials ($q < 0.01$) and lowered the starting point in the low- relative to medium-probability trials ($q < 0.01$). We found no difference in the others DDM parameters.

Alpha oscillations track human decision-making strategies

We corroborated that the low- versus high-probability condition were associated to a different suppression of alpha amplitude in posterior regions. Moreover, we assessed how individual differences over the tendency to shape alpha oscillations modulated the effect that prior exerted in decision-making. To this end, we partitioned the sample, through a median split approach (Fig.2A), between those who exhibited a strong reduction in alpha amplitude in the high- compared with the low-probabilty condition (i.e., the *believers*) versus those who showed a more nuanced modulation (i.e., the *empiricists*). The two groups showed different decision-making profiles:

the prior-dependent modulation of the decision criterion (Δ criterion $_{\text{believers}} = 0.88 \pm 0.10$, Δ criterion $_{\text{empiricists}} = 0.42 \pm 0.07$; $t_{78} = 3.78, p < 0.01; d = 0.85$) were greater in individuals prone to shifting alpha amplitude (Fig.2B), while the sensitivity ($d'_{\text{believers}} = 1.41 \pm 0.10$; $d'_{\text{empiricists}} = 1.35 \pm 0.09$; $t_{78} = 0.40, p > 0.70; d = 0.09$) were not distinguishable between the two groups. This result was also supported by Pearson's correlation, which demonstrated that the degree of alpha modulation correlates positively with the level of Δ criterion. Furthermore, we verified that the alpha effect in tracking predictive styles is spatially localized to electrodes contralateral to stimulus presentation (Fig.2C). These findings proved the reliability of alpha fluctuations in detecting the different weights that prior knowledge plays in establishing decision-making biases in the general population.

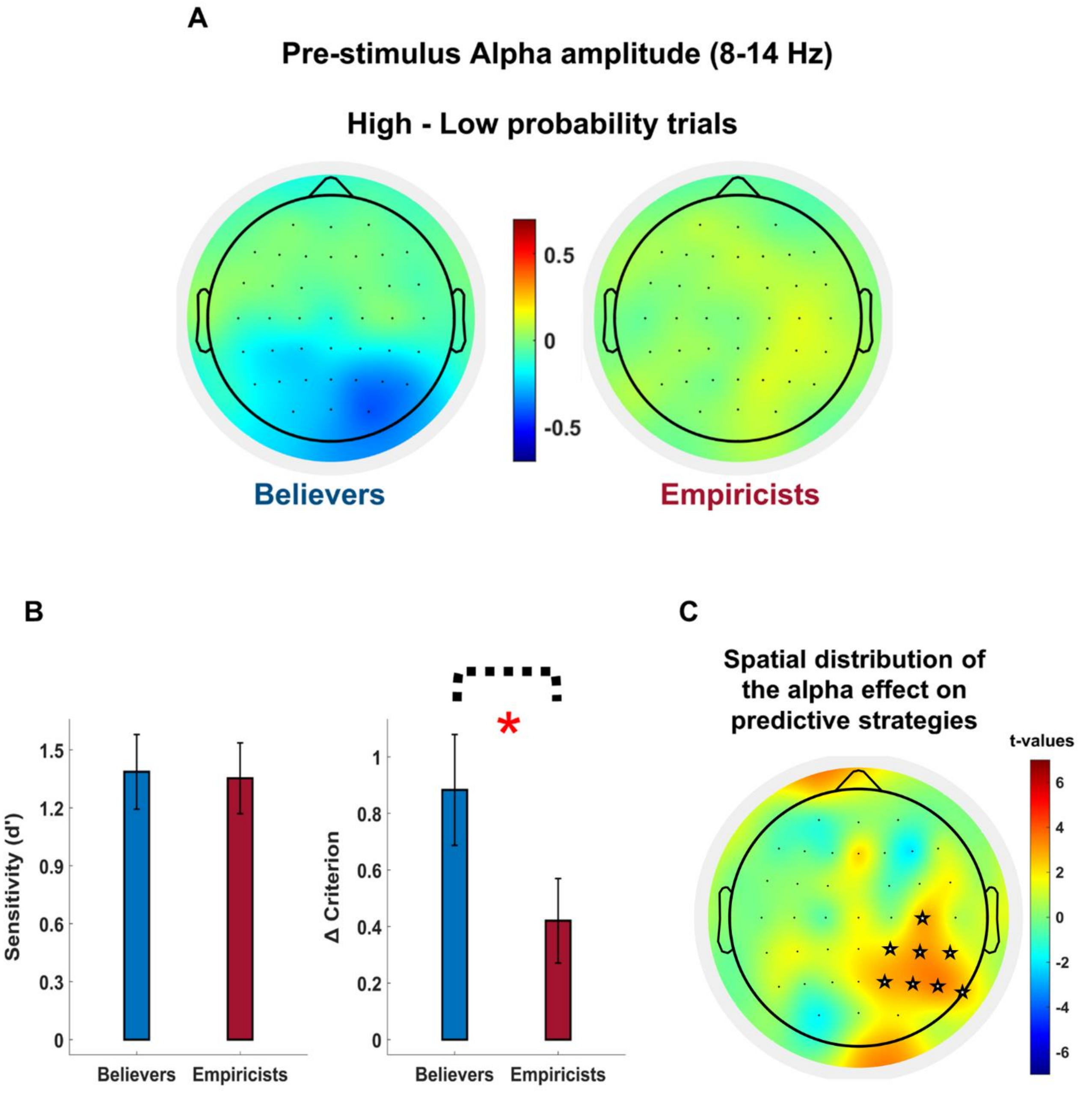

Figure 2. Electrophysiological correlates of prior processing.

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

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

To test whether individual position along the ASD-SSD axis could intercept the predictive style employed, we used principal component analysis to extract the component (i.e., PC2) showing opposite loading between the AQ and SPQ subscales. Then, we evaluated whether the PC2 individuals scores were significantly different between believers and empiricists. The independent sample t-test conducted showed the presence of a significant difference in the PC2 scores ($PC2_{believers} = 0.26 \pm 0.17$, $PC2_{empiricists} = - 0.26 \pm 0.13$; $t_{78} = 2.39$, $p = 0.02$; $d = 0.54$), proving that the believers were closer to the positive schizotypal end of the continuum, whereas the empiricists were more shifted toward the autistic pole of the continuum (Fig.3; Fig.S7).

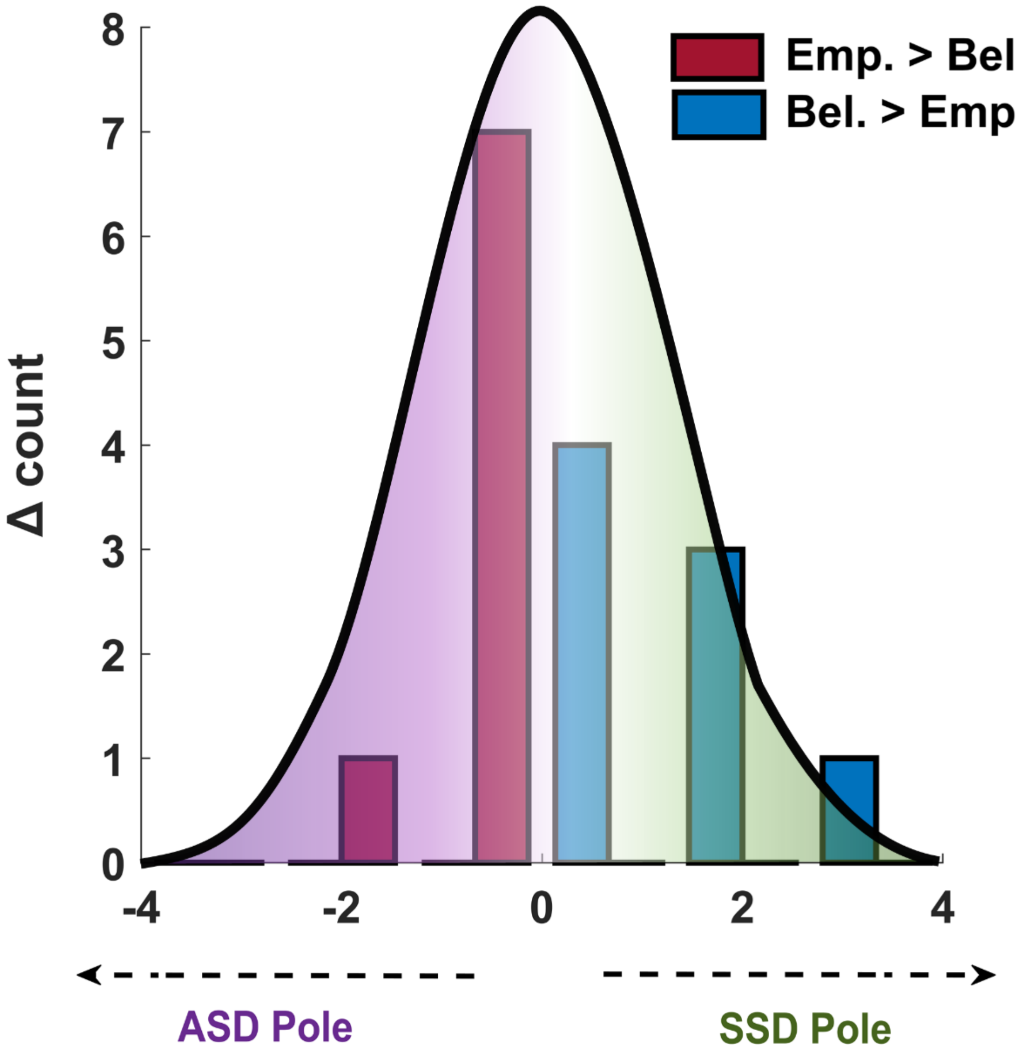

Figure 3. The position along the ASD-SSD continuum directs the adoption of the predictive strategy.

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

A very similar pattern of results emerged when comparing the AQ and SPQ subscale scores in the believers' group versus the empiricists' group: autistic and negative schizotypal traits exhibited a similar pattern of decision-making tendencies, being more prominent in the empiricist group (Fig. 4A); conversely, positive schizotypal traits (e.g., magical thinking) were more present in the believers' group (Fig. 4B).

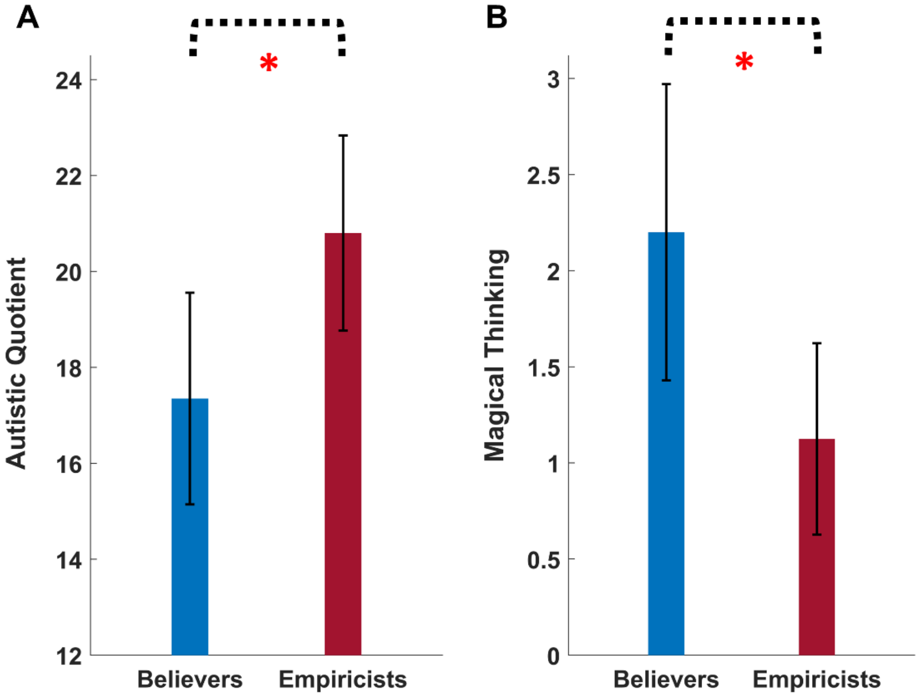

Figure 4. Positive autistic and schizotypal traits discriminate believers from empiricists.

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

Correlation analysis

To corroborate the results obtained from the median-split analysis, we also showed that the PC2 score is significantly correlated with Δ alpha amplitude (Fig.S8; $r = 0.24$, $p = 0.03$), proving that the closer the individuals are to the schizotypal (vs. autistic) pole of the continuum, the more (vs. less) biases their alpha amplitude in a prior-dependent fashion. Similarly, we demonstrated the presence of a positive relationship between proximity to the schizotypal pole and the magnitude of criterion modulation in the high- vs. low-probability condition (Fig.S8; $r = 0.28$, $p = 0.01$). Then, we performed a multiple linear regression analysis to better understand the relation between these variables by placing the ASD-SSD continuum factor, the Δ Alpha Amplitude and the interaction between these two variables as predictors of Δ criterion. The analysis showed that the regression was significant ($F_{3,76} = 4.94$, $p < 0.01$), with both Δ alpha amplitude ($\beta = 0.26$, $p = 0.02$) and the ASD-SSD continuum factor ($\beta = 0.33$, $p = 0.02$) [but not their interaction ($\beta = -0.18$, $p = 0.17$)] emerged as significant predictors of the prior-based modulation of the decisional criterion (Δ criterion).

Mediation analysis

To further understand the inter-relation between ASD-SSD continuum factor, Δ criterion and Δ Alpha Amplitude, we conducted a mediation analysis to examine whether Δ Alpha Amplitude mediated any effect that the ASD-SSD continuum factor exerted on the Δ criterion (Fig.5). We found a significant mediation effect (0.04, 95% CI: 0.001 – 0.083), whereby relatively greater Δ Alpha Amplitude mediated the positive association between ASD-SSD continuum factor and Δ criterion (i.e., lower Δ criterion in individuals closer to the ASD pole). Moreover, the analysis showed that there was significant residual direct effect of ASD-SSD continuum factor on Δ criterion (0.13, 95% CI: 0.003 – 0.256) suggesting that the impact of ASD-SSD continuum factor on Δ criterion are partially mediated by the Δ Alpha Amplitude.

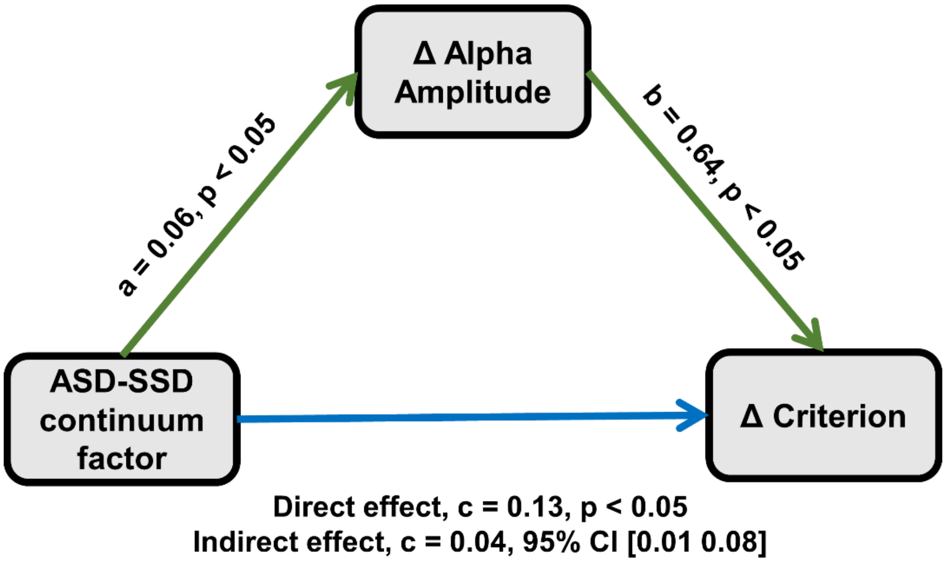

Figure 5. Mediation Analysis

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

Discussion

Humans develop a constellation of different representations of the external world, even in the face of the same sensory experience (Benwell et al., 2022; Karlaftis et al., 2019). According to the Bayesian framework, these differentiations could be grounded on a different integration of prior knowledge with new information coming from the external world: some people are more prone to base their inferences on accumulated models and experiences, while others tend to rely more on input presented in the here and now. In this research, we explored whether these different predictive styles could be also routed by dispositional factors related to autistic and schizotypal traits. In accordance with the autism-schizophrenia continuum model (Tarasi et al., 2022), ASD and SSD are associated with a diametrical behavioral/cognitive pattern resulting from a distinct weight given to priors and new sensory information (Andersen, 2022; Tarasi et al., 2021; Ursino et al., 2022). Positive SSD symptoms tend to be associated with priors-driven perception (Powers et al., 2016; Schmack et al., 2013; Stuke et al., 2021) and opposition toward evidence that contradicts preconceived beliefs (Woodward et al., 2007), whereas ASD is characterized by overweighting of external evidence (Brock, 2012; Karvelis et al., 2018) compared to prior knowledge (Schneebeli et al., 2022; von der Lühe et al., 2016). Therefore, we expected that adopting a predictive style that overweights vs. underweights prior models may be prompted by a predominance of schizotypal vs. autistic traits, respectively.

To investigate these hypotheses, we used data from humans performing a probabilistic detection task, while non-invasively recording their neural activity using EEG. We have shown that providing prior knowledge about the target probability created a strong response bias in human observer, without affecting their visual sensitivity. However, the degree of bias-shifting was highly different among participants. Using the electrophysiological data collected, we were able to identify a neural signature that distinguish individuals that overweight (*believers*) vs. underweight (*empiricists*) expectation-like information in perceptual inference: *believers* showed extensive shaping of alpha oscillations in perceptual regions, while *empiricists* showed a reduced modulation. This finding proves that alpha rhythms are a reliable electrophysiological index able to discriminate participants' predictive behavior, confirming the role this frequency band plays in shaping perceptual outcomes (Cecere et al., 2015; Di Gregorio et al., 2022; Ippolito et al., 2022; Romei et al., 2010; Ronconi et al., 2018; Samaha et al., 2020). According to the SDT framework, observers evaluate the presence vs. the absence of the stimulus by assessing whether the strength of the internal responses exceeds the decisional criterion. Following this framework, a voluntary regulation of pre-stimulus alpha oscillations could impact the criterion through a modulation of the excitability of the cerebral cortex (Jensen and Mazaheri, 2010). The reduction of alpha amplitude in high- vs. low-probability trials would increase the cortical excitability that, in turn, would magnify the strength of the internal responses making it easier to exceed the decisional criterion (Foxe and Snyder, 2011; Iemi et al., 2017; Samaha et al., 2020; Tarasi et al., 2022).

Importantly, we analyzed whether individuals adopting the believer vs. empiricist strategies showed differences in schizotypal vs. autistic traits. First, we performed a PCA to extract the dimension showing opposite loading between the AQ and SPQ subscales. The conducted analysis showed that the second component (PC2) showed diametrical saturations with the positive schizotypal and autistic scales, confirming the opposite nature between these two dimensions (Del Giudice et al., 2014; Dinsdale et al., 2013; Nenadić et al., 2021; Zhou et al., 2019). Crucially, we identified that PC2 scores were statistically different in the two groups: the empiricists showed negative mean values (i.e., they were more shifted toward the ASD pole), while the believers showed more positive values (i.e., they were more shifted toward the SSD pole).

It is important to emphasize that these findings contrast with some evidence pointing toward an opposite effect linked to reduced prior processing in SSD (Valton et al., 2019), as reflected by the reduced susceptibility to expectancy-driven illusions (e.g. the hollow-mask illusion (Dima et al., 2009)). This conflicting evidence could be interpreted through a hierarchical model of predictive coding (Schmack et al., 2017; Sterzer et al., 2018;

Stuke et al., 2019; Tarasi et al., 2022). According to this proposal, the weight assigned to predictive information in SSD could be subordinate to the hierarchical level from which it is generated: whereas predictions generated at lower levels of the cortical hierarchy (e.g., sensory areas) would have reduced precision, higher-order beliefs and explicit prior information (like the one employed in the current study) would be hyper-processed in the SSD population (Haarsma et al., 2020; Schmack et al., 2013).

Furthermore, we corroborated the results highlighted by the PCA analysis by investigating the contribution of AQ and SPQ subscales in orienting the adoption of predictive styles. First, we demonstrated that participants within the believers group manifested less autistic and negative schizotypal traits compared to the empiricists. The finding that negative schizotypal traits share similarities in cognitive style with autistic traits is in line with empirical research showing the presence of comparable cognitive and perceptual phenomena that tie these two dimensions together. For example, both negative schizotypy and autistic traits predicted weaker rubber hand illusion effects (Ide and Wada, 2017; Torregrossa and Park, 2022). Subsequently, we showed that believers manifested higher rate of positive schizotypal traits relative to the empiricists. In particular, magical thinking was the subscale of the SPQ that was most strongly expressed in the believers' group. Magical thinking is connected with increased susceptibility to psychosis (Chapman et al., 1994), anti-scientific attitudes (Tarasi et al., 2023), illusory perception (Elk, 2013; Peled et al., 2000; Riekki et al., 2013), and it is genetically connected to schizophrenia (Saarinen et al., 2022). Crucially, participants with higher magical ideation tend to rely on a limited amount of objective evidence to construct meaningful models, which are also overestimated (Brugger and Graves, 1997), and showed decreased activity in the cognitive evaluation network during the processing of evidence that contradicts a belief (Lavigne et al., 2020). Following these lines, a higher number of magical thinking would favor the adoption of the believer's style due to the propensity to promote the overestimation of the precision of prior knowledge, such as the expectation-like information provided in the task, at the expense of incoming information.

Finally, to better understand the relation between ASD-SSD continuum factor, Δ criterion and Δ Alpha Amplitude, we conducted a mediation analysis which proved that the influence exerted by the position along the

ASD-SSD continuum on behavior was mediated by the degree of alpha amplitude modulation. This finding suggests that ASD and SSD traits could shape the use of probabilistic priors through opposite modulation on alpha wave amplitude (Martínez et al., 2019).

The described results fit into the growing literature aimed at identifying the behavioral and electrophysiological signatures underlying bayesian processing (Bastos et al., 2020; Betti et al., 2021; Dzafic et al., 2021; Friedrich et al., 2022) and inter-individual differences in the predictive machinery (Andersen, 2022; Powers et al., 2018; Sterzer et al., 2018; Tarasi et al., 2022). For the first time, we have demonstrated that the position along the ASD-SSD continuum directs the predictive strategies adopted by individuals. This is particularly important because it shows that, even within the general population, it is possible to trace signs of the presence of different approaches toward predictive inference that depends on sub-clinical personality traits. Future studies should investigate whether the directionality of the effect played by position along the ASD-SSD continuum is maintained even when interoceptive priors are introduced, given their role in modulating decision-making outcomes (Migeot et al., 2022; Salamone et al., 2021). It should be noted that, in the task employed, both strategies led to the same result in terms of accuracy. For this reason, we conceive these styles as two different, but equally valid, strategies within the proposed experimental set-up. Follow-up studies should investigate whether different contexts can elicit performance gains/losses as a function of the predictive style promoted by the ASD and SSD traits. For example, the tendency to favor the believer predictive style would explain why positive schizotypal traits were correlated with a performance advantage when the prior knowledge aid to interpret a highly ambiguous bottom-up signal (Teufel et al., 2015), whereas the tendency to favor the empiricists predictive style would explain why AQ traits favor the perception of specific details when they are contained in global patterns (Conson et al., 2022; Cribb et al., 2016; Russell-Smith et al., 2012). Moreover, since these peculiarities in information processing and in neural regulation are already evident in the sub-clinical population, they could be important factors both in identifying markers that signal early risk toward the development of mental disorders, and in understanding the mechanisms contributing to the onset of manifest clinical forms along the ASD-SSD continuum. In this regard, it would be crucial for future studies to evaluate the behavioral and neural indices outlined involving patients with positive SSD symptoms and ASD patients. This would allow to evaluate the developmental trajectory of predictive strategies, assessing whether they become more rigid, inflexible, and context-independent as one approaches the ends of the continuum.

Study 6: Antivax attitude in the general population along the autism-schizophrenia continuum and the impact of socio-demographic factors.

from the published manuscript:

Tarasi, L., Borgomaneri, S., & Romei, V. (2023). Antivax attitude in the general population along the autism-schizophrenia continuum and the impact of socio-demographic factors. *Frontiers in Psychology*, *14*, 1059676.

Abstract

One of the most important inventions in human history is vaccines. However, to date a consistent amount of people exhibit a hesitant approach towards them and mixed results have emerged in the attempt to characterize which factors may play a role in predicting such negative attitude. Here, we aimed at investigating how the individual scoring along the autism-schizophrenic continuum component and socio-cultural factors (such as gender, education level and age) contribute towards vaccination attitudes in the general population. Multiple regression analysis revealed that the closer the individual lied on the positive schizotypal pole, the higher was their negative attitude toward vaccines. A diametric, more favorable disposition was found for individuals closer to the autistic end of the continuum. Furthermore, we reported that among the socio-cultural factors, only age can be considered a significant predictor of vaccination attitudes, with younger participants showing a more positive attitudes toward vaccination, while the level of education is an important protective factor in mitigating the negative impact that the proximity to the SSD pole and age play against vaccination disposition. These findings are relevant to improve targeted public health interventions, highlighting the crucial role of demographic, psychological, and social correlates in predicting anti-vax beliefs, which have the devasting potential to increase the spread of infectious disease.

Introduction

The development of vaccines has represented one of the most important innovations in the history of humanity and medicine, helping to prevent an estimated 3.5-5 million deaths each year (World Health Organisation, 2022). The relevance of vaccination became even more tangible with the emergence of the COVID-19 pandemic as the world's attention focused on the development of a new vaccine capable of contrasting this virus. Despite the unquestionable value of vaccines in counteracting the spread and reducing the number of hospitalizations and deaths due to virus-related infectious diseases (Bernal et al., 2021), a sceptical attitude toward vaccines and vaccination campaigns implemented by governments around the world is widespread in the general population (Freeman et al., 2020). In this regard, the concept of "hesitancy" has been defined as the behaviour of "delaying acceptance or refusal of vaccines despite the availability of vaccine services" (SAGE Working Group on Vaccine Hesitancy, 2014) and, recently, it has been included in the top-10 threats to global health (World Health Organisation, 2019). This hesitant approach has important practical repercussions at both individual (e.g., increased risk of suffering lethal effects from the virus) and socio-economic level (e.g., increased spending by health care systems) (Mullooly et al., 1994; Tenforde et al., 2021). In recent years, there are numerous lines of research investigating what factors determine attitudes toward vaccination (Yaqub et al., 2014). Research in this area is prompted by the fact that they represent serious risk factors regarding infectious diseases, as a negative attitude has been linked to actual vaccine uptake (Latkin et al., 2022). Socio-cultural factors, such as gender, education level and age appear to play a role in explaining vaccination attitudes (Bertoncello et al., 2020). However, the directionality of the effects is not fully understood due to the presence of mixed findings. For example, Chen et al. (2021) highlighted that the level of education was negatively associated with intention to vaccinate, whereas lower education levels were associated with vaccine hesitancy (Robertson et al., 2021) and higher conspiracy beliefs about COVID-19 (De Coninck et al., 2021) in other studies. Regarding gender, higher vaccine hesitancy rates (Morales et al., 2022) and lower vaccine intention (Zintel et al., 2022) have been reported in women compared to men, but opposite results are also reported. For example, in Latin America, the Caribbean, and high-income countries, women reported being less hesitant than men (Flor et al., 2022). Regarding the influence of age, some studies have highlighted that vaccine hesitancy was higher in younger age groups (Robertson et al., 2021) but others pointed in opposite direction showing that age was positively associated to vaccine hesitancy (Moscardino et al., 2022; Ouyang et al., 2022).

These mixed results could be due to the fact that vaccine attitude differs across time, country, and vaccine type. Thus, a variable predicting a particular vaccination attitude in a given context could cease to make a difference when contingencies change. For example, a worldwide survey demonstrated that the European region is the least confident towards vaccine safety, while Bangladesh, Ecuador, and Iran reported highest agreement that vaccines are important (Larson et al., 2016). Moreover, sociodemographic variables may impact only specific dimensions of vaccine attitude. For example, education increases confidence in the importance and efficacy of the vaccine, but not safety (Larson et al., 2016).

In addition to socioeconomic and cultural elements, psychological factors such as personality traits, and beliefs appear to direct attitudes toward vaccines (Hornsey et al., 2018). Among these factors, a critical element in dictating vaccinal attitude could be the type of predictive style adopted by the individual. According to Bayesian brain theories, our perception/decision arises from an integration-like mechanism between externally derived signal (sensory evidence) ascending the cortical hierarchy in a bottom-up flow and signal derived from internal model (prior belief) that descends the cortical hierarchy in a top-down flow. The balanced integration of these two sources of information would lead to adaptive choice and behavior (Tarasi et al., 2022b). Crucially, there are clinical/sub-clinical manifestations in which the decision-making process leans overly toward priors or sensory evidence. For example, the autism-schizophrenia continuum model (Tarasi et al., 2022d) posits that autism spectrum disorders (ASD) and schizophrenia spectrum disorders (SSD) would be associated with a different weight assigned to top-down and bottom-up information (Andersen, 2022; Tarasi et al., 2021b; Ursino et al., 2022), resulting in behavioural/cognitive patterns pointing in opposite directions. Specifically, whereas prior information would be overweighted in positive SSD, input-based information would be the core upon which

ASD relies in decision making. The evidence for this diametricality is manifold: positive schizotypy (which is characterized by the presence of ideas of reference, magical/bizarre thinking and unusual perceptual experiences) tends to be associated to belief-driven perception (Schmack et al., 2013), less deliberate decision-making processes (Leer et al., 2015) and resistance towards evidence that goes against pre-established beliefs (Buchy et al., 2007), whereas people with high autistic-like traits are characterized by overweighting of external evidence (Van de Cruys et al., 2014b), detail-oriented processing approach (Alink and Charest, 2020c) and deliberate and logical thinking style (Brosnan et al., 2016; Lewton et al., 2019). Importantly, these peculiarities in the predictive style that characterize positive SSD and ASD could subserve a different disposition toward vaccines. Since higher levels of positive schizotypy and delusion proneness have been associated to anti-scientific beliefs (i.e., telepathy) (Raine, 1991), to conspiracy theory about COVID-19 (Acar et al., 2022; Larsen et al., 2021), to prior-driven perception (Schmack et al., 2013) and individuals with psychotic disorders tend to refuse COVID-19 vaccination more than the general population (Hassan et al., 2022), we hypothesize that individuals lying toward the positive SSD pole of the continuum may show a general negative attitude toward vaccines. Furthermore, it is possible to speculate that the propensity for deliberate processing and the tendency to gather much evidence before making a decision observed in ASD may be related to a positive attitude toward vaccination, as the adoption of a deliberative and analytical thinking style increases the inclination to reject COVID-19 conspiracy theories/theorists (Swami and Barron, 2021). Evidence in support of this hypothesis comes from populations with clinical autism that show higher odds of being vaccinated for COVID-19 (Shea et al., 2022; Weinstein et al., 2021). However, the adoption of a deliberative cognitive style devoted to information gathering (Brosnan et al., 2014; Quinde-Zlibut et al., 2020) neither eliminates the possibility of developing erroneous beliefs (Georgiou et al., 2021) nor automatically implies a positive approach to vaccination as this also depends, for example, on the type of source and information channels from which the evidence on which the attitude rests is drawn.

To shed light on these hypotheses, the present study aims to explore, for the first time, whether positive schizotypal and autistic traits predispose to a particular attitude toward vaccination as measured by the Vaccination Attitudes Examination (VAX) Scale (Martin and Petrie, 2017), by assuming that being closer to the positive schizotypal vs. autistic side of the continuum could favour a negative vs. positive attitude toward vaccination. In the study we will also consider the possible role that gender, education level, and age play in these relationships given their highlighted role in the literature in moderating vaccination attitudes.

Materials and Methods

Participants

268 (Female = 186) individuals within the general population took part in the study by completing an online form. All participants signed a written informed consent prior to taking part in the study, which was conducted in accordance with the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna. Participants provided their demographic data, such as age, gender and education. The age of the sample ranges from 18 to 76 (M = 27.13, SD = 11.67) while participants' years of education range from 13 to 25 (M = 20.06, SD = 2.32).

Measures

Schizotypal traits

Subclinical traits associated with the SSD were measured with the Schizotypal Personality Questionnaire [SPQ, (Raine, 1991)]. This self-report questionnaire is composed of 74 questions divided in 9 subscales (ideas of reference, magical thinking, social anxiety, unusual perceptual experiences, constricted affect, no close friends, odd behavior, odd speech and suspiciousness) that can be further organized in 3 main factors (cognitive-perceptual, interpersonal and disorganization) in which participants are asked to answer questions regarding different aspects of their personality, behavioral preferences and cognitive styles, in addition to questions concerning sensorial experiences and beliefs, with “Yes” or “No” statements. We used the original scoring methods, assigned the response a binary code (no = 0; yes = 1).

Autistic traits

We used the Autism-Spectrum Quotient test [AQ (Simon Baron-Cohen et al., 2001a)]. This self-report questionnaire is composed of 50 questions divided in 5 subscales in which participants are asked, similarly to the

SPQ, to answer questions regarding different aspects of their personality, behavioral preferences, cognitive styles, as well as potential discomfort connected to specific sensorial experiences. Each AQ subscale is composed by 10 items addresses a psychological feature present in ASD: imagination (assesses imaginative ability), communication (assessing the weakness in communication skills), social skills (assessing the presence of poor social skills), attention to detail (assessing the exceptional attention to detail), and attention switching (assessing poor attention switching ability/strong focus of attention). The sum of the scores obtained in each subscale provides a global score, with higher values indicating higher levels of autistic traits. We used the original scoring methods, converting each item into a dichotomous response (agree/disagree) and assigned the response a binary code (0/1).

Autism-schizophrenic continuum

To identify the autism-schizophrenia axis, a principal component analysis (PCA) was performed on the correlation matrix of the AQ and SPQ subscales. To verify the adequacy of the dataset for the proposed analysis, the Kaiser-Mayer-Olkin (KMO) measure and the Bartlett's test were used. The first two principal components were extracted and we selected the second one which, according to previous literature (Del Giudice et al., 2014; Dinsdale et al., 2013; Nenadić et al., 2021; Zhou et al., 2019b), is supposed to capture the diametric relationship between these two conditions, as it is inversely loaded with schizotypal and autistic subscales.

Vaccination attitude

We used the 12-item Vaccination Attitudes Examination (VAX) scale (Martin and Petrie, 2017) to measures vaccine attitude. This self-report demonstrated good internal consistency, convergent validity, and construct validity (Wood et al., 2019). VAX is composed by four subscales (3 items each): mistrust of vaccine benefit (Vax-mistrust), worries about unforeseen future effects (Vax-worries), concerns about commercial profiteering (Vax-prof), and preference for natural immunity (Vax-natur). Responses are assigned by judging the degree of agreement with the twelve statements using a 6-level Likert scale (from "Strongly Agree" to "Strongly Disagree"). A higher score indicates more negative attitudes toward vaccinations.

Results

Analyses were conducted using SPSS 26 and RStudio v2021.

Principal component 2 tracks the diametric dimension between ASD and SSD.

To test whether individual position along the ASD-SSD axis could predicted vaccine attitude, we used principal component analysis (PCA) to extract the component showing diametric loading between the SPQ and AQ subscales. Bartlett's ($p < 0.01$) test and the Kaiser-Meyer-Olkin (KMO = 0.88) proved the adequacy of the data for the proposed analysis. According to previous literature, the second component condenses the dimensions that show a diametric pattern whereas the first component condenses the common features between these two personality traits. Our results pointed in this direction: the two components accounted for 53.5% of the variance, with the first dimension showing positive loadings with all subscales of the SPQ and AQ, especially the subscales indicating socio-communicative dysfunction. Conversely, the second component exhibited both negative and positive loadings with the two questionnaires. Specifically, the positive dimensions of the SPQ (ideas of reference, magical thinking and unusual perceptual experience) loaded positively on the second component, while all subscales of the AQ (except attention to detail) loaded negatively. Crucially, negative schizotypal subscales pointed in the same direction of the AQ dimensions. This psychometric results corroborate previous findings showing the presence of comparable cognitive and perceptual phenomena that tie these two dimensions together (Trevisan et al., 2020). This result confirmed the presence of a diametrical structure, with autistic traits and positive schizotypal traits placed at the opposite ends of a single continuum.

The position along the ASD-SSD continuum and Age predicted vaccinal attitude

We performed a series of multiple linear regression analyses (using the enter method) to understand the relation between the ASD-SSD continuum factor and demographical data with Vax scores (Table 1). Therefore, we placed the total Vax score or Vax subscales as the dependent variable and entered the PC2 scores (Fig. 1) and demographic indices as predictors. We found no multicollinearity problems in the multiple regressions conducted (max VIF value: 1.014).

The analysis showed that:

1) In the first regression, we entered Vax total score as the dependent variable. Results showed that the regression was significant ($F_{4, 263} = 5.52$, $p < .01$, $R^2 = .08$). As can be seen in Table 1, both the ASD-SSD continuum factor and Age emerged as significant predictors of a general negative attitude towards vaccination.

2) In the second regression, we considered as dependent variable the subscale Vax-mistrust. The regression was again significant ($F_{4, 263} = 2.44$, $p = .047$, $R^2 = .04$) but only the ASD-SSD continuum factor emerged as significant predictor of increased distrusting of vaccine benefit.

3) In the third regression, we considered as dependent variable the subscale Vax-prof. The regression was again significant ($F_{4, 263} = 5.11$, $p < .01$, Adj. $R^2 = .07$) with both the ASD-SSD continuum factor and Age predicting a greater tendency to have concerns about commercial profits related to vaccines. In addition, a trend very close to the statistical threshold emerged that pointed to a reduced tendency to associate vaccine spread as being motivated by economic rather than public health concerns as educational levels rise.

4) In the fourth regression, we considered as dependent variable the subscale Vax-worries. The regression was again significant ($F_{4, 263} = 8.44$, $p < .01$, $R^2 = .11$). Again, the ASD-SSD continuum factor and Age emerged as predictors of increased worry about vaccine-related future adverse events.

5) In the fifth regression, we considered as dependent variable the subscale Vax-natur. The regression showed only a trend toward statistical significance ($F_{4, 263} = 1.82$, $p = .12$, $R^2 = .03$), but the ASD-SSD

continuum factor significantly predicted a preference for natural exposure to viruses rather than through vaccination practices.

	Vax		**Vax-Mistrust**		**Vax-worries**		**Vax-profit**		**Vax-natural**	
	β	*p*	β	*p.*	β	*p.*	β	*p.*	β	*p.*
ASD-SSD continuum factor	**0.23**	**0.00**	**0.19**	**0.00**	**0.22**	**0.00**	**0.21**	**0.00**	**0.12**	**0.04**
Education	-0.06	0.34	0.01	0.80	-0.04	0.52	-0.11	0.07	-0.05	0.44
Gender	0.03	0.60	0.02	0.70	0.08	0.15	0.02	0.70	-0.03	0.66
Age	**0.16**	**0.01**	0.00	0.99	**0.25**	**0.00**	**0.14**	**0.02**	0.10	0.10

** β = Standardized beta; p = p-value.

Table 1

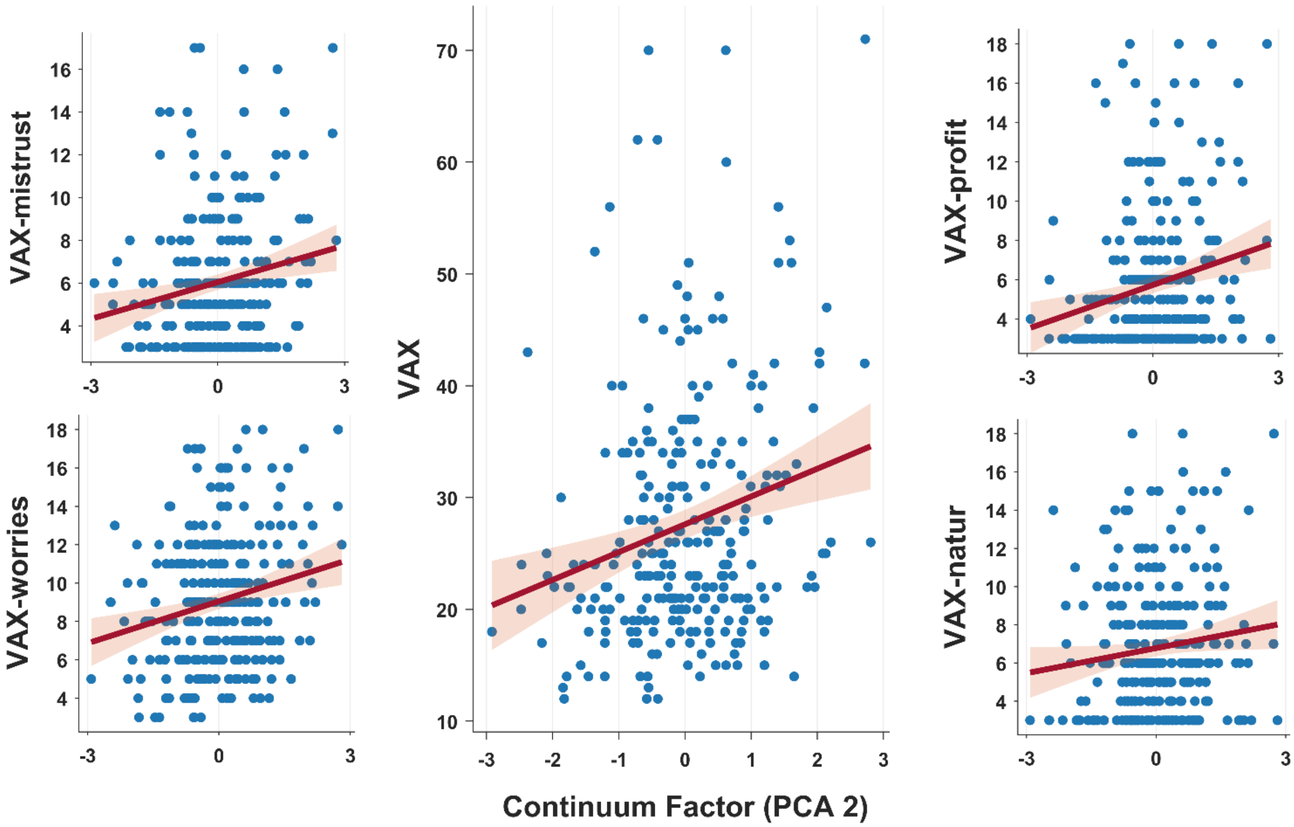

Figure 1. Graphical representation of the relationship between individuals' scores on the ASD-SSD continuum factor *(PC2, x-axis) and attitudes toward vaccination. Multiple regressions conducted showed that proximity to the positive schizotypal (vs. autistic) pole promoted widespread negative (vs. positive) attitudes toward vaccination.*

All in all, the regressions carried out showed that there are two main predictors that succeed in intercepting individual attitudes toward vaccination. The first and most important is the ASD-SSD continuum factor, which is a significant predictor for all Vax subscales and for a general negative attitudes toward vaccination. In addition, we determined that the magical thinking subscale appears to be the dimension along the continuum most strongly associated with a negative disposition toward vaccination. The second main predictor was age, which was found to be related to a general negative attitude toward vaccination, increased fear of long-term harms, and concerns about commercial gains related to vaccine dissemination.

Education levels moderate the relationship between the ASD-SSD continuum factor, age and vaccination attitude

Having assessed the relationship between the ASD-SSD continuum factor, age and negative attitudes toward vaccination, we have explored, using a moderator analysis conducted in RStudio, whether contextual variables related to the level of education attained could have a protective effect, dampening the effect that the proximity to the SSD pole and age have on attitudes toward vaccination. The analyses were carried out by mean-centering the predictors and calculating 95% confidence interval (CI) based on 2000 bootstrap iterations and assessing whether it overlapped with the zero value. The conducted analyses disclosed:

1) The presence of a significant interaction between the ASD-SSD continuum factor and education level considering the Vax-worries subscale (b = - 0.17, 95% CI = [- 0.355; - 0.003]); therefore, PC2 scores correlated with a concern about vaccine-related adverse events in a different fashion according to education level (Fig. 2). Specifically, higher levels of education dampen the effect that the proximity to the SSD end of the continuum has on scores in the Vax-worries subscale.
2) The presence of a significant interaction between age and education level considering the Vax-worries subscale (b = - 0.014, 95% CI = [- 0.028; - 0.003]); thus, lower levels of education magnify the impact that age has on Vax-worries subscale.
3) The presence of a significant interaction term between age and education level considering the Vax-profit subscale (b = - 0.019, 95% CI = [- 0.028; - 0.008]); again, level of education appears to have a protective effect on vaccine attitude, as a high level is associated with a dampening of the positive association between age and concerns about vaccine-related profits. It should be noted that both moderation analyses are equally significant when removing individuals who are still in educational age.

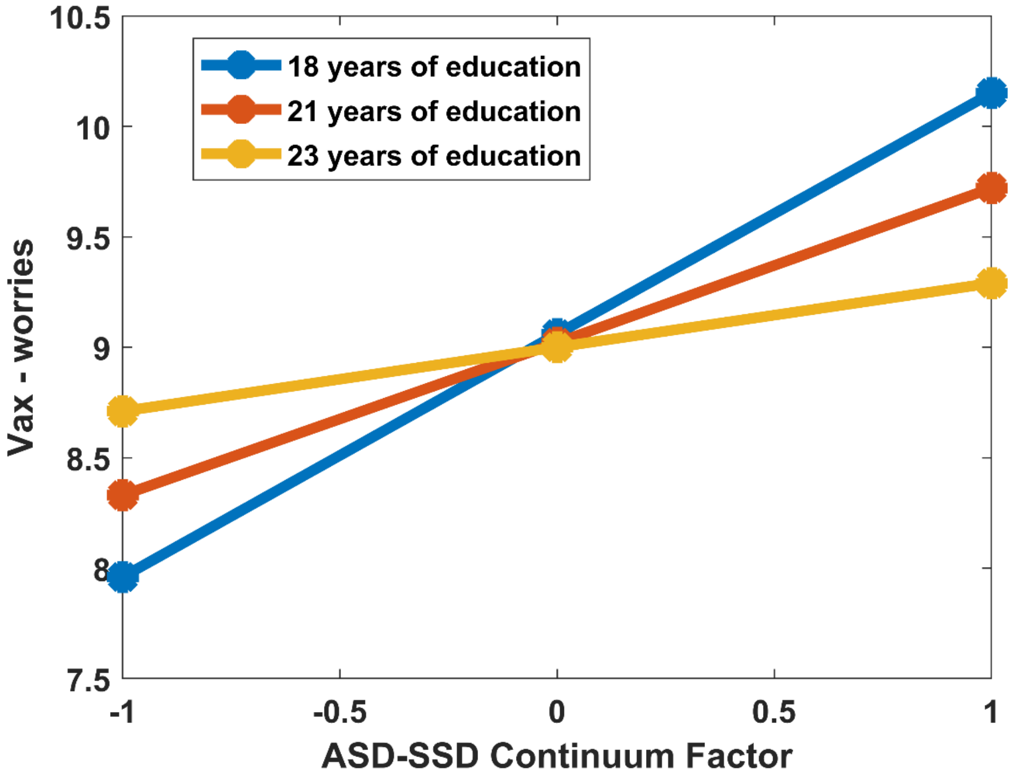

Figure 2. From the graph, it is possible to visualize how the education level factor interacts with the ASD-SSD continuum factor *in explaining attitudes toward vaccination. In particular, the ASD-SSD continuum factor is related to increased concern about vaccine-related adverse events in a different way depending on education level. Specifically, higher levels of education mitigate the effect that the proximity to the SSD pole exerts on Vax-worries subscale scores.*

Discussion

Vaccine hesitancy has been designated as one of the threats to global health by the World Health Organization and has been a strikingly salient issue during the COVID-19 pandemic. This work sought to shed light on the factors that lead to negative attitudes toward vaccines in an adult population. In particular, our study investigated how sociodemographic characteristics and personality traits dictate disposition toward vaccination.

First, we proved that the placement of individuals along the ASD-SSD continuum affected vaccine attitudes. Specifically, the closer the individual was to the schizotypal axis (positive scores in PC2) the more negative attitudes toward vaccines were displayed, whereas disposition was more favorable in participants closer to the autistic end of the continuum (negative scores in PC2). This relationship was statistically significant in all dimensions probed by the Vax questionnaire, demonstrating that position along the ASD-SSD axis pervasively shapes vaccine disposition.

It is noteworthy that not all schizotypal subscales loaded positively with principal component 2, but only the subscales measuring positive symptoms. Positive schizotypal symptoms are genetically related to schizophrenia (Saarinen et al., 2022) and are featured by a number of unusual tendencies and experiences such as odd beliefs, ideas of reference and delusions (Lenzenweger, 2006) which typically does not misrepresent reality as much as in psychosis, but are configured as a sub-threshold psychotic form (American Psychiatric Association, 2013). These unusual sets of thoughts, such as having faith in telepathy, sixth sense, and paranormal phenomena often conflict with mainstream beliefs (Raine, 1991). Thus, the proximity to the SSD pole of the continuum could cause a negative bias against vaccination because of the tendency to escape the culturally provided worldview (e.g., the scientific perspective) and turn to non-traditional channels of information (e.g., conspiracy websites). This could, in turn, lead to the generation of conspiracy-like beliefs about vaccines that fuel a hostile attitude. Crucially, scoring on measures of belief in conspiracy theories are positively predicted by individual schizotypal traits (Darwin et al., 2011), and adoption of a conspiracy perspective on coronavirus is associated with hesitancy toward the COVID-19 vaccine (Allington et al., 2021) and with decreased institutional trust, reduced support for government regulations and physical distancing measures (Pummerer et al., 2022).

Following a Bayesian perspective, these idiosyncrasies manifesting in the SSD pole of the continuum may result from an imbalance in the weight placed on belief-driven (overweighted) and sensory evidence-driven (underweighted) information (Tarasi et al., 2022d). Higher level of delusion-proneness was positively related to a tendency to gather insufficient evidence when forming beliefs (Leer et al., 2015), to a predisposition to establish meaningful patterns where there are none present (i.e., apophenia) (Blain et al., 2020) and to manifest a bias against disconfirmatory evidence (Woodward et al., 2007). Therefore, positive SSD features could promote the formation of non-evidence-based beliefs, which would subsequently be overweighted in the decision-making process, as testified by studies showing that a greater tendency for delusional beliefs is associated with prior-driven decision-making (Schmack et al., 2013). At the neural level, the over-weighting of prior information relative to disconfirmed sensory evidence could stem from an imprecision of bottom-up signaling (Tarasi et al., 2022d). For instance, in both schizophrenia and schizotypy, a reduction in the speed of oscillations in the alpha band (IAF) has been consistently observed (Fuggetta et al., 2014; Ippolito et al., 2022a; Murphy and Öngür, 2019; Ramsay et al., 2021; Trajkovic et al., 2021). Individual Alpha Frequency is a crucial marker involved in the precise encoding of incoming evidence (Coldea et al., 2022; Di Gregorio et al., 2022; Samaha and Postle, 2015), segregation of sensory information (Cecere et al., 2015; Cooke et al., 2019; Ronconi et al., 2018b; Sharp et al., 2022; Wutz et al., 2018b) and shown to be associated with long integration windows between sensory modalities leading to high proneness in crossmodal illusory perception (Fenner et al., 2020; Ferri et al., 2018; Fotia et al., 2021; Haß et al., 2017). Crucially, Ramsay et al. (2021) showed that SSD individuals exhibited reduced alpha speed compared to the control group and that this reduction was predictive of lower sensitivity in a visual task and correlated with impaired global cognition. Thus, it is possible that an imprecision in the input signal processing triggers cascade mechanisms that would lead the top-down flow (carrying the belief information) to prevail by directing the activity of the lower brain areas (Dzafic et al., 2021; Schmack et al., 2013; Tso et al., 2021).

Moreover, the study has shown that proximity to the ASD pole of the continuum fosters a positive attitude toward vaccines. This pattern might depend on the fact that the ASD pole is characterized by the tendency to systematization (Baron-Cohen et al., 2003), and hyperponderance of external inputs (Brock, 2012; Karvelis et al., 2018b) that would be processed in a more analytical and deliberative way (Brosnan et al., 2016; Lewton et al., 2019). Follow-up studies will be useful to examine whether this positive attitude is actually underpinned by the assumption of a more analytic thinking style as one approaches the autistic end of the continuum.

Looking at sociodemographic variables, only age was found to be a significant predictor of vaccination attitudes. In our sample, young age was shown to be associated with more positive attitudes toward vaccination. This finding is particularly surprising considering that virus infections tend to have potentially problematic outcomes as age increases. Indeed, previous studies have found that older people are more likely to report that they would take a vaccine relative to the younger categories (Lazarus et al., 2021) which instead showed higher levels of hesitancy in the UK population (Allington et al., 2021). However, it should be noted that increasing age heightens susceptibility to misinformation. For example, age is a strong predictor of online fake news dissemination, with users over the age of 65 sharing nearly seven times as many articles from fake news domains as the younger age group (Guess et al., 2019). Therefore, it is conceivable that the enormous amount of false information proliferated about vaccines in the recent years has an increasingly detrimental effect on vaccinal attitudes as age increases.

In addition, although there is some evidence of greater vaccine hesitancy in women than men (Morales et al., 2022), no gender-dependent difference emerged in our sample. However, the one small trend that emerged points to an increased fear of future vaccine-related adverse events in the female gender. This relationship is not surprising because women are more likely to express concerns about vaccine safety, which may also explain the trend toward higher vaccination rates in male (Bish et al., 2011). It is conceivable that, by obtaining a larger sample, the relationship between female gender and perceived risks of long-term adverse events may emerge significantly.

Finally, our exploratory analysis showed that level of education plays a protective role, mitigating the negative effect that being close to the schizotypal axis and age have on attitudes toward vaccination. In fact, with lower levels of education, both proximity to the SSD pole of the continuum and age predict extremely negative attitudes toward vaccination, while with high values of education this relationship is more nuanced. Specifically, education level attenuates the relationship between ASD-SSD continuum factor scores, age and the concern about vaccine-related adverse events (*Vax-worr*) and the relationship between age and concerns about vaccine-related profits (*Vax-prof*). Older people or individuals closer to the SSD pole tend to assume an association between vaccines and hidden risks. This relationship could be brought into play because of conspiracy-type thinking, which links vaccines to risks that manufacturers do not declare. A higher level of education might make individuals more prone to engage in more elaborate, nuanced reasoning and more ready to cast doubt on the validity of their beliefs. In addition, individuals with higher education tend to be more analytically oriented compared with the students with lower level of education (Aarnio and Lindeman, 2005) and this might make it easier for them to seek evidence-based information that counteract the belief about vaccine-related risk, e.g., evidence about the rigid safety steps and protocols that vaccines must prove to have passed before being put on the market. This finding emphasizes that the level of education is an important protective factor that succeeds in mitigating the effect that psychological or demographic variables have on a maladaptive attitude such as a negative vaccination disposition, resulting in benefits at the individual (e.g., reduced risk of adverse events) and social (e.g., reduced cost of care) level.

One limitation of the study regards that, although the online form used for data collection allowed us to reach people from different socio-demographic background, the data sample analysed has an average age of around 27 years old and an average level of education of 20 years old. This testify to the fact that the majority of participants are young and educated adults. These limitations can be overcome in future studies by employing differentiated data collection methods and/or a larger sample size. In addition, data were collected on individuals within the general population. Follow-up studies should assess whether a diametric pattern of vaccine attitudes might also emerge by considering individuals at the extreme ends of the continuum (patients with schizophrenia and autism).

In summary, the proposed study revealed that anti-vax attitudes may be favoured by proximity to the schizotypal pole of the ASD-SSD continuum, whereas being close to the autistic pole promotes the adoption of a more positive perspective toward vaccination. In addition, demographic factors such as age play a role in shaping vaccination attitudes. Finally, we highlighted the protective role played by education in mitigating the negative impact that schizotypal traits and age have toward vaccines. These findings offer a new understanding of the factors that motivate people to want to reject the science on vaccinations. Understanding these underlying motivations opens up new opportunities in terms of promoting resilient strategies against antivax attitudes by improving tailored public health interventions to reduce the risk deriving from maladaptive attitudes toward vaccines.

General conclusion

The present thesis aimed to push the boundaries of understanding regarding the pivotal role played by neural oscillations in modulating perceptual inference and decision-making processes. Additionally, it delved into exploring how variations in Autistic and Schizotypal traits shape individual differences in the neuro-behavioral mechanisms underpinning Bayesian inference. To achieve these goals, we explored various pathways to address the underlying issue comprehensively.

Initially, the thesis began with a foundational exploration, systematically reviewing existing literature regarding the role held by ASD and SSD in shaping perceptual inference. This process resulted in the development of a novel bio-behavioral model conceptualizing ASD and SSD as extreme yet diametrically conditions, each shaping predictive inference in opposite ways. Along this continuum, the way sensory information integrates with prior knowledge undergoes alteration: proneness to ASD spectrum lead towards heightened evaluation of sensory evidence, while SSD traits result in an overweighting of prior information. Importantly, along the thesis it has been demonstrated that variating the balance between sensory and prior information not only influences perceptual outcomes in controlled laboratory settings but also shapes decision-making attitudes in practical real-world scenarios, such as perspective toward vaccination.

Furthermore, employing advanced computational models and state-of-the-art EEG analyses, we uncovered the oscillatory mechanisms governing predictive inference. Alpha oscillations (8-14 Hz) emerged as pivotal in determining the weight assigned to prior information. Crucially, variations along the ASD-SSD spectrum delineate distinct patterns in this marker, indicative of diverse predictive styles across the continuum. Additionally, we have identified patterns of intrinsic brain functionality, that delineate different interactions between top-down information flows carrying priors (projected in a feedback loop) and bottom-up pathways conveying incoming sensory inputs (projected in a feed-forward manner). The resolution of this trade-off, favoring bottom-up information flow over top-down, as individual autistic traits increase, suggests that specific brain configurations predispose individuals to adopt certain predictive styles.

Understanding Human Perception through Bayesian brain theory

In Study 1, we structured a novel biobehavioral model that, for the first time, framed Autism and Schizophrenia within a common theoretical framework linked to Bayesian brain theories. These perspectives, including the predictive coding theory (Rao and Ballard, 1999), serve as a fundamental framework that explicates the active and constructive nature inherent in human perception. They illuminate the concept that our brains do not merely passively absorb sensory input but instead constantly anticipate and shape our understanding of the world. Specifically, predictive model suggests that the cognitive system generates predictions based on prior knowledge and expectations, continuously comparing these predictions with incoming sensory information. Any mismatches between the forecasted and actual input drive adjustments, refining our perception and guiding our actions. In essence, predictive coding portrays perception as a dynamic, ongoing process where our brains actively construct and update our understanding of the environment based on a constant interplay between expectations and incoming sensory signals.

In study 4, we made a step forward, by uncovering the specific impact prior information exert in a perceptual decision-making task in the visual modality. Our results revealed intriguing behavioral evidence, indicating participants' ability to integrate expectation-related information into their decision-making process. Specifically, manipulating perceptual expectations influenced individual response strategy without affecting objective performance in the task. Notably, participants shifted their criterion to a more liberal position when presented with a cue indicating a high probability of the target's presence, whereas the opposite trend was observed with a low probability cue. This evidence bolsters the idea that expectations actively shape perceptual content, prompting participants to respond congruently to prior information regardless of the actual stimulus occurrence. This evidence is in line with previous research showing that priors affect response rate (Bang and Rahnev, 2017), reaction times (Mulder et al., 2012), and metacognition (Sherman et al., 2015) but have a negligible (Wyart et al., 2012) or even detrimental effect on perceptual sensitivity (Rahnev et al., 2011). The immediate question that arises is how this finding can be linked to the hypothesized role of prior information in optimizing perceptual decision-making. In fact, considering its lack of impact on enhancing objective performance, doubts may arise regarding its optimizing function. However, optimizing perception does not necessarily mean perfecting it entirely. In our task, consider the advantage of adapting the behavioral response based on prior knowledge while maintaining the same level of accuracy in the task. This adaptability allows to base decision on expectations about stimulus presence, enabling a reliance on this information to guide your response without necessitating full processing of the stimulus to its maximum extent. This strategic utilization of prior information streamlines decision-making, utilizing expectations to efficiently shape responses without exhaustive processing, ultimately optimizing the perceptual process through energy savings to achieve the same results.

Brain rhythms are crucial for the coding of prior predictions

The understanding of the neural mechanisms behind predictive processing remains limited in the current literature, despite its significance in explaining decision-making phenomena and individual cognitive differences. To bridge this current gap, in Study 4, we showcased the pivotal role of alpha amplitude modulation in sensory regions as a critical marker for prior utilization. Indeed, we mapped the neural signature of the strategy shift observed at the behavioral level described in the previous section. Specifically, liberal and conservative trials were characterized by low and high posterior alpha amplitude, respectively.

In Study 1, we detailed a rhythm-based implementation of Bayesian inference, hypothesizing that interactions between prediction and prediction-error units occur through inter-area rhythmic synchronization within different frequency bands. Our findings in Study 4 build upon this framework by revealing that the local impact of alpha amplitude in prior exploitation depends on network-level brain activation that follow prior presentation. Specifically, synchronization in the alpha-band within the parieto-occipital network participates in transmitting predictive-like information and is associated with the enhanced use of prior expectations by regulating alpha amplitude modulation. Heightened connectivity was connected to increased alpha modulation. This suggests that prior processing occurring at a network level might utilize alpha amplitude modulation to effectively integrate prior information into the decision-making processes. Conversely, we have outlined a specific role of theta synchronization in checking prior implementation. Specifically, fronto-parietal theta mediated a supervisory process of the predictive machinery in the task, dampening the effect that prior information plays in decision-making, by reducing the differentiation of alpha amplitude based on the provided priors.

Finally, these findings outlined in study 4 aided in tracing the neurofunctional mechanisms underlying the differences in predictive styles existing in the general population. Crucially, an imbalance between alpha and theta synchronization leads to interindividual differences favoring priors overweighting (*believers*) vs. prioritization of sensory input (*empiricist*) strategy, respectively. Specifically, fronto-parietal theta coupling, mediating a supervisory process of the predictive machinery, was enhanced in *empiricists*. Conversely, parieto-occipital alpha synchronization, underpinning the conveyance of expectation-like information, was heightened in *believers*.

Unraveling Predictive Theory: Understanding Diametric Decision-Making Styles Across the ASD-SSD Continuum

In the bio-behavioural model established in study 1, we hypothesized that interindividual differences in predictive strategies could be driven by the position along the Autistic Spectrum Disorder (ASD) - Schizophrenic Spectrum Disorder (SSD) continuum. Specifically, in the model we have assumed that perceptual styles seen in ASD and SSD may stem from a differential weight assigned to prior vs. sensory information. ASD is linked to a heightened focus on external evidence over prior knowledge (Karvelis et al., 2018; Van de Cruys et al., 2014). Individuals with high autistic traits tend to rely more on objectively displayed stimuli rather than predictive expectations (Skewes et al., 2015b). Additionally, ASD shows reduced reliance on anticipatory neural responses in multisensory tasks (Ronconi et al., 2023) and lacks posterior alpha desynchronization in response to behaviorally-relevant targets (Keehn et al., 2017). Conversely, in SSD, maladaptive perceptual inference is often due to an over-reliance on prior information compared to sensory evidence (Kafadar et al., 2022; Schmack et al., 2013). Powers et al. (2017) identified a positive correlation between the severity of hallucinations and the number of conditioned hallucinations during a visual-auditory conditioning task, suggesting a dependence on overweighted prior information in perception. Similar findings were observed in individuals at high clinical risk for psychosis, exhibiting behaviors consistent with hyper-precise priors (Kafadar et al., 2020). Moreover, abnormal modulation of alpha activity has been linked to distorted expectations during social interactions in schizophrenic patients (Billeke et al., 2015). Building on the theoretical structured proposed in study 1, study 5 aimed to empirically investigate whether an individual's position along the ASD-SSD continuum correlates with the predictive style adopted in the perceptual decision-making task employed in study 4. First, we were able to replicate the distinction between individuals that overweight (*believers*) vs. underweight (*empiricists*) expectation-like information in perceptual inference: *believers* showed extensive shaping of alpha amplitude oscillations in perceptual regions, while *empiricists* showed a dampened modulation. These behavioral distinctions corresponded with varying degrees of strategy modulation: *believers* adjusted their criterion based on prior information, whereas *empiricists* maintained a more consistent criterion regardless of the provided prior. Significantly, our investigation unveiled distinct positions along the ASD-SSD axis among individuals who embraced the empiricist and believer strategies. *Empiricists* were notably aligned more toward the ASD pole, while *believers* showed a greater inclination toward the SSD pole. Crucially, mediation analysis underscored that the influence of positioning along the ASD-SSD continuum on behaviour was mediated by alpha amplitude modulation, indicating that ASD and SSD traits could potentially shape the use of probabilistic priors by exerting opposite effects on alpha wave amplitude modulation (Martínez et al., 2019), as predicted in study 1.

This discovery marks the very first instance where the position along the ASD-SSD continuum was found to govern the predictive strategies adopted by individuals. This finding is particularly significant as it suggests that, within the general population, subtle traces of divergent approaches to predictive inference exist, contingent upon sub-clinical personality traits. Notably, in the utilized task, both strategies yielded similar accuracy rates, positioning these styles as two distinct yet equally valid strategies within the experimental framework used in study 4 and 5. Follow up studies should assess whether different contexts prompt performance enhancements or reductions based on the predictive style promoted by ASD and SSD traits. For instance, the inclination toward the believer predictive style may elucidate why positive schizotypal traits correlated with improved performance when prior knowledge facilitated the interpretation of highly ambiguous bottom-up signals (Teufel et al., 2015).

Conversely, the preference for empiricist predictive style could elucidate why Autistic traits foster data-driven decision-making (Brosnan et al., 2016; Lewton et al., 2019).

Furthermore, these distinct information processing peculiarities and neural regulatory patterns, evident in the sub-clinical population, might serve as pivotal markers signalling early risks for the development of mental disorders. They could also offer insights into the mechanisms contributing to the emergence of clinical manifestations along the ASD-SSD continuum. Subsequent studies should evaluate these behavioural and neural indices involving individuals exhibiting positive SSD symptoms and ASD patients, aiming to trace the developmental trajectory of predictive strategies. This investigation is needed to explore whether these strategies become more rigid, inflexible, and context-independent (and thus maladaptive) toward the ends of the continuum.

Decisional style along the ASD-SSD axis is capable of impacting real-life perspective such as vaccination attitudes

In everyday environments, concepts, beliefs, and models regarding the environment are regularly shared through social interactions, communications, and peer encounters, forming fundamental frameworks for individuals to understand the world around them. Recently, there has been heated discourse around mass vaccination efforts, sparking significant division between those advocating for vaccination and those harbouring more skeptical views. Study 6 revealed a correlation between individuals' positions along the ASD-SSD continuum and their attitudes toward vaccines. Closer proximity to the SSD end correlated with more negative vaccine attitudes, while those closer to the ASD end demonstrated a more favourable disposition.

Drawing from the Bayesian perspective proposed in study 1, these distinctive attitudes among SSD individuals could result from an imbalance in valuing belief-based (overvalued) versus sensory evidence-driven (undervalued) information. Traits associated with SSD, such as a tendency to form beliefs with insufficient evidence (Leer et al., 2015), inclination toward finding patterns where none exist (apophenia) (Blain et al., 2020), and a bias against contradictory evidence (Woodward et al., 2007), might influence the creation of non-evidence-based beliefs which would subsequently be overweighted in the decision-making process, as testified by studies showing that a greater tendency for delusional beliefs is associated with prior-driven decision-making (Schmack et al., 2013). Conversely, proximity to the ASD end of the continuum correlated with a positive attitude toward vaccines. This inclination might stem from the predictive style linked to the ASD pole characterized by the tendency to systematization (Baron-Cohen et al., 2003) and hyperponderance of external inputs (Brock, 2012; Karvelis et al., 2018) that would be processed in a more analytical and deliberative way (Brosnan et al., 2016; Lewton et al., 2019). Future research could explore whether this positive attitude indeed aligns with a more analytical thinking style characteristic of individuals closer to the autistic end.

Additionally, study 6 highlighted the protective role of education against negative vaccine attitudes linked to proximity to the SSD axis. Lower levels of education correlated with extremely negative vaccine attitudes in those closer to the SSD end, while higher education levels moderated this relationship. Higher education might foster more elaborate, critical reasoning, more ready to cast doubt on the validity of their beliefs. In addition, individuals with higher education tend to be more analytically oriented compared with individuals with lower level of education (Aarnio and Lindeman, 2005) and this might make it easier for them to seek evidence-based information that counteract the belief about vaccine-related risk, e.g., evidence about the rigid safety steps and protocols that vaccines must prove to have passed before being put on the market. This underscores the pivotal role of education in offsetting extreme predictive styles, effectively countering the intrinsic tendencies observed in SSD. This, in turn, holds promise for reducing adverse events and alleviating societal healthcare costs.

The trade-off between feedback and feedforward connections is modulated by individual autistic trait as predicted by the ASD-SSD continuum model

Studies 4 and 5 have indicated that the neural signatures underlying the integration of priors in the decision-making process are modulated by ASD-SSD traits, aligning with the predictions of Study 1. Studies 2 and 3 delved into understanding how effective brain connectivity varies across the continuum, specifically exploring how individual autistic traits might influence the prevalence of forward versus backward signaling in brain information flows. Once again, this theoretical investigation stems from the model theorized in Study 1, which, drawing from biologically grounded interpretations of predictive coding, postulates that one's position along the continuum maps the prevalence of the directionality of brain connections. Briefly, predictive coding could be implemented in a hierarchical-like structure in which predictions are feedbacked from higher to lower brain regions, while prediction errors follow a feed-forward pathway in an opposite direction (Bastos et al., 2012; Friston, 2010; Rao and Ballard, 1999). In Study 1, the hypothesis proposed that variations in the prevalence of directional connections might account for the differing emphasis placed on prior information versus sensory evidence. Consequently, it was expected that one's position along the ASD-SSD continuum might be associated with a different prevalence in connectivity directionality. Specifically, a tendency towards SSD traits might lead to a prevalence of feedback connectivity, while a tendency towards ASD traits might result in a dominance of feedforward connectivity.

This is specifically what we revealed in study 2 and 3 in which individuals with higher autistic traits exhibited stronger ascending connections from occipital regions and stronger incoming connections toward frontal areas (i.e., bottom-up connections) compared to those with lower autistic traits. Conversely, there is notably reduced connectivity flowing in the opposite direction. Specifically, as the level of autistic traits increases, a noticeable decline in the quantity of top-down connections originating from frontal regions was observed.

This pattern of over-representation of feed-forward information flow and diminished top-down signaling aligns with the sensory characteristic observable in individuals with ASD. In fact, ASD are more influenced by bottom-up visual information (Amso et al., 2014) and less constrained by top-down prior information, leading to an increased veridical representation of the external world (Karvelis et al., 2018). Crucially, this directionality pattern in connectivity may reflect a hierarchical organization within the processing stream, with a hyper-representation of bottom-up connections (especially from the occipital towards the frontal lobes) involved in sensory processing and hypo-representation of top-down connections reflecting context modulation, and prior knowledge, planning, and attention. The observed connectivity organization strongly aligns with the hypothesis proposed in Study 1, suggesting that individuals with ASD might struggle to rely on predictions of the external environment due to the dominance of sensory information over internal expectations. Empirical evidence from Studies 2 and 3 demonstrated that variations in bottom-up connectivity, thereby influencing the effect of sensory input on the overall internal model, are more pronounced in individuals exhibiting higher autistic traits, even within a healthy population. An important and novel aspect of these results is that these highlighted characteristics in brain organization are present even at rest. This suggests an inherent and consistent tendency within the neural system favoring the signaling of bottom-up information over top-down information in ASD individuals. Furthermore, an intriguing avenue for further exploration would involve investigating whether and how the altered directionality pattern observed in resting-state connectivity across the autistic side of the continuum also manifests during task performance, such as decision-making tasks, providing a neural substrate underlying the highlighted peculiarities observed at the behavioral level. Moreover, a crucial future direction involves exploring the validity of the hypothesis formulated for SSD. Within the proposed model, individuals with SSD traits are hypothesized to exhibit a prevalence of top-down connections over bottom-up ones. Investigating this reversal in connectivity patterns across the spectrum would elucidate the contrasting neural mechanisms between ASD and SSD traits, offering valuable insights into the manifestation of distinct neurodevelopmental traits in directional connectivity.

Final Remarks

The exploration across the six studies unravelled the intricate relationship between human perception, decision-making, and the underlying neurofunctional mechanisms interlinked within the framework of the Bayesian brain theory.

Study 1 established the foundational framework of the thesis by situating ASD and SSD within the predictive coding paradigm. This conceptual model elucidates the active and constructive nature of human perception, highlighting the dynamic process through which sensory input and prior information are integrated.

Building upon this, Study 4 delved into exploring the precise impact of prior information on decision-making, elucidating how expectations shape perceptual contents without affecting objective performance. The neural underpinnings of these processes uncovered in Study 4 brought alpha amplitude modulation to the forefront, showcasing its pivotal role in prior utilization within decision-making process. Moreover, brain synchronization in the alpha and theta bands ensures the active modulation of this brain index, involving an interaction between process facilitating (mediated by parieto-occipital alpha coupling) vs. supervising (mediated by fronto-parietal theta coupling) prior utilization. Importantly, the trade-off between alpha and theta synchronization shapes predictive tendencies across the general population. This culminated in identifying distinct decision-making styles, namely the *empiricists* (who underutilize prior information) and the *believers* (who overweight prior information).

Crucially, Study 5 shed light on how subclinical traits influence predictive strategies in perceptual decision-making tasks. It emerged that an individual's position on the ASD-SSD continuum shapes the adopted predictive strategy: ASD traits lean towards adopting an empiricist decision-making style, while SSD traits steer towards the believer's predictive style.

The implications have far-reaching effects on real-world scenarios, as evidenced in Study 6, where attitudes toward vaccination correlated with an individual's position on the ASD-SSD continuum. The research also underscored the potential impact of education in tempering extreme predictive styles, particularly among SSD-oriented individuals.

Studies 2 and 3 enriched this understanding by revealing the neural connectivity patterns associated with ASD traits. These patterns showcased an inclination toward bottom-up processing and reduced top-down signalling, mirroring the emphasis on sensory information over prior expectations observed at the behavioural level as reviewed in study 1 and empirically evidenced in study 5. This aligns with the hypothesized hierarchical predictive coding structure, substantiating the differences in information flow across the continuum.

Ultimately, this comprehensive exploration not only elucidates the intricacies of human perception and decision-making but also offers glimpses into potential markers for mental health risks and their developmental trajectories. The integration of predictive styles along the ASD-SSD continuum within decision-making contexts offers a nuanced understanding of diverse cognitive strategies within the population. The journey through these studies unravels the complex interplay of perception, cognition, and neural mechanisms, illuminating the varied pathways by which individuals navigate and interpret the world around them.

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